The Burrowing Barnacles (Cirripedia, Acrothoracica) of South Africa

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Abstract

The Acrothoracica of South Africa are reviewed for the first time, 50 years after the last publication on this group appeared. A new host category for acrothoracicans is described in Chapter 1, as *Weltneria spinosa* was collected from coralline red algae. This finding was not an isolated event, as this species was found inhabiting four different species of coralline algae across a range of sites up to 900 km apart. These are the first unequivocal records of living acrothoracicans burrowing into coralline red algae. Further inspections of coralline algae in this and other regions will likely reveal many more new host records and possibly new acrothoracican species. In Chapter 2 a systematic account and key to all known South African acrothoracicans are given, with each description accompanied by scanning electron microscopy, light microscopy and a distribution map. The number of known South African acrothoracicans is increased from four to eight species, as three new records and two undescribed species are added to the fauna, while one existing record is determined to be a *nomen nudum*. Chapter 3 examines patterns of distribution and host specificity. All species except one saw a range extension, some of which were > 500 km, while all species had additional hosts described. The species with the most hosts was *W. spinosa,* which was reported from 13 hosts that included gastropods, chitons and coralline red algae. South Africa thus now includes 11.27% of the world's acrothoracican species, with 62.50% of these endemic. Moreover, 75% of South African acrothoracicans were endemic to specific provinces. However, these values are likely to change substantially as more sites are sampled both within the region and in neighbouring countries. In conclusion this dissertation shows that South Africa has more acrothoracican species, occupying more hosts across wider distributional ranges than previously thought. Although this study serves as a valuable baseline it should be expanded on through future sampling, specifically focusing on areas

(Delagoa, Namaqua and offshore bioregions) and hosts (especially corals) not yet sampled in South Africa.

General Introduction

The Acrothoracica are one of three suborders within the Cirripedia, along with the Rhizocephala and the more familiar Thoracica (Fig. 1). The Acrothoracica are known as the 'burrowing barnacles', whereas the Rhizocephala are a group that parasitizes decapod crustaceans and the Thoracica are the conventional shelled sessile and stalked barnacles. In the Acrothoracica the females burrow into calcareous objects, including mollusc shells, corals, thoracican skeletons, bryozoans, echinoderms and limestone (Tomlinson, 1969; Kolbasov, 2009) and they are generally accompanied by dwarf males that either attach to the female, or to the burrow wall (Chan et al., 2014; Lin, Kolbasov and Chan, 2016).

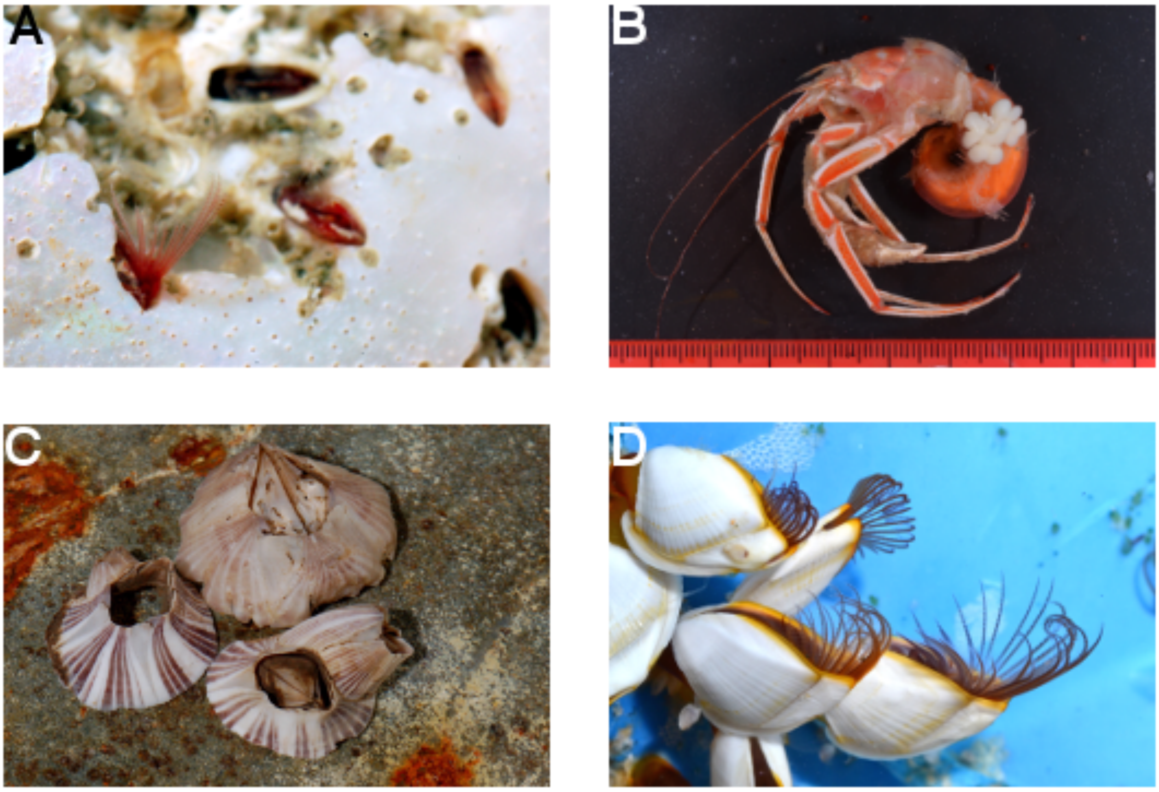

Fig. 1: Representatives of the three Superorders of the Cirripedia. A – Acrothoracica in their burrows; B – Rhizocephala on a hermit crab; C – Sessile thoracicans on a rock; D – Stalked thoracicans on a floating object washed ashore. Photos by CL Griffiths.

The Acrothoracica consists of two orders; the Cryptophialida and the Lithoglyptida (Kolbasov, Newman and Høeg (in Kolbasov, 2009). The females of the order Cryptophialida are characterised by a narrow, long-necked operculum, a small aperture, a tongue-shaped labrum, no caudal appendages and a special gastric mill at the end of the stomach (Kolbasov, 2009). Conversely, the Lithoglyptida are characterised by having a wide aperture, a sac-like mantle with well-developed mouth cirri, a large, saddle-like labrum and lack a special gastric mill at the end of the stomach (Kolbasov, 2009; Chan, Kolbasov and Cheang, 2012; Chan, Hsieh and Kolbasov, 2014). The Cryptophialida consist of the single family Cryptophialidae, Gerstaecker, 1866 with two genera, *Australophialus* Tomlinson, 1969 and *Cryptophialus* Darwin, 1854, comprising a total of 21 species. The Lithoglyptida are made up by two families, the Lithoglyptidae, Aurivillius, 1892 and the Trypetesidae, Krüger, 1940 and collectively consist of nine genera and 49 species (Kolbasov, 2015).

Globally, the overwhelming majority of literature on the Cirripedia refers to the Thoracica and in South Africa the situation is no different. The Thoracica of South Africa have been reviewed twice, once by Barnard (1924) and more recently by Biccard (2012), while almost no literature exists on either the Acrothoracica or Rhizocephala of South Africa. Only descriptions on the four known acrothoracican species (Noll, 1883; Berndt, 1907; Barnard, 1925; Tomlinson, 1967) and three rhizocephalan species (Day, 1939; Boschma, 1958a, b) exist, with some mentions in other global literature regarding South African acrothoracicans (Barnard, 1924; Tomlinson, 1969; Kolbasov and Newman, 2005; Kolbasov and Høeg, 2007; Kolbasov, 2009; Chan, Kolbasov and Cheang, 2012). Since all these reports are based on isolated records and no directed surveys of the acrothoracican fauna of the region have ever been conducted, no reliable information exists on the biogeography and host specificity of the

Acrothoracica of South Africa, making it very likely that additional unreported species are present in regional waters.

The purpose of this dissertation is to provide a preliminary overview of the diversity, biogeography and different host species colonized by the Acrothoracica of South Africa. The results are presented in the form of three chapters, as detailed below. Each chapter is presented in the form of a paper formatted as a journal publication. There is thus some inevitable overlap between chapters. The abstracts of each of the chapters have, however, been consolidated into a single abstract at the start of the dissertation and the reference lists similarly consolidated into a single list at the end of the dissertation. The three chapters are as follows:

Chapter 1: Coralline Red Algae – A New Host Taxon for Burrowing Barnacles (Cirripedia, Acrothoracica). This describes, for the first time globally, the occurrence of live acrothoracican barnacles in coralline algae and discusses the implications of this discovery.

Chapter 2: The Acrothoracica of South Africa – A Taxonomic Review. This chapter re-describes the existing three species known from the region, describes three species recorded within our political borders for the first time and two species new to science. Where possible, species descriptions include a diagnosis, description, distribution, information on host species, remarks, SEM images, light microscopy and a distribution map. A key to these species from the region is also included.

Chapter 3: Diversity, Biogeography and Host Specificity of South African Acrothoracica. This chapter gives an indication of the diversity of regional acrothoracican species, their distribution patterns around the South African coastline and host species in South Africa.

These 3 main or 'substantive' chapters are supported by this short introduction and a brief synthesis.

Chapter 1: Coralline Red Algae – A New Host Taxon for Burrowing Barnacles (Cirripedia, Acrothoracica)

Introduction

The Acrothoracica are shell-less cirripedes that burrow into a variety of calcareous marine substrata (Tomlinson, 1969; Kolbasov, 2009; Chan, Hsieh and Kolbasov, 2014). They have separate sexes, as females occupy burrows and dwarf males attach directly to the females, or to the burrow walls (Kolbasov, 2009). They are poorly known, mostly due to their inconspicuous nature, although several recent publications (Kolbasov, 2009; Chan, Hsieh and Kolbasov, 2014) have greatly enhanced knowledge of the group. Acrothoracicans are widespread in their geographical and depth distributions. Most are found intertidally (72%), but others occur in the deep ocean to depths of 3000 m (Kolbasov, 2009).

To date, acrothoracicans have been reported to burrow only into the calcium carbonate skeletons or shells of marine animals, including molluscs (gastropods, bivalves and chitons), corals, thoracican barnacles, echinoderms, and bryozoans; or into limestone and firm calcareous sediments (Tomlinson, 1969; Newman, 1974; Kolbasov, 2009; Chan, Hsieh and Kolbasov, 2014). There have been no unequivocal previous records of living acrothoracicans occurring in coralline red algae, although Thomas and Stevens (1991) report numerous *Balanodytes thomasi* (Kolbasov & Newman, 2005) on constructional lips and cup reef rims, which typically consist of an algal mat, crustose coralline algae and vermetid gastropods, as well as hard corals and limestone. It is not clear from this paper, however, whether *B. thomasi* was collected from the crustose coralline algae component of the samples. There is also a report of unoccupied burrows of an unidentified acrothoracican in Australian rhodoliths (free-living nodules in which corallines comprise > 50% of the structure – Foster,

2001) by Bassi et al. (2013). Thus there have been no confirmed reports of living acrothoracicans existing in crustose coralline red algae, despite the widespread distribution and variation in morphology of coralline red algae (Adey and Macintyre, 1973; Johansen, 1981; Woelkerling, 1988; Littler and Littler, 2013), and the apparent suitability of at least some thicker forms as habitat for species that burrow into calcium carbonate substrata (Chenelot et al., 2011). Coralline red algae belong to three orders (Corallinales, Hapalidiales, Sporolithales: subclass Corallinophycidae) and may occur as either geniculate (articulated) or non-geniculate (non-articulated, encrusting, crustose) forms (Le Gall et al., 2010; Nelson et al. 2015), although there is no taxonomic basis for this separation. Non-geniculate or encrusting species are morphologically diverse, and their thickness can vary from a few microns to several centimetres (Littler and Littler, 2013). They can occur as crusts, as free-living rhodoliths, or can be endophytic or parasitic (Johansen, 1981).

This study is the first to report on and identify living acrothoracicans burrowing into coralline red algae, thus revealing a major new habitat type that should be explored for this group of barnacles.

Methods

During 2017/2018 we surveyed the acrothoracican fauna of several sites around the South African coast, collecting a variety of potential host species and substrata at each site. Amongst the samples examined were 20 beach-cast rhodolith specimens collected from the intertidal zone of Algoa Bay. These were returned to the University of Cape Town, where they were examined under a dissecting microscope and manually cracked to expose any acrothoracicans. Some specimens were also decalcified with HCl to reveal acrothoracicans whose apertures were not detected by microscopic examination. Rhodoliths were prepared for identification following Maneveldt and van der Merwe (2012). Due to the degraded nature of the material, DNA sequencing was not possible and specimen identification was based solely on morphological and anatomical features, using Maneveldt, Chamberlain and Keats (2008).

Note that in this paper both botanical and zoological nomenclature systems are used, as appropriate. When citing authorities for animal species, we use the International Commission on Zoological Nomenclature system (Ride et al., 1999), while for coralline algal species the International Code of Nomenclature for algae, fungi, and plants (Shenzhen Code) is used (Turland et al., 2018).

Results

In total, 30 live *Weltneria spinosa* Berndt, 1907 and 12 additional empty *W. spinosa* burrow holes were found in the 20 rhodoliths examined (Eastern Cape: Summerstrand, 34°00’54.2”S, 25°41’34.7”E, *leg. T. Botha, J. Landschoff and C. Griffiths*, CA01-CA20). All 30 live specimens were found burrowed into a single rhodolith specimen which was attributed to the genus *Lithophyllum* Philippi attaining a maximum density of 7 per cm^2 (Fig. 1.1A, B). The remaining 12 empty burrows were distributed amongst five of the remaining rhodoliths. The species forming one of these rhodoliths was determined as *Neogoniolithon brassica-florida* (Harvey) Setchell and L.R.Mason (CA14), but the remaining specimens could not be identified due to their degraded and possibly fossilised state (decalcification of other rhodoliths rendered them useless for identification).

In addition, acrothoracicans were discovered in several encrusting coralline algal specimens from the University of the Western Cape (UWC) collections were examined (herbarium abbreviations follow Thiers, 2018). Twelve *W. spinosa* were found burrowed in two specimens of a lumpy species, tentatively identified as *Lithophyllum neoatalayense* Masaki (Eastern Cape: Morgans Bay, 32°43'28.53"S, 28°18'51.08"E, 12.vii.2010, *leg. G.W. Maneveldt and E. van der Merwe*, UWC 10/231 Qolorha, 32°38'29.69"S, 28°25'39.25"E, 13.vii.2010, *leg. G.W. Maneveldt and E. van der Merwe*, UWC 10/231). However, this identification is subject to genetic verification. Additionally, a single *W. spinosa* was found burrowed in a specimen of the thick, discoid *Heydrichia woelkerlingii* R.A.Townsend, Y.M.Chamberlain and Keats (Western Cape: Cape Agulhas, L'Agulhas, 34°49'26.58"S, 20° 1'0.84"E, 15.vi.2010, *leg. G.W. Maneveldt and E. van der Merwe*, UWC 10/131, Fig. 1.1C). Numerous additional live specimens of *W. spinosa* were also observed in large colonies of another unidentified non-geniculate coralline algal species photographed (but not collected) at Miller's Point, False Bay, in which 5 *W. spinosa* was found per cm^2 (Fig. 1.2).

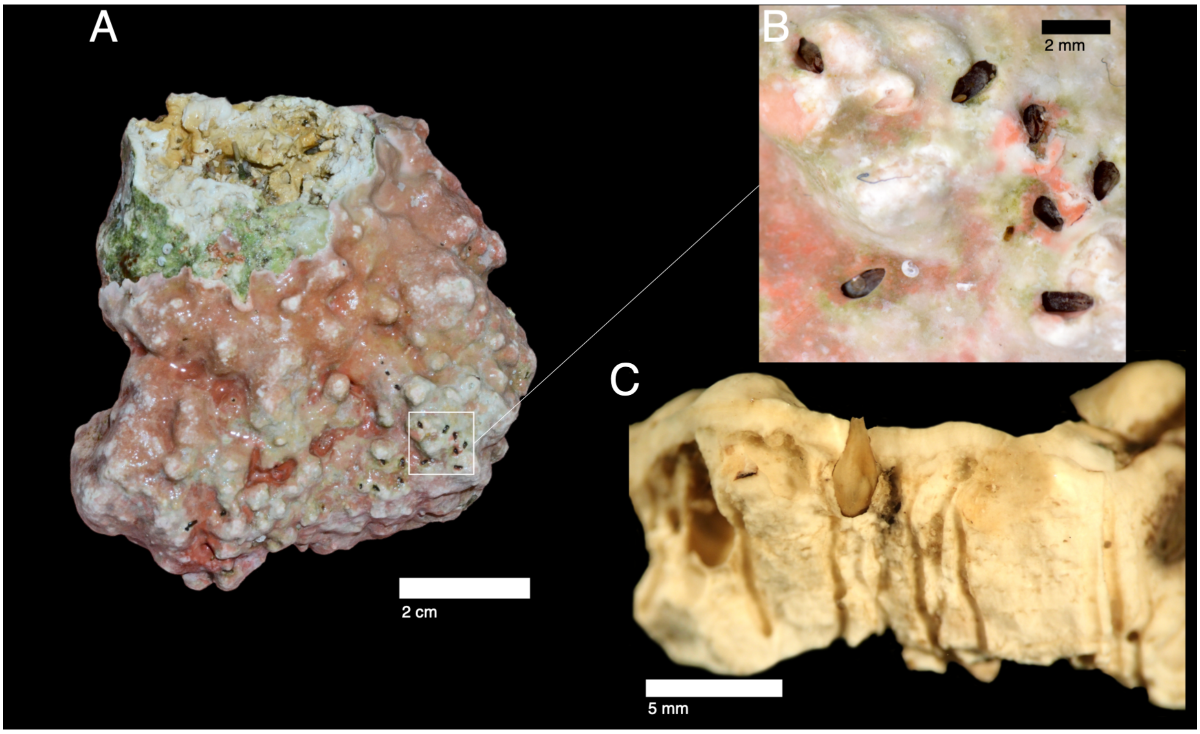

Fig. 1.1: A – Rhodolith (*Lithophyllum* sp.) from Algoa Bay hosting 30 live acrothoracicans; B – Magnified view (1 x 1 cm) showing burrows containing live female *Weltneria spinosa*; C – Vertical section through *Heydrichia woelkerlingii* (UWC 10/131) showing burrow and intact female *Weltneria spinosa.*

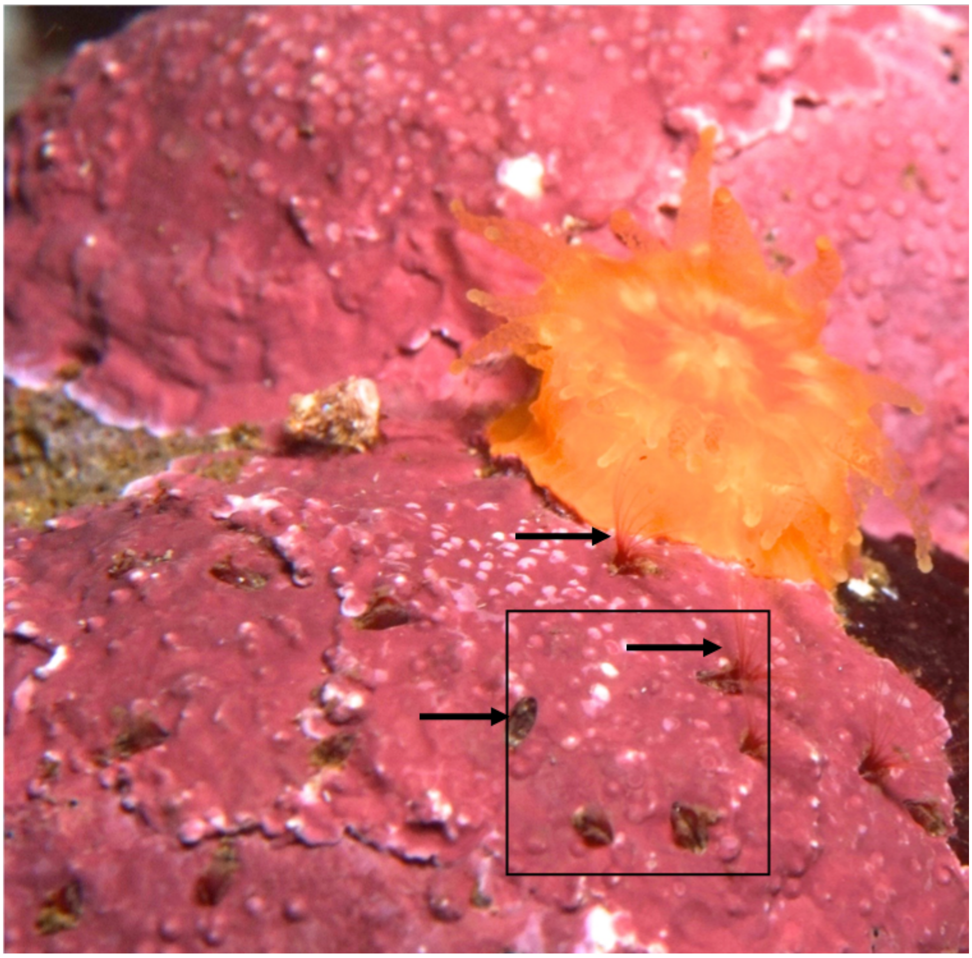

Fig. 1.2: Several live *Weltneria spinosa* burrowed in an unidentified species of non-geniculate coralline red alga, some feeding using their extended cirri. The square represents 1 x 1 cm. Photographed at Miller's Point, False Bay by Georgina Jones.

Discussion

This study provides the first unequivocal evidence of an acrothoracican species occupying several different species of coralline red algae, thus documenting a new habitat type for this group of barnacles. Coralline red algae are heavily calcified organisms, as calcite is deposited within their cell walls (Aguirre, Riding and Braga, 2000). It is therefore, not surprising that acrothoracicans have been discovered in this group of hosts, as they are well known to burrow in a wide variety of other calcareous marine substrata (Tomlinson, 1969; Kolbasov, 2009). Moreover, coralline red algae are already known to host several other groups of endobionts, especially burrowing polychaetes (Chenelot, Jewett and Hoberg, 2011). While most species of coralline red algal are too thin to be suitable hosts for acrothoracicans, many thicker smooth or thick knobbly crusts, as well as rhodoliths (since they typically also occur as superimposed thalli – GW Maneveldt, *per. obs*.), are thick enough to ensure that the animals can entirely immerse and protect themselves within their burrows (see Fig. 1.1C).

Coralline red algae are widespread globally, occurring in both warm and cold waters (Adey and MacIntyre, 1973; Johansen, 1981; Littler and Littler, 2013; Riosmena-Rodríguez, Nelson and Aguirre, 2017). Moreover, in terms of area covered, they are reported to have the broadest range of any marine algae globally, occupying a range of habitats within the photic zone, as well as extending to the greatest depths known for marine algae (Steneck, 1986). Rhodoliths are also common in all the world's oceans and rhodolith beds are thought to be amongst the most extensive of all benthic communities dominated by marine macrophytes (Foster, 2001; Riosmena-Rodríguez, Nelson and Aguirre, 2017).

The fact that these discoveries of acrothoracicans living in coralline algae are not isolated or anomalous observations is demonstrated by the fact that they are reported here from three locations up to 900 km apart and involving at least four different non-geniculate coralline algal species. It seems likely that examination of a range of thick coralline algal growth forms, from various habitats around the world, will reveal numerous additional new records and possibly new species of acrothoracicans, some of which might prove to be exclusive to the coralline algal habitat type.

Chapter 2: The Acrothoracica of South Africa - A Taxonomic Review

Introduction

The Acrothoracica are a Superorder largely of shell-less barnacles within the Infraclass Cirripedia, along with the Thoracica (conventional shelled sessile and stalked barnacles) and Rhizocephala (obligate parasitic barnacles that occur on decapod crustaceans). Acrothoracicans are more commonly known as 'burrowing barnacles', as the females bore into calcareous objects, such as mollusc shells, corals, thoracican barnacles, bryozoans, echinoderms, limestone and firm calcareous sediments (Tomlinson, 1969; Newman, 1974; Kolbasov, 2009) and more recently were found in coralline red algae (Chapter 1). They are different from thoracicans, as they have a soft carapace, generally lacking calcareous plates and they have a single pair of chitinous plates that guard the aperture (Chan, Hsieh and Kolbasov, 2014). They have reduced terminal cirri (3 – 5 pairs), a pair of mouth cirri and some species have caudal appendages (Kolbasov and Newman, 2005; Chan, Hsieh and Kolbasov, 2014).

Acrothoracicans have separate sexes (Darwin, 1854), with the females occupying self-made burrows and the dwarf males either attached to the females, or the burrow itself (Kolbasov, 2009). They are small animals, most being less than 5 mm in size. The females are on average roughly ten times bigger than the males (Klepal, 1987). Thus, due to the inconspicuous and highly reduced nature of the males, most of the research done on this group has been focused on females.

The life cycle of acrothoracicans comprises at least four naupliar stages, a cypris larval stage, a juvenile stage and adulthood (Kolbasov, Høeg, Chan, 2014). Larvae are free-living while juveniles and adults are epibiotic. The naupliar larvae All acrothoracican families release their young as cyprids, except the Trypetesidae (of which none have been found in South Africa, albeit two genera are known from southern Madagascar) that releases lecithotrophic planktonic nauplii that undergoes four naupliar stages until they become cyprids (Murphy and Williams, 2013; Southward, 2017). Male cyprids then settle on females, or female-occupied burrows, where they develop into dwarf males (Darwin, 1854; Southward, 2017), whereas females settle onto a calcareous substrate, and subsequently excavate a burrow to occupy. The burrow is created using spines and multifid scales (Lin, Kolbasov and Chan, 2016), possibly facilitated by chemical dissolution (Tomlinson, 1969).

The Acrothoracica are the most primitive group of barnacles and have a fossil record that extends back to the Devonian, or even the Ordovician (Chan, Hsieh and Kolbasov, 2014; Kolbasov, 2015), with several species from extinct and living genera being described in the fossil record (Tomlinson, 1969). However, no fossil species have been described from Africa and only extant species are known from this region.

The mid-1750's to late 1800's is considered to be the start of marine systematic research in South Africa (Clark, 1923), and during this era most work was carried out via large European expeditions that collected in South African waters. Most of these specimens were then catalogued in European museums and subsequently described and often well illustrated (Griffiths, 1999; Griffiths et al., 2010). From about 1900 onwards research was undertaken mostly by South African researchers, such as J. D. F. Gilchrist and his followers, including the prolific K. H. Barnard. By the 1970's, most common marine invertebrate and fish taxa in South Africa had been described, and many regional identification guides were compiled during this time until the 2000's (Griffiths et al., 2010). Unfortunately, a number of taxa still remain very poorly documented, of which the Acrothoracica are a good example. At the start of this dissertation, extremely little was known about the South African acrothoracicans and apart from the original species descriptions (Berndt, 1907; Barnard, 1925; Tomlinson, 1969), no further taxonomic work had been conducted over the past 50 years. Moreover, there has never been a dedicated study on the acrothoracican fauna of South Africa. The reason for the lack of research on this group was well illustrated by Griffiths (1999), who showed that the number of species descriptions is closely related to the number of taxonomists working on the groups and their career spans. Prior to the 2000's only one or two taxonomists made any significant contribution to the taxonomy of the regional Cirripedia, and the number of known species had remained virtually the same since their descriptions in the 1900's. Conversely, the Amphipoda, for example, shows an almost linear increase in species descriptions over the same time, as there has remained an almost unbroken sequence of taxonomists working on this group (Griffiths, 1999). More recently cirriped research in South Africa was revived, as Biccard (2012) produced a dissertation on the taxonomy, systematics and biogeography of thoracican barnacles, which was the first review on this group in South Africa in 88 years.

Over the last 30 years, the tools of taxonomy have changed considerably, with several new techniques being employed. One particularly useful technique for smaller crustaceans is Scanning Electron Microscopy (SEM), which has been particularly successfully employed in acrothoracican taxonomy since Turquier (1978) and subsequently implemented by Smyth (1986), Kolbasov (1999; 2000a, b), Kolbasov and Høeg (2000) and in the major revision by Kolbasov and Newman (2005). In these studies, the use of SEM has revealed several ultrastructural characters of taxonomic value. These characters are useful in differentiating between subfamilies of the Lithoglyptidae and the relationships between different genera and families within the Lithoglyptinae (Kolbasov and Newman, 2005). Furthermore, the monograph by Kolbasov (2009) almost exclusively relied on SEM and not conventional drawing techniques. Chan, Hsieh and Kolbasov (2014) also used SEM particularly effectively, along with light microscopy, to elucidate differences between species. Based on the proven effectiveness of SEM in describing species in this group, this chapter will also implement this technique to differentiate and describe species comprising the acrothoracican fauna of South Africa.

Prior to this study there were 90 described species of cirripedes in South Africa, of which only four were acrothoracicans (Kolbasov, 2009), three rhizocephalans (Day, 1939; Boschma, 1958a, b) and the remaining 83 thoracicans (Biccard and Griffiths, 2016). This study reports an additional five species, of which two are new to science, while one of the previous records is determined to be a *nomen nudum*. Therefore, this study brings the total number of acrothoracicans in the region to eight and of cirripedes to 94.

History of research

The first acrothoracican was described by Hancock (1849) called *Alcippe lampas*. This species was placed in the Lepadidae by Charles Darwin, who in 1854 described a species of his own, *Cryptophialus minutus*, for which he erected the order Abdominalia. Noll (1872) then moved *A. lampas* in the Abdominalia with *C. minutus*. Subsequently, two genera were described by Noll (1872) and Aurivillius (1892), namely *Kochlorine* and *Lithoglyptes* respectively. However, in 1905 Gruvel proposed that the name of the group be changed to Acrothoracica, as it had become apparent that the cirri were attached at the end of the thorax and not the abdomen, as Darwin had previously thought. He then included the genera *Alcippe, Cryptophialus, Kochlorine* and *Lithoglyptes* in this order. This was accepted by Berndt (1907) and he later added two orders, the Pygophora and the Apygophora. The

Pygophora consisted of the families Lithoglyptidae and Cryptophialidae and were characterised by having biramous terminal cirri and an anus, while the Apygophora was made of the family Trypetesidae, which has uniramous cirri and no anus. These two orders remained unchanged for a century, until Kolbasov, Newman and Høeg (In Kolbasov, 2009) proposed the current taxonomic structure. The changes were made after detailed inspection of the females, dwarf males and cyprids. Kolbasov (2002b) investigated the differences between the dwarf males of the three families. He concluded that his findings did not correspond to the Pygophora and Apygophora. Rather, the dwarf males can be grouped into two groups based on morphological traits. Kolbasov (2002b) remarked that the Lithoglyptidae and the Trypetesidae made up the first group, as they both have dense cuticular projections and complicated body forms (Lin, Kolbasov and Chan, 2016). He further concluded that the Cryptophialidae can be placed in a separate group characterised by circular cuticular ribs and teeth (Kolbasov, 2002b). A later study by Kolbasov and Høeg (2007) examined the cypris larvae of the three families. They concluded that the larvae of the Cryptophialidae were different to that of the Lithoglyptidae and Trypetesidae, as they showed several apomorphies. They had smaller and simpler carapaces, thoraxes and antennules, and also had no swimming appendages (Kolbasov and Høeg, 2007). Thus, Kolbasov, Newman and Høeg felt this was overwhelming evidence to change the systematics of the group to the current state, with the Acrothoracica split into two orders, the Cryptophialida and Lithoglyptida (Kolbasov and Newman, 2005; Kolbasov, 2009; Kolbasov, 2015).

The Cryptophialida consist of the monotypic family Cryptophialidae, Gerstaecker, 1866 with two genera, *Australophialus* Tomlinson, 1969 and *Cryptophialus* Darwin, 1854, and currently include 21 species. The Lithoglyptida are made up of two families, the Lithoglyptidae, Aurivillius, 1892 and Trypetesidae, Kruger, 1940 together comprises nine genera and 49 species (Kolbasov, 2015). The females of the order Cryptophialida are characterised by an operculum with a long, narrow neck, which is the main characteristic feature, lateral and reinforcing bars, a small burrow aperture, a tongue-shaped labrum, rudimentary mouth cirri, no caudal appendages and a special gastric mill at the end of the stomach (Kolbasov, 2009; Chan, Hsieh and Kolbasov 2014). The males of the Cryptophialida are bottle-shaped, with the posterior end elongated in mature males, along with an apertural slit and attachment antennules lacking a stalk (Kolbasov, 2009). Juvenile males are more rounded and lack an elongated posterior end. A charactersistic feature of males of this order are the presence of mantle teeth at the posterior end (Kolbasov, 2009). The cypris larvae of the Cryptophialida is fundamentally different to that of the Lithoglyptida, as they have a small carapace with ornamented deep pits, hexagonally arranged ridges and few, long setae and lack frontolateral pores (Kolbasov, Chan and Høeg, 2014). They have a rudimentary thorax and thoracopods that is not suitable for swimming, along with lattice organs that are plate-shaped with no terminal pore. The Lithoglyptida are characterised by having a wide aperture, a sac-like mantle, well-developed mouth cirri, a large, saddle-like labrum, elongated burrow aperture and lack a special gastric mill at the end of the stomach (Kolbasov, 2009; Chan, Kolbasov and Cheang, 2012; Chan, Hsieh and Kolbasov, 2014). The males of the Lithoglyptida are pear/bottle-shaped, with simple attachment antennules and an apertural slit at the posterior end (Kolbasov, 2009). Often the apertural slit margins are surrounded dense seta-like denticles that protect the entrance to the mantle cavity. Similar to the Cryptophialida, mature males have an elongated posterior end. The males also have lateral projections similar to lobes, that act as sheaths for the penis and testis (Kolbasov, 2009). The cypris larvae of the Lithoglyptida a well-developed carapace that totally encloses the body (Kolbasov, Høeg and Chan, 2014). They have fronotlateral pores, lattice organs with a large terminal pore. They also have six pairs of natatory thoracopods and a small but distinct abdomen and telson, developed for swimming (Kolbasov, Høeg and Chan, 2014). The family Lithoglyptidae consists of three subfamilies, the Berndtiinae Utinomi, 1950 (caudal appendages present or absent, five pairs of terminal cirri), the Lithoglyptinae Aurivillius, 1892 (caudal appendages present, four pairs of terminal cirri) and the Kochloroninae Gruvel, 1905 (caudal appendages present, three pairs of terminal cirri) (Chan, Hsieh and Kolbasov, 2014).

In the following account taxa are arranged in alphabetical order starting with the higher denomination. Each species is entered under the correct and most updated binomen. Subsequently, the binomen is followed by the original author's name, year of publication and previous synonyms are given in historical order. The latest taxonomic reference and any supplementary useful references are given for each species. Included in each species description is a short diagnosis, a list of hosts occupied by the species, the distribution of the species, as well as remarks. Accompanying each species description are a series of plates with photographs and light microscopy along with a map showing its regional distribution. Moreover, there are SEM images of each species showing taxonomically important features. Only females were considered in this study, as few males were observed (for some species none were seen) and both light microscopy and SEM's did not yield feasible images of dwarf males.

Thus, the following account lists all previously known and recently discovered species of South African Acrothoracica and is the first work of its kind for this region. During the last century, two monographs have been published on the Acrothoracica globally (Tomlinson, 1969; Kolbasov, 2009) and these included the known South African species at the time. Unfortunately, the latest monograph is published in Russian and only figure legends and a brief summary are in English. This makes the use of this publication difficult, for many researchers, particularly those in the Southern African region. Thus, an updated guide to the Acrothoracica of South Africa will prove to be useful for taxonomists working on this group.

Methods

Study Area

The sampling for this study was focused on the three main coastal provinces of South Africa - the Western Cape, Eastern Cape and KwaZulu-Natal. Several shore collections within the Western Cape were made throughout the duration of this study, as these were easily accessible to the author, while two single dedicated trips were made to sample within each of the other two provinces during 2017. Overall collection sites ranged from Melkbosstrand (33°44'08.1"S, 18°26'15.2"E), just North of Cape Town on the west coast, to Isipingo (29°59'44.1"S, 30°57'00.8"E) just North of Durban on the east coast (Fig. 2.1).

Fig. 2.1: Map of the South Africa depicting the sampling sites, along with the two major currents along the coast.

Host collection

Field work consisted of hand collections in the intertidal zone on rocky shores, or in the subtidal zone by snorkelling (< 5 m). Where possible, ten individuals of each of the larger gastropod, bivalve, polyplacophoran and thoracican species from each of the three provinces were randomly collected, in most cases living molluscs were collected, but rarely unoccupied shells were included. The host genera collected included *Argobuccinum*, *Atrina*, *Austromegabalanus*, *Burnupena*, *Crepidula*, *Charonia*, *Dinoplax*, *Fusinus*, *Haliotis*, *Mancinella*, *Ranella*, *Purpura*, *Scutellastra*, *Tenguela* and *Turbo*. In the Western and Eastern Cape certain crustose coralline algae species were also collected and examined for acrothoracicans (see Chapter 1 for methods on these), while some additional coralline specimens were examined from the collections held at the University of the Western Cape. Furthermore, some individual acrothoracicans were extracted from mollusc specimens obtained from the East London Museum, or donated by divers.

Extraction and processing

After the collection of host specimens, they were examined microscopically and where possible, the positions of the barnacles on the host were noted and subsequently all visible barnacles were carefully extracted using a vice and/or wire cutter to crack the shells and forceps to remove the barnacles. After all visible barnacles were extracted, shells were treated in 2% HCl to extract any unnoticed specimens (Tomlinson, 1969; Chan, Kolbasov and Høeg, 2016). This method is not ideal, as it does not preserve some of the calcareous plates that are characteristic features of some acrothoracicans. Moreover, acid treated specimens are unsuitable for DNA analyses. However, for small species like the Cryptophialida, this method is extremely useful, specifically for acquiring frequency data. Once extracted, all specimens were preserved in 96% ethanol. Species identifications were done using morphological analyses of both external and internal features. Specimens of each of the species were sent to Dr. Benny Chan at Academia Sinica in Taiwan for DNA extraction, but unfortunately extraction was unsuccessful.

For dissections and light microscopy, specimens were boiled in 10% KOH for several minutes, until translucent. Subsequently specimens were carefully transferred to a solution of ethanol, freshwater and glycerol. This was left for several days at ambient temperature, which allowed the ethanol and freshwater to evaporate, leaving only the specimens in a glycerol solution. Light microscopy images were acquired using a Nikon Stereoscopic Zoom Microscope SMZ1500 with a Nikon DS Camera Control Unit DS-U3 and DS-5M Camera head with the NIS Elements Documentation and Digital 3D Imaging program, or with a Leica DM750 compound microscope using the Leica Application Suite (LAS) EZ.

SEM Imaging

Specimens for SEM examination were cleaned thoroughly using a small paintbrush under a Leica ES2 dissecting microscope. Subsequently the specimens were placed in Hexamethyldisilazane for 10 minutes. They were then transferred to a petri dish and air-dried in a fume-hood for several minutes. Thereafter these specimens were sputter-coated with gold-palladium and images were taken using the TESCAN MIRA-3 Scanning Electron Microscope (5 kV). Images were edited using GIMP (https://www.gimp.org).

Maps

Maps were created using R Software (R Core Team, 2018).

Body structure and terminology

The main morphological features of a female acrothoracican are illustrated in Fig. 2.2 and the principal body parts are defined as follows:

Terminal cirri – Biramous (except in Trypetesidae it is uniramous) cirri located at the posterior end of the thorax used for feeding. Does not include first pair of cirri (mouth cirri), which is adjacent to the mouthparts.

Opercular bars – Pair of chitinous bars located at the mantle sac opening often with spines, nodules and setae and often ends with posterior processes. Some species have a globular or drop-shaped orificial knob below the dorsal side of the opercular bars.

Posterior processes – Pair of large spines, often hooked at the ventral end of the opercular bar, often with spines and setae along the length.

Mouthparts – Consists of a labrum and paired mandibles with mandibular palps, maxillae and maxillules.

Mantle – Sac in which the somatic body of females are embedded, attached to the substrate via an attachment disk. Surface often with setae, spines, teeth and multifid scales.

Caudal appendages – Pair of appendages at the base of the last pair of terminal cirri (found in most species of the Lithoglyptidae).

Comb collar – An array of large setae that is underlying to the ventral half of the opercular bar.

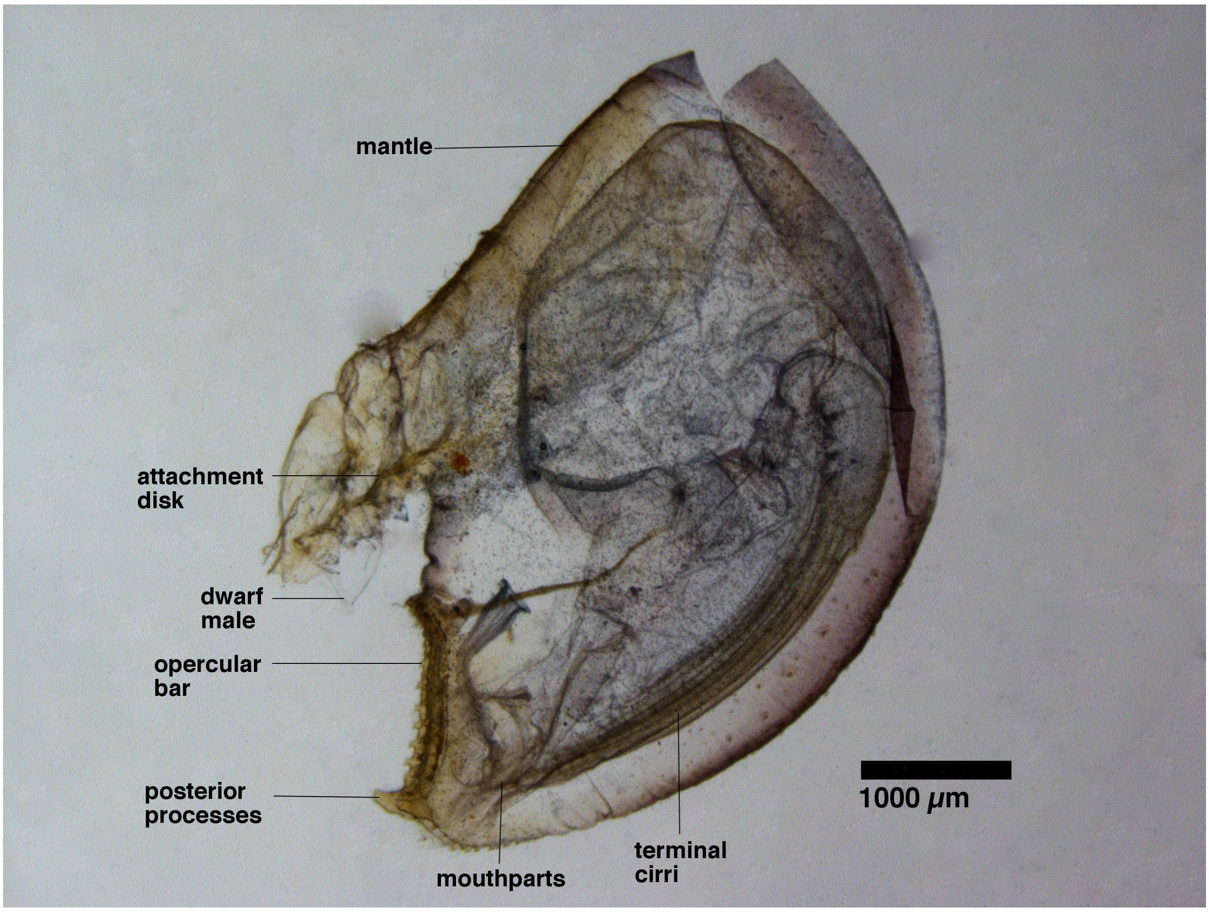

Fig. 2.2: External and internal anatomy of a female acrothoracican (*Weltneria spinosa*).

Key to the Acrothoracica of South Africa

1a. Mantle bottle-like, elongated neck with operculum and small aperture, labrum elongated and tongue-like, rudimentary mouth cirri ……………………… **(Order: Cryptophialida) 2**

1b. Operculum without elongated neck, wide aperture, large saddle-like labrum, well developed mouth cirri……………………………………………. **(Order: Lithoglyptida) 4**

2a. Females with four pairs of terminal cirri and one dorsal thorax process ………………………………………………………………. **(Genus: *Australophialus*) 3**

2b. Females with three pairs of terminal cirri and two dorsal thorax processes

………………………………………………….. **(Genus: *Cryptophialus*) not found in SA**

3a. Females with an indentation one-third the distance from the rostral end on the apertural margin………………………………………………………… ***Australophialus turbonis***

3b. Lacks distinctive notch in the opercular margin in *A. turbonis*, rather has a margin with small bifid teeth…………………………………………………. ***Australophialus utinomii***

4a. Females with well-developed opercular bars and operculum with large rows of multifid scales, comb collar developed, biramous terminal cirri……….... **(Family: Lithoglyptidae) 5**

4b. Females with indistinct opercular bars and operculum without large rows of multifid scales, reduced comb collar, uniramous cirri …...... **(Family: Trypetesidae) not found in SA**

5a. Five pairs of terminal cirri……………………….……….... **(Subfamily: Berndtiinae) 6**

5b. Four pairs of terminal cirri……………………………… **(Subfamily: Lithoglyptinae) 8**

5c. Three pairs of terminal cirri….……………………….. **(Subfamily: Kochlorininae) 10**

6a. Without caudal appendages……………………..……. **(Genus: *Berndtia*) not found in SA**

6b. With caudal appendages…………………………………….…. **(Genus: *Weltneria*) 7**

7a. Opercular bar with large hook-like posterior processes……………… ***Weltneria spinosa***

7b. Opercular bar with a broad opercular area, with sharp posterior processes with some spines on them, opercular bar with row of small bifid and simple teeth…. ***Weltneria hirsuta***

8a. Caudal appendages without pedestals……………………..……….…. **Balanodytes 9**

8b. Caudal appendages with basal pedestal, with a pair of hook-like posterior processes and a pair of posterior setose processes……………………….. ***Auritoglyptes* not found in SA**

8c. Caudal appendages with basal pedestal, with no posterior processes of opercular bars, but with small posterior lobes…………………...……….… ***Lithoglyptes* not found in SA**

9a. Posterior processes of opercular bar straight, with a spine branching off at the apex (slightly anteriorly facing) with simple, straight spine on apex, lateral bars absent……………………………………………………… ***Balanodytes n. sp.***

9b. Posterior processes of opercular bars recurved (strongly anteriorly bent), with feeble lateral bars ……………………………………………….…. ***Balanodytes flexuosus***

10a. Opercular bar with long, thin lance-shaped teeth (8 – 13), with a prominent, globular orificial knob…………………………………………………… ***Kochlorine bocqueti***

10b. Opercular bar with short, broad arrowhead-shaped teeth (5 - 8), with an oval underdeveloped orificial knob……………………….……………***Kochlorine n. sp.***

Systematic Account

Superorder **ACROTHORACICA** Gruvel, 1905

Cryptosomata Hancock, 1849: 313

Abdominalia Darwin 1854: 310

Acrothoracica Gruvel, 1905: 310

Diagnosis: Small, soft-bodied barnacles. Females burrow into calcareous substrates (molluscs, corals, limestone, thoracicans, etc.). Minute dwarf males either attached to the female or her burrow. Lack calcareous shell plates, but possess a single pair of chitinous plates, also known as opercular bars, near the aperture. Have 3 – 5 pairs of terminal cirri, with a single pair of mouth cirri, adults have reduced abdomen. Caudal appendages present (some lithoglyptids) or absent (all cryptophialids).

Remarks: Currently the Acrothoracica consist of two orders, the Cryptophialida and the Lithoglyptida (Kolbasov, 2009).

Order **CRYPTOPHIALIDA** Kolbasov, Newman and Høeg (Cited in Kolbasov, 2009)

Cryptophialida Kolbasov, Newman and Høeg, in Kolbasov, 2009: 241. Chan, Hsieh and Kolbasov, 2014: 2.

Diagnosis: Main characteristic feature females with long, narrow-necked operculum, with small circular aperture, tongue-shaped labrum, no caudal appendages and special gastric mill at end of stomach. Rudimentary mouth cirri, with developed lateral and reinforcing bars.

Thorax with one or two whip-like dorsal processes, no caudal appendages (Chan, Hsieh and Kolbasov, 2014). Posterior end of dwarf males with circular, cuticular ribs and frequently with mantle teeth. Simple attachment attenules without a stalk. Cypris larvae possesses rudimentary thorax and thoracopods, carapace covers the body incompletely. Burrow opening rounded and small.

Remarks: The Cryptophialida consists of the monotypic family Cryptophialidae.

Family **CRYPTOPHIALIDAE** Gerstaecker, 1866

Cryptophialidae Gerstaecker, 1866: 534.

Diagnosis: As for Cryptophialida.

Remarks: Contains the genera *Australophialus* Tomlinson, 1969 and *Cryptophialus* Darwin, 1854 with five and 16 species respectively. In South Africa, only *Australophialus* observed.

Genus ***Australophialus,*** Tomlinson, 1969

Australophialus Tomlinson, 1969: 117.

Diagnosis: Characterised by having four pairs of terminal cirri and one whip-like dorsal body process (Chan, Hsieh and Kolbasov, 2014).

Remarks: Globally, there are currently five species in this genus, two of which are found in South Africa (both endemic).

Australophialus turbonis (Barnard, 1925)

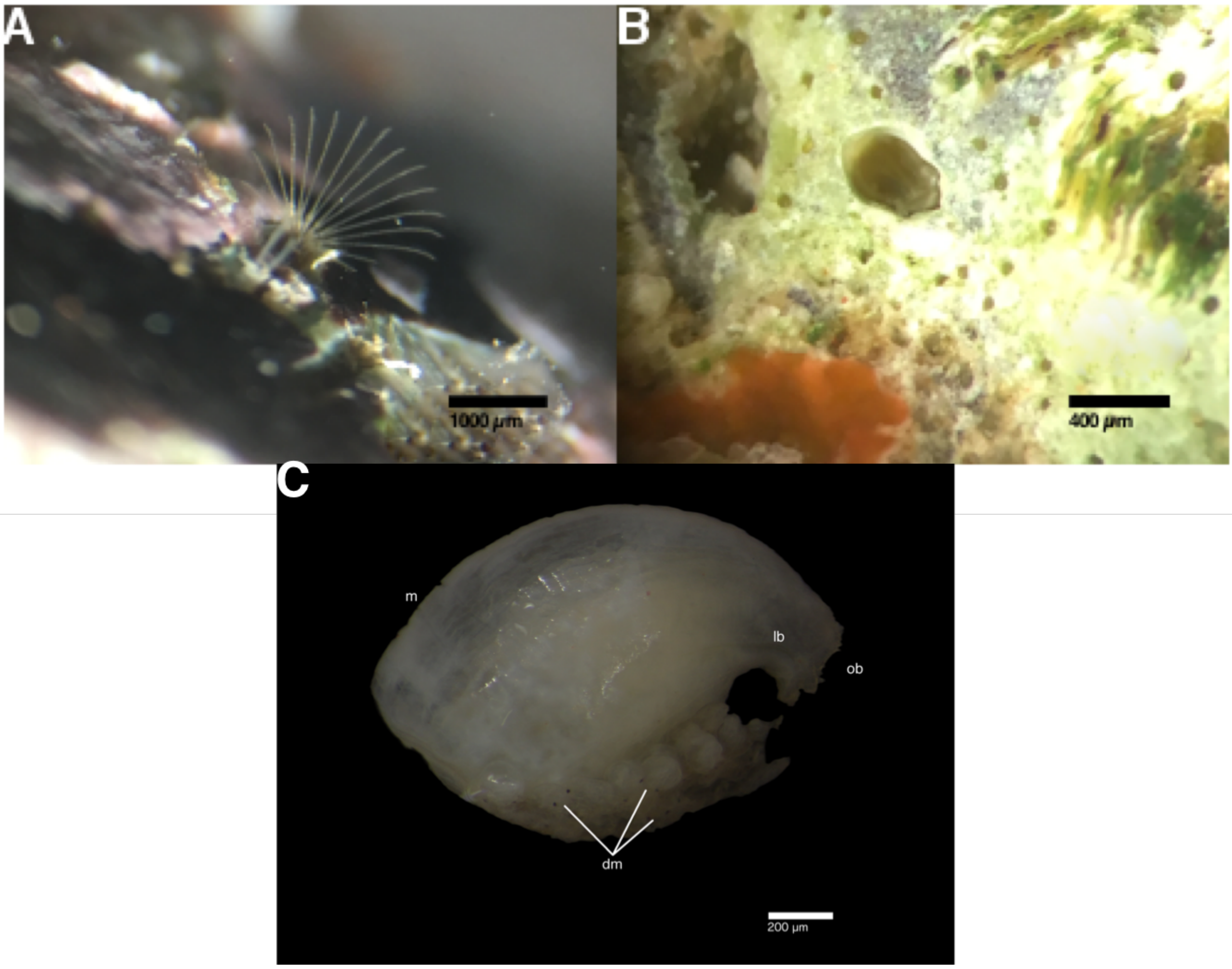

Fig. 2.3: *Australophialus turbonis*, female. A – Female feeding using terminal cirri in *Turbo sarmaticus*; B – Burrow in *Burnupena cincta*; C - Lateral view of a whole specimen. Abbreviations: *ob* – opercular bar, *lb* – lateral bar, *m* – mantle, *dm* – dwarf males.

Cryptophialus turbonis Barnard, 1925: 5; Newman and Ross (1971): 26.

Australophialus turbonis Tomlinson, 1969: 121 - 125, Fig. 33; Tomlinson, 1987: 66, Fig. 3; Kolbasov and Høeg, 2007: 129, Fig. 3 (F), Fig. 4 (K), Fig. 10 (A); Kolbasov (2009): 207,

Fig. 3 (*а*), Fig. 7 (*в*), Fig. 19 (*б*), Fig. 20 (*б, е, ж*), Fig. 21 (*и*), Fig. 22 (*б*), Fig. 24 (*б*), Fig. 28 (*б, е*), Fig. 38 (*ж*), Fig. 50 (*а*), Fig. 52 (*г*), Fig. 55 (*ж*), Fig. 59 (*а*), Fig. 126.

Material examined: SAMC-A091103, False Bay, Western Cape, South Africa, February 2017, 30 specimens in 3 *Turbo cidaris* shells. SAMC-A091104, Wooleys Pool, False Bay, Western Cape, South Africa, 30 January 2017, 3 specimens in 2 *Turbo sarmaticus* shells. SAMC-A091105, False Bay, Western Cape, South Africa, January and February 2017, 308 specimens in 4 *Turbo sarmaticus* shells (19 not deposited, used for dissections, SEM's, light microscopy and genetic analyses). SAMC-A091106, Melkbosstrand, Western Cape, South Africa, 28 February 2017, 1 specimen in a *Fusinus ocelliferus* shell. SAMC-A091107, Melkbosstrand, Western Cape, South Africa, 28 February 2017, 2 specimens in a *Haliotis midae* shell. SAMC-A091108, Bloubergstrand, Western Cape, South Africa, April 2017, 2 specimens from 2 *Argobuccinum pustulosum* shells. SAMC-A091109, False Bay, Western Cape, South Africa, 15 March 2017, 1 specimen in a *Burnupena cincta* shell. SAMC-A091110, False Bay, Western Cape, South Africa, 15 March 2017, 1 specimen in a *Burnupena cincta* shell. SAMC-A091111, False Bay, Western Cape, South Africa, 27 September 2018, 17 specimens from 3 *Crepidula porcellana* shells. SAMC-A091112, False Bay, Western Cape, South Africa, 15 March 2017, 1 specimen in a *Burnupena cincta* shell.

Diagnosis: Australophialid with a notch one-third distance from rostral end on apertural margin, otherwise similar to other South African australophialid, *Australophialus utinomii*.

Description: Female, mantle bottle-shaped, with characteristic elongated neck of all Cryptophialids (Fig. 2.3C; 2.5A). Length 1 – 3 mm (mean = 1.95 mm), width 0.6 – 1.6 mm (mean = 1.19 mm). Opercular bars about 300 μm long and well-armed on margins by long, simple spines and setae, with nodules on flat surface of opercular bar (Fig. 2.4A, D). Distinct notch on opercular bar about one-third from rostral end (Fig. 2.4D, F; 2.5B). An infolded velum with lamellae extends into comb collar, which is composed of long, fine projections, ending in bristles (Fig. 2.4E). Lateral surfaces of operculum with dense rows of multifid scales, with setae (Fig. 2.4B). Mantle surface striated with no obvious projections, other than small teeth that are mostly bifid and uniformly distributed. Large reinforcing bars present, with one extending dorsally toward attachment area on dorsal end of aperture. A pair of lateral bars extends from apertural notch downward along mantle on either side (Fig. 2.5B), with fewer teeth on lateral bars, as is normal for this genus. Attachment area masked by layers of previous moults (cemented exuviae) that forms a hard disk onto which males attach (Tomlinson, 1969). Similar to *W. spinosa*, has a light reddish and white colour when examined fresh and turns light brown/white when preserved in alcohol (Fig. 2.3C). Burrow oval-shaped (Fig. 2.3B), averaging 0.3 x 0.25 mm.

Terminal cirri with four pairs, without caudal appendages (Fig. 2.5C). One whip-like dorsal body process (Fig. 2.5D). Mouth cirrus (paired) reduced and consists only of small processes with a couple of bristles (Tomlinson, 1969). Characteristic of the genus, labrum elongated and tongue-shaped and extends out of aperture, with setae at tip (Fig. 2.5F). Mouthparts typical of the genus, with ovate maxilla with distal setae (Fig. 2.5E). Mandible with three teeth on cutting edge. Maxillule with no notch, no dense and long setae (Fig. 2.5E). Mandibular palp elongated, with setae at distal end. Mature attached males averaging 0.45 x 0.25 mm. As many as 17 males attached to a single female.

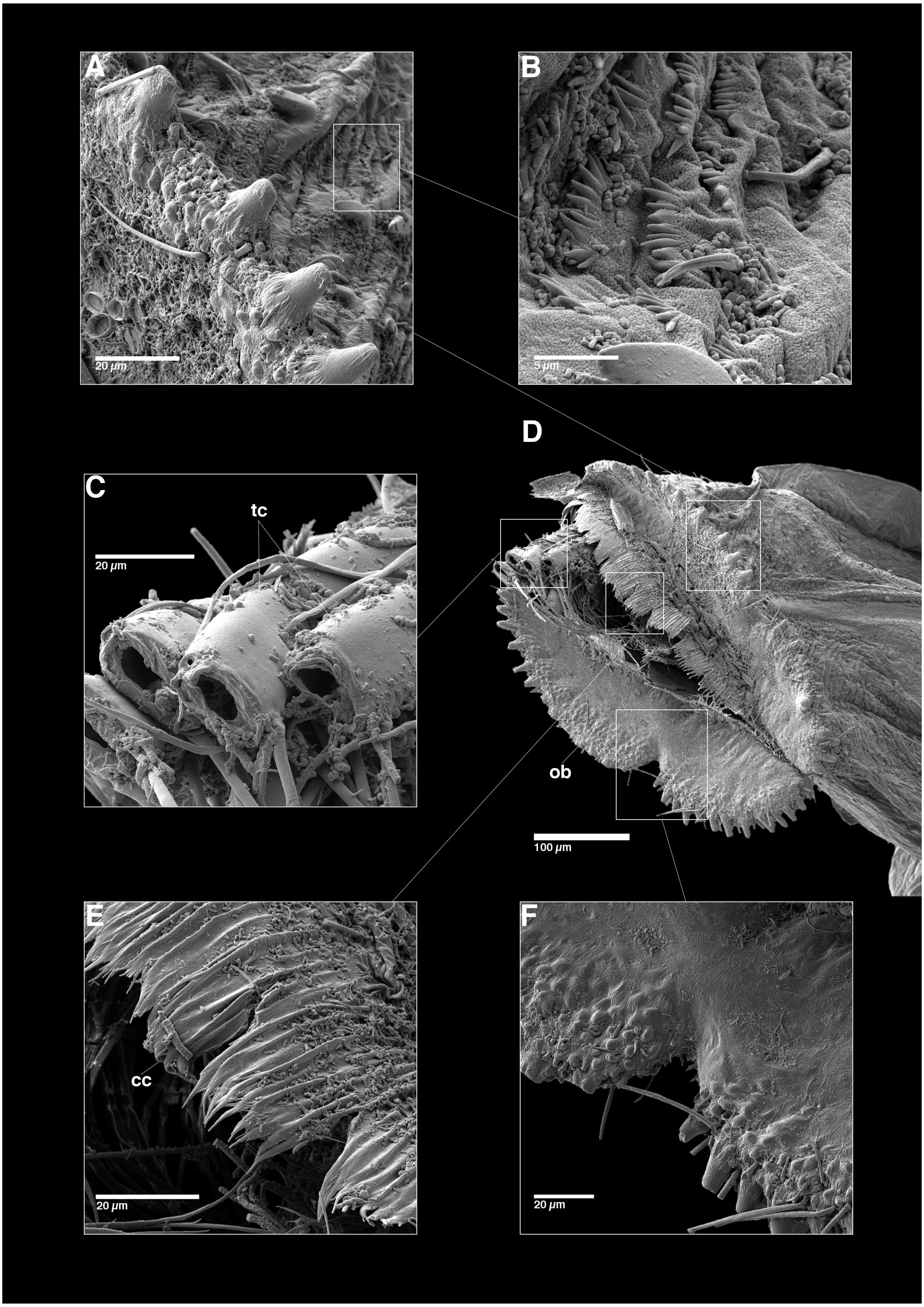
A
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Fig. 2.4: *Australophialus turbonis* collected from *Turbo sarmaticus* from False Bay. Scanning electron microscopy of general morphology and external features, female. A – Spines on margin of opercular bar; B – Multifid scales; C – Posterior end of terminal cirri; D – Opercular area; E – Comb collar; F – Diagnostic notch on opercular bar. Abbreviations: *cc* – comb collar, *ob* – opercular bar, *tc* – terminal cirri.

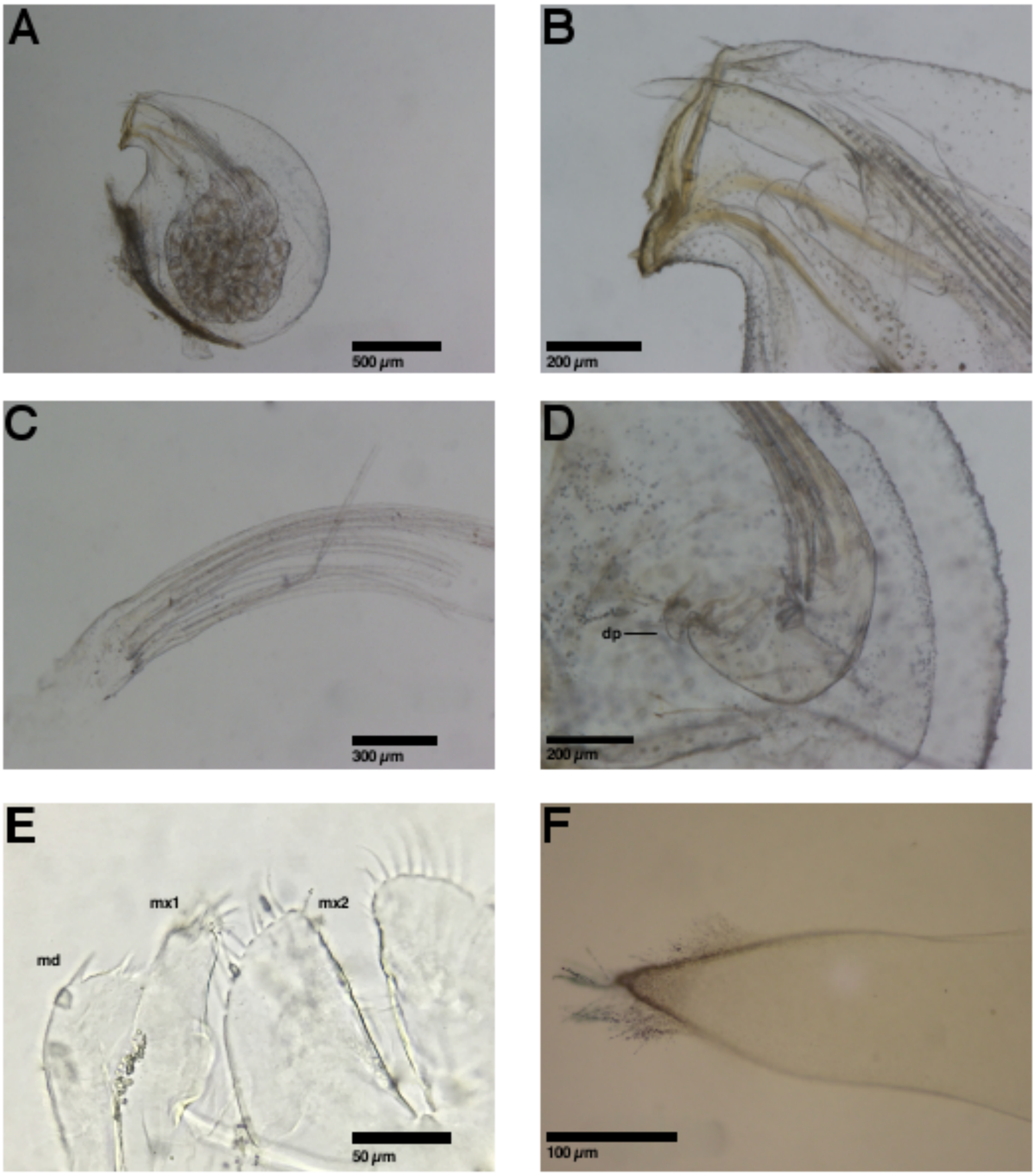

Fig. 2.5: *Australophialus turbonis* collected from *Turbo sarmaticus* from False Bay. Light microscopy of showing external features and cirri, female. A – Lateral view of whole specimen; B – Opercular area, lateral view showing opercular bars with notch, labrum and lateral bars; C – Terminal cirri; D – Dorsal body process; E – Mouthparts including the mandible, maxillule and maxilla; F – Labrum. Abbreviations: *dp* – dorsal body process, *md* – mandible, *mx1* – maxillule, *mx2* - maxilla.

Hosts: Type host *Turbo sarmaticus* Linnaeus, 1758. Previously known to bore into shells of *Burnupena cincta* (Röding, 1798) and *Burnupena limbosa* (which is a subspecies of *B. cincta*). New hosts reported here are *Argobuccinum pustulosum* (Lightfoot, 1786), *Crepidula porcellana* Lamarck, 1801*, Fusinus ocelliferus* (Lamarck, 1816), *Haliotis midae* Linnaeus, 1758 and *Turbo cidaris* Gmelin, 1791.

Distribution: Type locality False Bay (34°07'57.8"S, 18°26'44.1"E), South Africa. Ranges from Paternoster (32°48’28.90”S, 17°53’29.05”E) to Hermanus (34°25’1.62”S, 19°14’55.46”E). Endemic to the Western Cape (Fig. 2.6).

Fig. 2.6: *Australophialus turbonis.* Distribution records on the South African coastline.

Remarks: *Australophialus turbonis* was previously reported from the Western Cape in various hosts and at Umpangazi in KwaZulu-Natal (Tomlinson, 1969) from *Purpura persica* (Linnaeus, 1758) (previously *Thais rudolphi*). However, it was probably misidentified as *A. utinomii,* which is morphologically similar to *A. turbonis* (see below). *Australophialus turbonis* is only known from the Western Cape and was not found in either the Eastern Cape nor KwaZulu-Natal, whereas *A. utinomii* was found in the Eastern Cape around East London, as well as in KwaZulu-Natal. Moreover, *A. utinomii* is also known from two *Purpura* Bruguiére, 1789 species (see below), while this is not a known host for *A. turbonis*. Commonly found in association with *Weltneria spinosa*.

Australophialus utinomii Tomlinson, 1969

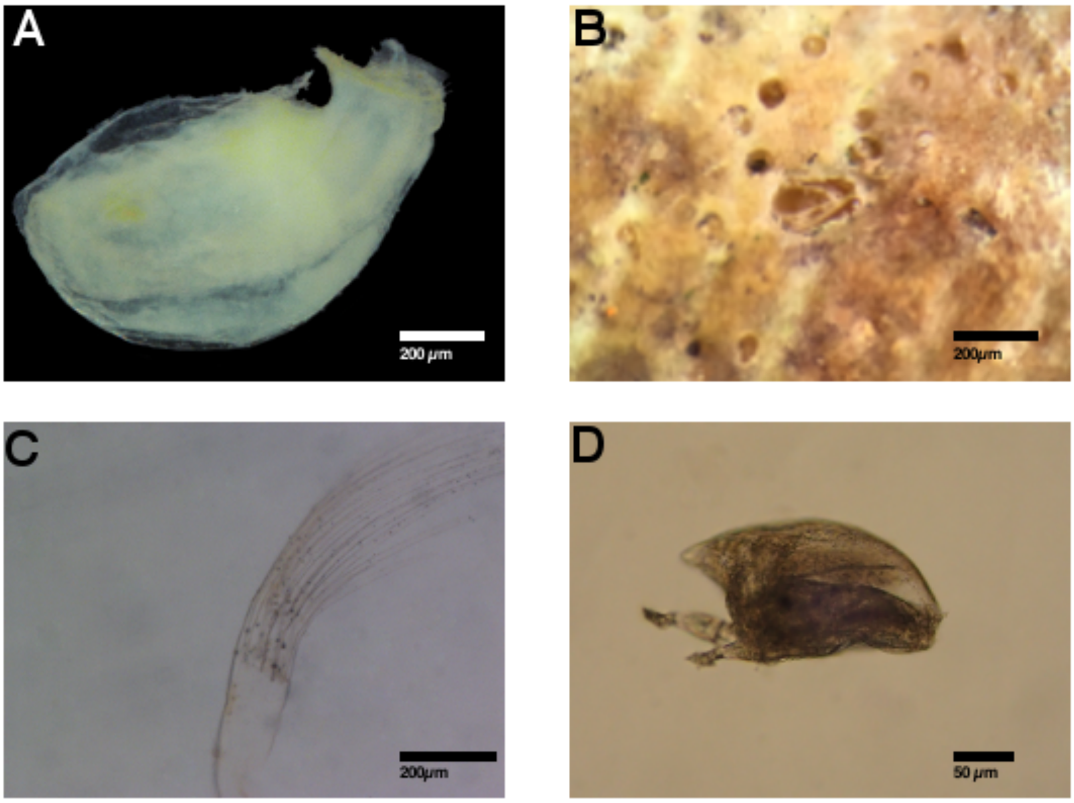

Fig. 2.7: *Australophialus utinomii* from *Ranella gemmifera* from Gonubie, female. A - Lateral view of whole specimen; B –Burrow opening; C - Terminal cirri; D – Cypris larva.

Australophialus utinomii Tomlinson, 1969: 119 – 121; Kolbasov, 2009: 208, Fig. 127.

Material examined: SAMC-A091096, near East London, Eastern Cape, South Africa, April 2017, 79 specimens in 7 *Burnupena cincta* shells (four not deposited, used for SEM's and genetic analyses). SAMC-A091097, near East London, Eastern Cape, South Africa, April 2017, 29 specimens in 5 *Burnupena cincta* shells (11 not deposited, used for SEM's and genetic analyses or not deposited). SAMC-A091099, Gonubie, Eastern Cape, South Africa, 27 April 2017, 6 specimens in *Mancinella capensis* shell. SAMC-A091098, Chintsa West, Eastern Cape, South Africa, 26 April 2017, 6 specimens in 2 *Dinoplax gigas* shell plates.

SAMC-A091100, near East London, Eastern Cape, South Africa, April 2017, 7 specimens on 3 *Turbo sarmaticus* shells. SAMC-A091101, near East London, Eastern Cape, South Africa, April 2017, 81 specimens from 4 *Turbo sarmaticus* shells (4 not deposited, used for dissections). SAMC-A091102, Gonubie, Eastern Cape, South Africa, 27 April 2017, 4 specimens on *Ranella gemmifera* shell. SAMC-A091093, Isipingo, KwaZulu-Natal, South Africa, 21 September 2017, 44 specimens in *Purpura panama* shell (only 34 deposited, 10 used for dissections). SAMC-A091091, Banana Beach, Port Shepstone, KwaZulu-Natal, South Africa, 20 September 2017, 35 specimens from 2 *Purpura panama* shells. SAMC-A091092, Banana Beach, Port Shepstone, KwaZulu-Natal, South Africa, 20 September 2017, 5 specimens in *Purpura panama* shell. SAMC-A091094, Banana Beach, Port Shepstone, KwaZulu-Natal, South Africa, 20 September 2017, 7 specimens in *Purpura bufo* shell. PP08, Banana Beach, Port Shepstone, KwaZulu-Natal, South Africa, 20 September 2017, 2 specimens from a *Purpura panama* shell. SAMC-A091095, Port Shepstone, KwaZulu-Natal, South Africa, 19 September 2017, 1 specimen from *Dinoplax validifossus* shell plate.

Diagnosis: Similar to *A. turbonis* but without the distinctive notch in the opercular margin, instead margin with small bifid teeth.

Description: Female, body shape characteristic of cryptophialids, with mantle bottle-like and neck elongated (Fig. 2.7A). Length 0.65 – 2 mm (mean = 1.18 mm), width 0.4 – 0.95 mm (mean = 0.68 mm). Opercular bars with average length 0.35 mm, with plenty of setae and simple, bifid and rarely trifid spines on margin (Fig. 2.8D, E). Large spines and setae present on caudal region of opercular bar (Fig. 2.8B). Rostral end of opercular bar elongated with several spines and setae (Fig. 2.8E). Comb collar consisting of small projections fused at the bases (Fig. 2.8A). Surface of opercular area striated (as is whole of mantle), with small multifid scales (Fig. 2.8F). A pair of lateral bars support either side of mantle, these bars pointed and associated with 3-4 rows of small spines. An internal reinforcing bar found within apertural region at dorsal end. Colour light brown/white when fresh, becoming slightly paler when preserved in alcohol. Burrow opening small, oval-shaped (Fig. 2.7B).

Four pairs of biramous, multi-segmented terminal cirri present (Fig. 2.7C). A pair of rudimentary uniramous, unsegmented mouth cirri present on ventral thorax area, posterior to mouth. Labrum pronounced and extends far beyond opercular area; large in comparison to others of this genus (Fig. 2.8D). Mouthparts typical of genus, a pair of mandibles with palps present, along with a pair of maxillae and maxillules. One dorsal body process present. Females with maximum of four dwarf males recorded. Dwarf males 0.29 x 0.16 mm. Cypris larvae 0.25 x 0.15 mm (Fig. 2.7D).

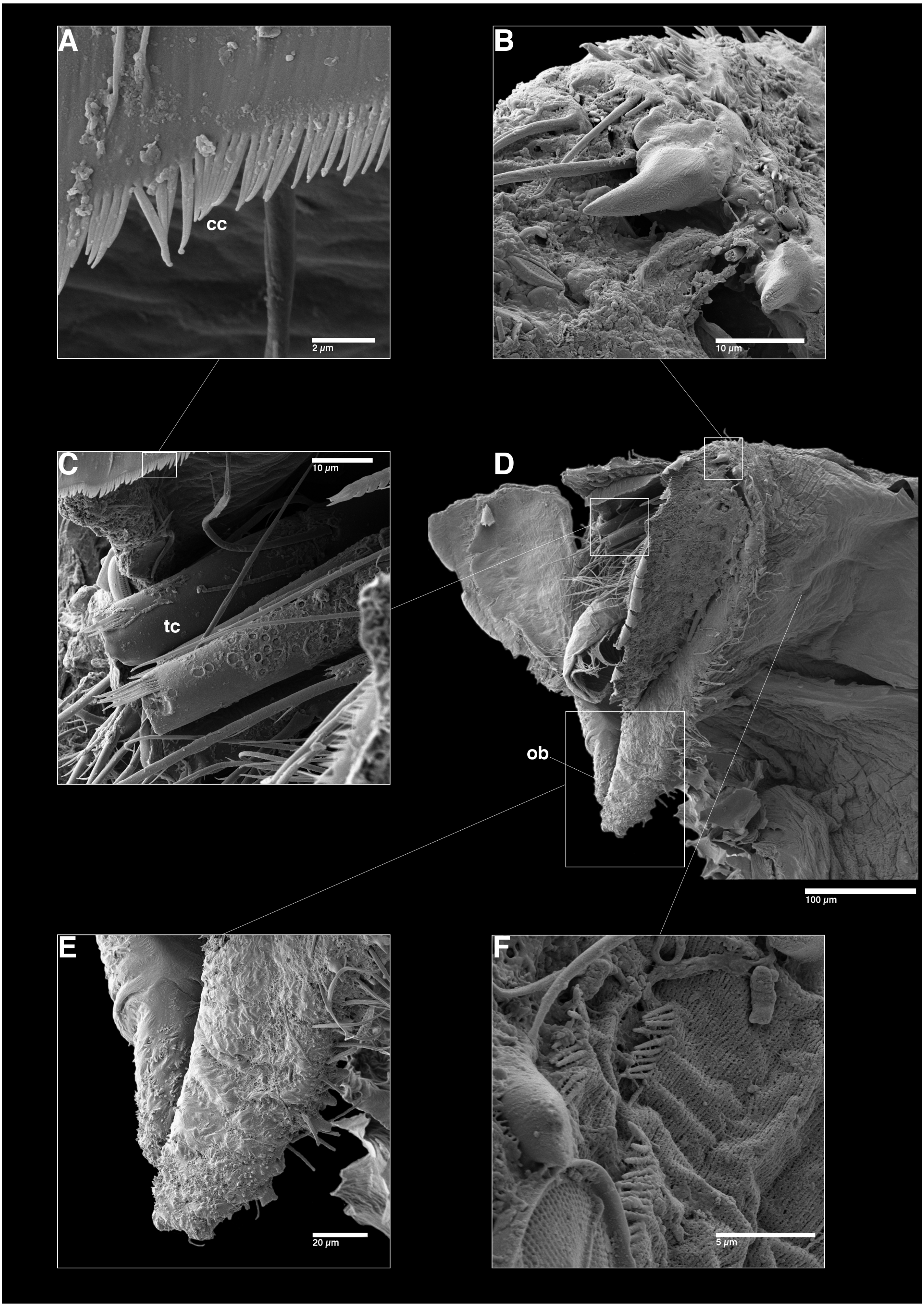
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Fig. 2.8: *Australophialus utinomii* from *Burnupena cincta* near East London. Scanning electron microscopy of general morphology and external features, female. A – comb collar; B – Magnified view of spine at caudal margin of opercular bar; C – Terminal cirri protruding out of aperture; D - Opercular area, fronto-lateral view; E – Rostral area of opercular bar with spines and setae; F – Surface of lateral opercular area with multifid scales. Abbreviations: *cc* – comb collar, *ob* – opercular bar, *tc* – terminal cirri.

Hosts: Previously known from *Dinoplax gigas* (Gmelin, 1791). Additional hosts in the Eastern Cape include *Burnupena cincta, Mancinella capensis* (Petit de la Saussaye, 1852)*,* *Ranella gemmifera* (Euthyme, 1889) and *T. sarmaticus*. Additional hosts in KwaZulu-Natal include *Dinoplax validifossus* Ashby, 1934*, Purpura bufo* Lamarck, 1822 and *P. panama* (Röding, 1798).

Distribution: Type locality is Qolora (32°41'50.5"S, 28°22'25.1"E), Eastern Cape, roughly 50 km east of East London. Ranges from Gonubie (32°56'33.8"S, 28°02'00.9"E) to Isipingo (29°59'44.1"S, 30°57'00.8"E). Endemic to the Eastern Cape and KwaZulu-Natal (Fig. 2.9).

Fig. 2.9: *Australophialus utinomii.* Distribution on the South African coastline.

Remarks: Common, often in association with *Kochlorine bocqueti, Kochlorine n. sp.* and *Weltneria spinosa*. Attempts to dissect this species were unsuccessful.

Order **LITHOGLYPTIDA** Kolbasov, Newman and Høeg (Cited in Kolbasov, 2009)

Lithoglyptida Kolbasov, Newman and Høeg in Kolbasov, 2009: 239; Chan, Hsieh and Kolbasov, 2014: 12.

Diagnosis: Females with wide aperture, sac-like mantle, well-developed mouth cirri, large, saddle-like labrum and lack special gastric mill at end of stomach (Kolbasov, 2009; Chan, Kolbasov and Cheang, 2012; Chan, Hsieh and Kolbasov, 2014). Females have an operculum without a neck, with opercular bar less than aperture length. Thorax without long dorsal processes. Burrow shape elongated. Males have surfaces with several cuticular denticles and lack mantle teeth. Cypris larvae with developed thorax and thoracopods with an unperforated carapace with fronto-lateral pores.

Remarks: Consists of two families, the Lithoglyptidae and Trypetesidae. No species of the Trypetesidae known from South Africa.

Family **LITHOGLYPTIDAE** Aurivillius, 1892

Lithoglyptidae Aurivillius, 1892: 133. Kolbasov, 2009: 147; Chan, Hsieh and Kolbasov, 2014: 13.

Diagnosis: Females have well-developed opercular bars, comb collar, thoracic lappets and mouth appendages; protopod mouth cirri, biramous multi-segmented terminal cirri, caudal appendages present in some species, intestine with anus. Dwarf males pear-shaped with a pair of lobes at base of attachment antennules (Chan, Hsieh and Kolbasov, 2014).

Remarks: Consist of three subfamilies: Berndtiinae, Lithoglyptinae and Kochlorininae, all present in South Africa.

Subfamily **BERNDTIINAE** Utinomii, 1950

Berndtiidae Utinomi, 1950: 457.

Weltneriinae Kolbasov and Newman, 2005: 40.

Diagnosis: Females with 5 pairs of terminal cirri. Caudal appendages present in *Weltneria,* but not in *Berndtia*.

Remarks: Currently there are two genera described from this monophyletic subfamily, *Berndtia* Utinomi, 1950 and *Weltneria* Berndt, 1907. No species of *Berndtia* are reported from Africa (Kolbasov, 2009), however further investigation of coral species could potentially reveal their presence, as corals are their preferred substrate (Chan, Hsieh and Kolbasov, 2014).

Genus ***Weltneria*** Berndt, 1907

Diagnosis: Females with five pairs of biramous terminal cirri, two-segmented caudal appendages. This is considered plesiomorphic, as this represents the ground pattern for all thecostracans (Kolbasov and Newman, 2005). Lateral bars weak or absent, orificial knob absent. Dwarf males pear-shaped, tapering towards the top, no lateral projections, attachment antennules with stalk absent (Chan, Hsieh and Kolbasov, 2014).

Remarks: At present, there are 12 *Weltneria* species globally. Two of these are present in South Africa, of which *W. spinosa* is endemic.

***Weltneria spinosa* Berndt, 1907**

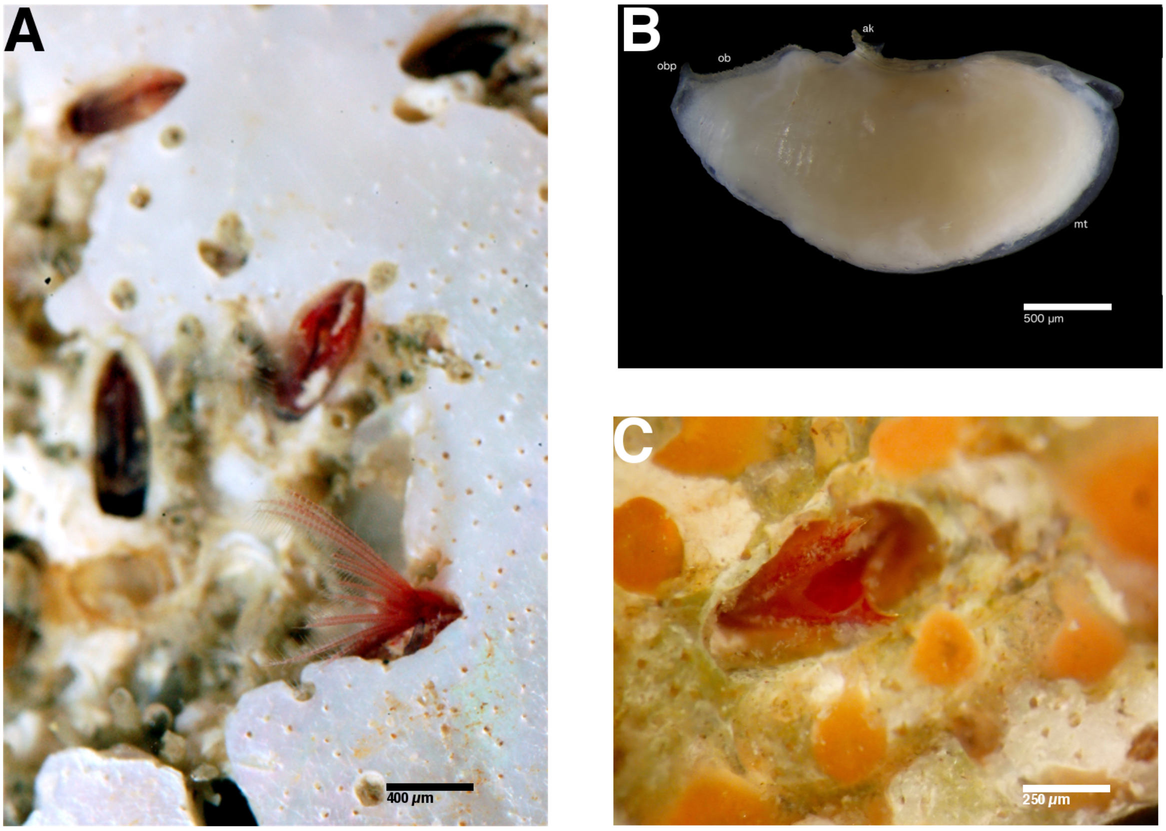

Fig. 2.10: *Weltneria spinosa* collected from *Turbo sarmaticus* from False Bay, female. A - Female feeding using cirri; B - Lateral view of whole specimen; C - Natural colouration showing opercular bars with posterior processes of opercular bar. Abbreviations: *ak* – attachment knob, *mt* – mantle, *ob* – opercular bar, *obp* – posterior process of opercular bar.

Weltneria spinosa Berndt, 1907: 289; Tomlinson, 1969: 32-36, Fig. 1; Tomlinson, 1987: 65, Fig. 2; Kolbasov and Høeg, 2007: 129, Fig. 3 (A), Fig. 5 (A, F), Fig. 7 (A), Fig. 8 (C), 1 Fig. 9 (E), Fig. 11 (E); Kolbasov, 2009: 174 (In Russian), Fig. 2 (*а*), Fig. 5 (*ж*), Fig. 14 (*е, ж*), Fig. 25 (*г*), Fig. 28 (*б*), Fig. 37 (*а*), Fig. 39 (*е*), Fig. 49 (*а*), Fig. 51 (*а*), Fig. 53 (*а, е, ж, з, и*), Fig. 55 (*в*), Fig. 56 (*б, и*), Fig. 58 (*б*), Fig. 60 (*б*), Fig. 85.

Material examined: SAMC-A091113, False Bay, Western Cape, South Africa, January and February 2017, 34 specimens from 6 *Turbo sarmaticus* shells (5 not deposited, used for genetic analyses). SAMC-A091114, False Bay, Western Cape, South Africa, January and February 2017, 376 specimens from 8 *Turbo sarmaticus* shells (10 not deposited, used for dissections and light microscopy). SAMC-A091115, Chintsa West, Eastern Cape, South Africa, April 2017, 25 specimens from 4 *Turbo sarmaticus* shells (2 not deposited, used for SEM's). SAMC-A091116, Gonubie, Eastern Cape, South Africa, April 2017, 105 specimens from 5 *Turbo sarmaticus* shells. SAMC-A091117, Gonubie, Eastern Cape, South Africa, 27 April 2017, 12 specimens from a *Haliotis midae* shell. SAMC-A091118, Gonubie, Eastern Cape, South Africa, 27 April 2017, 223 specimens from a *Haliotis midae* shell (3 not deposited, used for genetic analyses). SAMC-A091119, Melkbosstrand, Western Cape, South Africa, 28 February 2017, 13 specimens from a *Haliotis midae* shell. SAMC-A091120, Gonubie, Eastern Cape, South Africa, 27 April 2017, 30 specimens from *Ranella gemmifera* shell. SAMC-A091121, Gonubie, Eastern Cape, South Africa, 27 April 2017, 6 specimens from *Ranella gemmifera* shell. SAMC-A091122, False Bay, Western Cape, South Africa, 19 February 2017, 1 specimen from *Argobuccinum pustulosum* shell (2 not deposited, used for SEM's). SAMC-A091123, False Bay, Western Cape, South Africa, 17 February 2017, 9 specimens from *Argobuccinum pustulosum* shell. SAMC-A091124, False Bay, Western Cape, South Africa, 14 March 2017, 11 specimens from *Argobuccinum pustulosum* shell. SAMC-A091125, False Bay, Western Cape, South Africa, 14 March 2017, 3 specimens from *Argobuccinum pustulosum* shell. SAMC-A091126, Melkbosstrand, Western Cape, South Africa, 28 February 2017, 5 specimens from *Turbo cidaris* shell. SAMC-A091127, Melkbosstrand, Western Cape, South Africa, February 2017, 30 specimens from 2 *Turbo cidaris* shells. SAMC-A091128, Chintsa West, Eastern Cape, South Africa, 26 April 2017, 3 specimens from a *Dinoplax gigas*. SAMC-A091129, False Bay, Western Cape, South Africa, 15 March 2017, 2 specimens from *Burnupena cincta* shell. SAMC-A091130, East London surrounds (Gonubie, Chintsa West), Eastern Cape, South Africa, April 2017, 8 specimens from 2 *Mancinella capensis* shells (2 not deposited, used for genetic analyses). SAMC-A091131, Gonubie, Eastern Cape, South Africa, 27 April 2017, 51 specimens from *Mancinella capensis* shell. SAMC-A091132, Summerstrand, Eastern Cape, South Africa, 4 July 2017, 6 specimens from *Mancinella capensis* shell. SAMC-A091133, L'Agulhas, Western Cape, South Africa, 15 June 2010, 1 specimen in *Heydrichia woelkerlingii*. SAMC-A091134, Summerstrand, Algoa Bay, Eastern Cape, South Africa, 4 July 2017, 30 specimens in *Lithophyllum sp.* SAMC-A091135, Morgan Bay, Eastern Cape, South Africa, 13 July 2010, 12 specimens from *Lithophyllum neoatalayense* Masaki. SAMC-A091136, False Bay, Western Cape, South Africa, 4 August 2016, 4 specimens from *Scutellastra tabularis* shell.

Diagnosis: Females with pair of large hooks forming posterior processes of operculum, inner and outer margins of operculum with entire or bifid teeth. Also characterised by presence of pair of weak and irregular lateral bars.

Description: Female, body oval-shaped (Fig. 2.10B; 2.12A). Length 2.1 – 4.7 mm (mean = 2.98 mm), width 1.05 – 2.85 mm (mean = 1.69 mm). Opercular bars on average 0.87 mm long, with pair of large posterior processes at top of operculum that have several simple teeth and setae on them (Fig. 2.11B, D; 2.12B). Both inner and outer margins of operculum lined with bifid or entire teeth and setae (Fig. 2.11C, D, E). Rostral end of opercular bar with simple spines and setae (Fig. 2.11E). Lateral surface of operculum lined with several teeth, setae and large multifid scales (Fig. 2.11B, F). Comb collar consists of long feather-like projections (Fig. 2.11A). Developed orificial knob absent. Feeble lateral bars present running down mantle near operculum (Fig. 2.12A). Row of mostly bifid spines running down ventral surface on mantle. Females bright red when fresh, cirri also bright red (Fig. 2.10A, C). Aperture looks like typed apostrophe, with one end having more pointed tapered slit (Fig. 2.10C).

Five pairs of terminal cirri, with pair of two-segmented caudal appendages (Fig. 2.12C, D), two conical processes present (Fig. 2.12C). Mouth cirri with four-segmented posterior ramus shorter than five-segmented anterior ramus, both with long setae (Fig. 2.12G). Labrum saddle-shaped, mandibular palp trapezoid, with dense setae (Fig. 2.12H). Mandible with three teeth, excluding inferior angle (Fig. 2.12E), first tooth separated from second and third teeth by large notch, inferior angle with several small spines and setae. Maxillule with single notch in middle of outer margin, two long cuspidate setae below notch, with three short, sharp setae above notch (Fig. 2.12F). Male, much smaller than female, average of 0.66 x 0.32 mm, with as many as four on a single female.

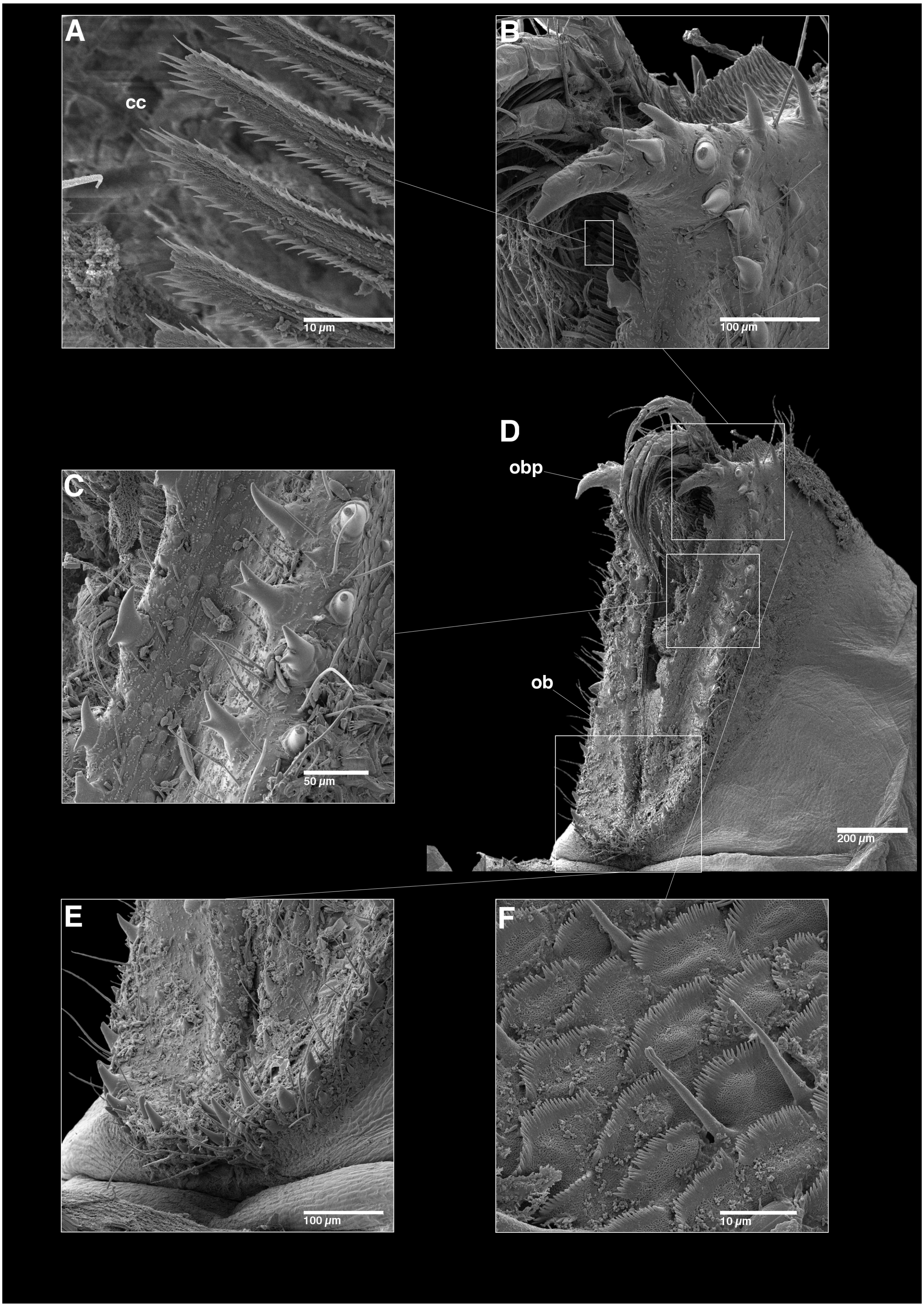
A
cc
10 µm
B
100 µm
C
50 µm
D
obp
ob
200 µm
E
100 µm
F
10 µm

Fig. 2.11: *Weltneria spinosa* from *Argobuccinum pustulosum* from False Bay. Scanning electron microscopy of external morphology around opercular area, female. A – Comb collar; B – Upper area of opercular bar showing posterior process; C – Two rows of bifid teeth on opercular bar with setae; D – Opercular area; E – Rostral end of opercular bar with simple spines and setae; F – Multifid scales. Abbreviations: *cc* – comb collar, *ob* – opercular bar, *obp* – posterior process of opercular bar.

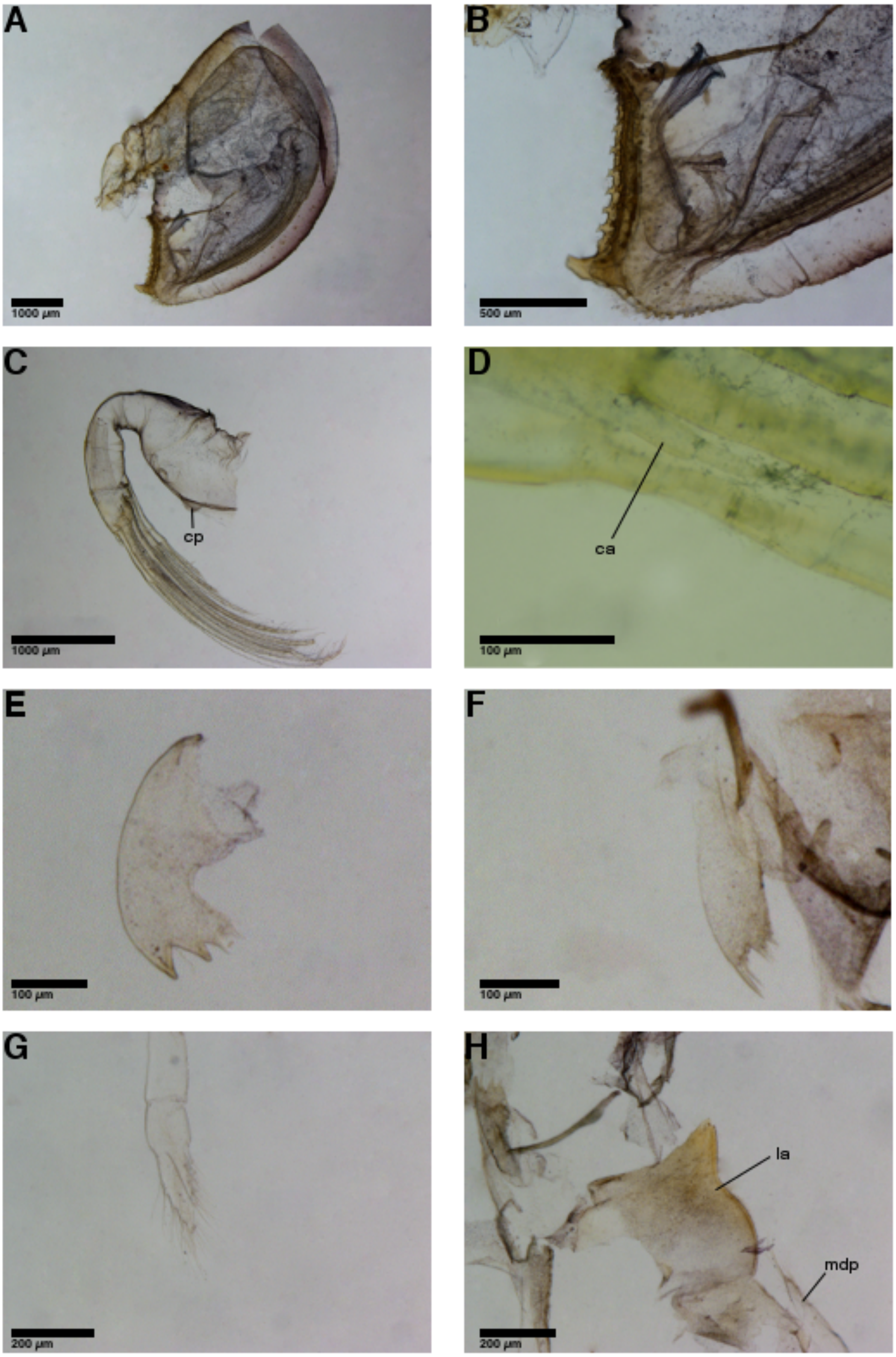

Fig. 2.12: *Weltneria spinosa* from *Turbo sarmaticus* from False Bay. Light microscopy of external mantle and internal structures, female. A – Lateral view of whole specimen; B –

Lateral view of opercular area; C – Terminal cirri; D – Caudal appendage; E – Mandible; F – Maxillule; G – Mouth cirri; H – Labrum and mandibular palp. Abbreviations: *ca* – caudal appendage, *cp* – conical process, *la* – labrum; *mdp* – mandibular palp.

Hosts*:* *Haliotis midae* is the type-host. Also known from *Argobuccinum pustulosum* and *Turbo sarmaticus.* New hosts in the Western Cape include *Burnupena cincta*, *Dinoplax gigas*, the giant limpet *Scutellastra tabularis* (Krauss, 1848) and *Turbo cidaris*. Also collected in the Eastern Cape from two new hosts, *R. gemmifera* and *M. capensis* as well as from *T. sarmaticus* and *H. midae*. Also found inhabiting coralline red algae (Chapter 1) in the Eastern Cape in a rhodolith (*Lithophyllum sp.*), a discoid species, *Lithophyllum neoatalayense* Masaki, 1968 also from *Heydrichia woelkerlingii* Townsend, Chamberlain and Keats, 1994 in the Western Cape.

Distribution: Type locality Hermanus (34°25’1.62”S, 19°14’55.46”E) in the Western Cape. Ranges from Melkbosstrand (33°44'08.1"S, 18°26'15.2"E) to Qolorha (32°50'08.0"S, 28°07'09.5"E). Endemic to Western and Eastern Cape (Fig. 2.13).

Fig. 2.13: *Weltneria spinosa*. Distribution along the South African coastline.

Remarks: *Weltneria spinosa* Berndt, 1907 is the type species of the genus *Weltneria.* It is the most commonly found acrothoracican in South Africa, with up to 235 individuals found in a single *Haliotis midae* shell. Often found in the same host along with *Australophialus turbonis* in the Western Cape and *Australophialus utinomii* and *Kochlorine bocqueti* in the Eastern Cape. In the Western Cape empty burrows of this barnacle are often occupied by the unique amphipod, *Ampelisca excavata* K. H. Barnard, 1926, which appears to be restricted to and anatomically adapted to live in this specialised niche (Gray and Barnard, 1970). This amphipod was found in *W. spinosa* holes on both *T. sarmaticus* and in great abundances on the coralline algae *H. woelkerlingii.*

***Weltneria hirsuta* (Tomlinson, 1963)**

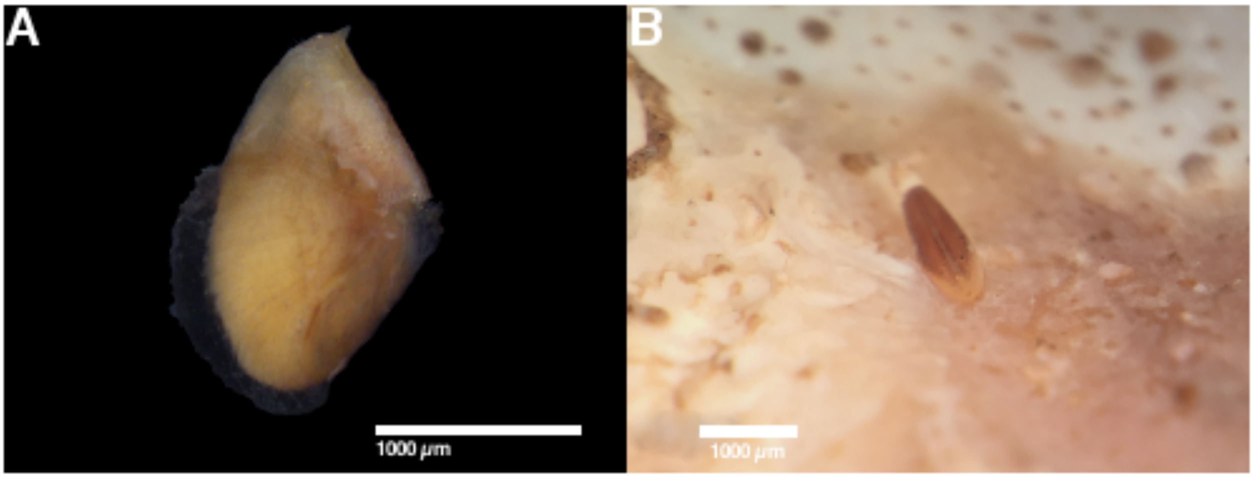

Fig. 2.14: *Weltneria hirsuta* from *Charonia lampas* from Kwelera Bay, female. A – Lateral view of whole specimen; B – Burrow opening.

Lithoglyptes hirsutus Tomlinson, 1963b: 299, Figs. 1 – 7.

Utinomia newmani Tomlinson, 1963a: 265: 265, Fig. 1 - 5.

Weltneria hirsuta Kolbasov, 2009: 173 (In Russian), Fig. 8 (*а*), Fig. 12 (*а*), Fig. 14 (*б*), Fig. 15 (*а*), Fig. 17 (*в*), Fig. 18 (*е*), Fig. 26 (*г*), Fig. 37 (*б, в*), Fig. 39 (*а*, *в*), Fig. 82; Chan, Hsieh and Kolbasov, 2014: 49, Fig. 42, Fig. 43.

Material examined: ELMC 0421, Kwelera Bay, Eastern Cape, 7 January 1986, 14 specimens on *Charonia lampas* shell (7 specimens not deposited, used for SEM's, dissections and genetic analyses).

Diagnosis: *Weltneria* with opercular bars that has numerous sharp simple teeth and long setae, opercular bars terminates in a tapered conspicuous spine-shaped posterior process.

Description: Female, length 1.6 – 2.5 mm (mean = 2.05 mm) and width 1 – 1.7 mm (mean = 1.31 mm). Body oval-shaped, except opercular area flat surface, not rounded (Fig. 2.14A; 16A). Opercular bars broad, concave on outer surface, average of 1.05 mm, with large dorsal surface and pair of posterior processes (Fig. 2.15C, D) with simple spines along edges and down lateral surface of opercular area (Fig. 2.15C, A, F). Opercular bars have small aperture with almost no internal structures visible (Fig. 2.15C). Row of simple and bifid teeth on either side of opercular bars, with several other randomly distributed on dorsal surface (Fig. 2.15A). Comb collar of long feather-like projections (Fig. 2.15B). Several bifid and trifid teeth present on surface of mantle. Developed orificial knob absent. Lateral surface below opercular bars with spines, setae and broad multifid scales, similar to those of *W. spinosa* (Fig. 2.15E, F). Opercular knob and lateral bars absent. Mantle surface with several randomly-distributed bifid teeth. Live colour unknown, dark brown/orange when preserved in ethanol (Fig. 2.14A). Burrow oval-shaped, opercular bars well-fitted to burrow (Fig. 2.14B).

Terminal cirri five pairs with two-segmented caudal appendages, with setae at end segment (Fig. 2.16B, C). Mouth cirri with three-segmented posterior ramus shorter than four-segmented anterior ramus (Fig. 2.16E) Both rami with setulated setae. Labrum saddle-shaped, bullate, upper edge convex and armed with developed dorsal process, while anterior edge horseshoe-shaped, smooth (Fig. 2.16D). End of mandibular palp trapezoid, with dense simple setae as well as setae that have small sparse setules on tip (Chan, Hsieh and Kolbasov, 2014). Mandible with three major teeth becoming smaller toward inferior angle, with first upper tooth separated from the rest. Inferior angle with several denticles and inferior angle ended in two large denticles (Chan, Hsieh and Kolbasov, 2014). Maxillule with single notch, two large cuspidate and small setae above notch and more than five sharp setae at margin below notch (Fig. 2.16F). Lateral surfaces with dense serrate setae. Maxilla sub-triangular with plenty simple setae on outer margin and apex (Fig. 2.16E).

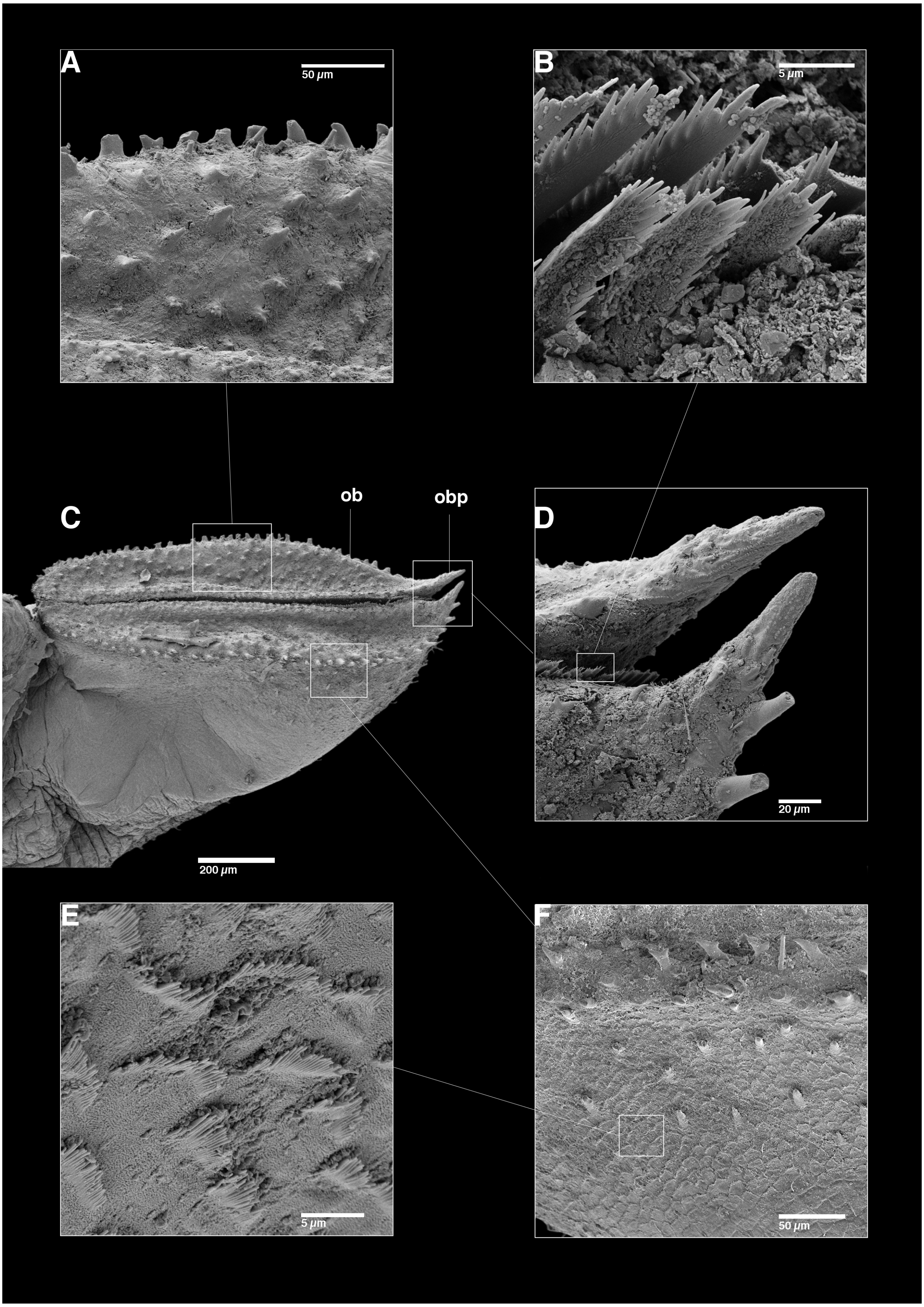

Fig. 2.15: *Weltneria hirsuta* collected from *Charonia lampas* from Kwelera Bay. Scanning electron microscopy of external features, female. A – Row of teeth on opercular bar, with nodules; B – Comb Collar; C – Opercular area, lateral view showing opercular bars; D – posterior processes of opercular bar; E – Multifid scales; F – Surface below opercular area showing bifid teeth and spines. Abbreviations: *ob* – opercular bar, *obp* – posterior process of opercular bar.

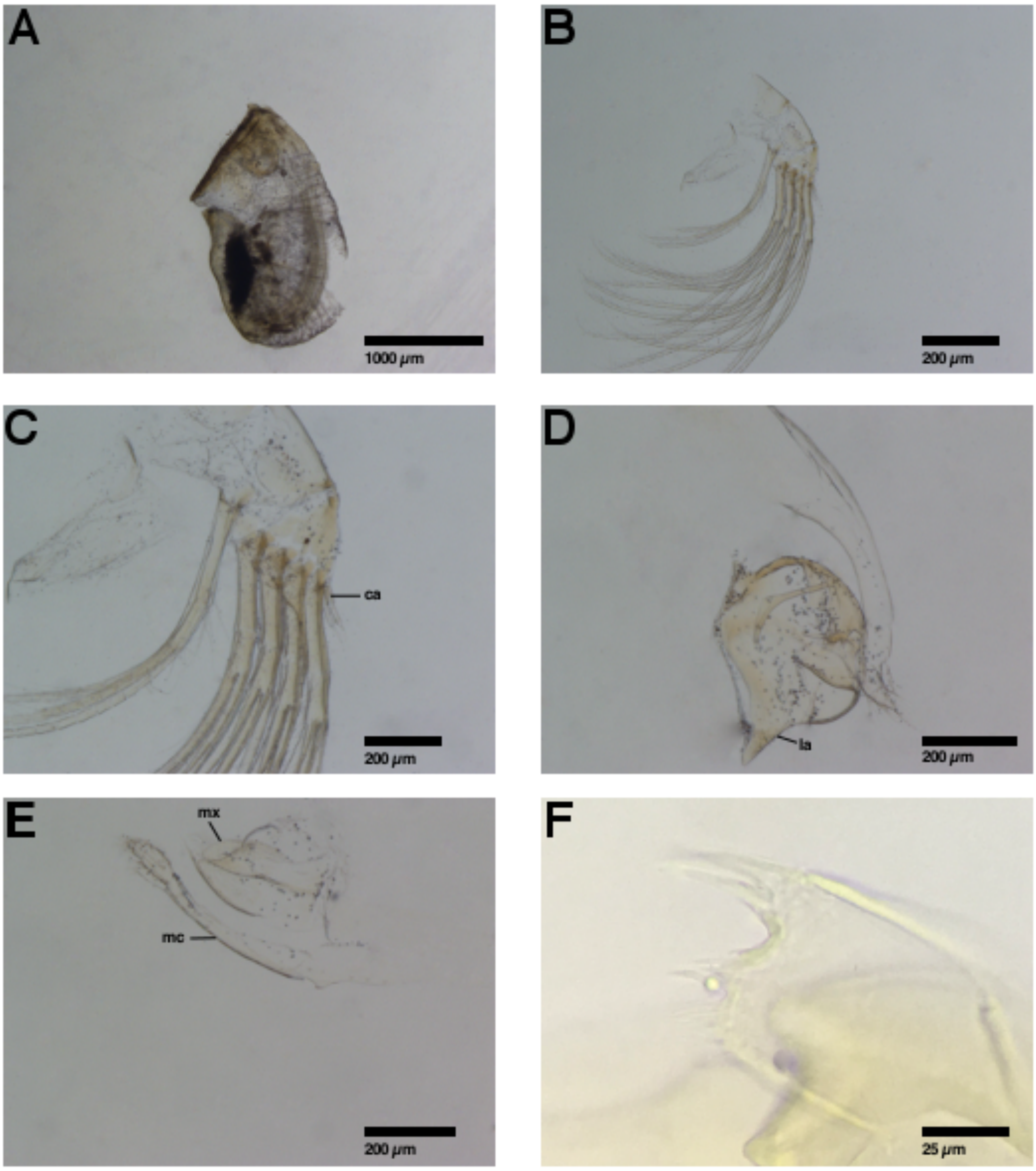

Fig. 2.16: Female *Weltneria hirsuta* from *Charonia lampas* from Kwelera Bay. Light microscopy of whole specimen and some internal structures, female. A – Lateral view of whole specimen; B – Five pairs of terminal cirri; C – Terminal cirri with caudal appendages; D – Mouth cirri and labrum; E – Mouthparts including mouth cirri and maxilla; F – Maxillule. Abbreviations: *ca* – caudal appendage, *la* – labrum, *mc* – mouth cirri, *mx* - maxilla.

Hosts: Originally found in two corals, *Psammocora* Dana, 1846 and *Porites* Link, 1807 in Hawaii and shell of *Bursa* Röding, 1798 in Japan and *Murex* Linnaeus, 1758 in Taiwan (Chan, Hsieh and Kolbasov, 2014). Found in South Africa in *Charonia lampas* (Linnaeus, 1758) from Kwelera Bay, collected in 1986 and stored in the East London Museum (ELMW0952).

Distribution: Type locality is Hawaii (Chan, Hsieh and Kolbasov, 2014). Japan, Taiwan and a single sample in South Africa from Kwelera Bay (32°50'08.0"S, 28°07'09.5"E), near East London, Eastern Cape. In South Africa only occurs in the Eastern Cape (Fig. 2.17).

Fig. 2.17: *Weltneria hirsuta.* Distribution along the South African coastline.

Remarks: Live colour unknown, and some mouthparts could not be dissected out, as only 14 individuals were available from a single sample held at the East London Museum and collected in 1986. Individuals were in bad condition.

Subfamily **Lithoglyptinae** Aurivillius, 1892

Lithoglyptinae Aurivillius, 1892: 133; Kolbasov and Newman, 2005: 41; Kolbasov, 2009: 240.

Diagnosis: Lithoglyptid with 4 pairs of terminal cirri and with caudal appendages. Dwarf males can be bottle-shaped, pear-shaped or with wing-like lateral projections, with simple attachment antennules, or with long attachment stalk.

Remarks: There are currently 3 genera in this subfamily, *Auritoglyptes*, *Balanodytes* and *Lithoglyptes*. Only *Balandoytes* found in South Africa.

Genus ***Balanodytes*** Utinomii, 1950

Balanodytes Utinomi, 1950: 453, 458; Chan et al., 2013: 226.
Armatoglyptes Kolbasov and Newman, 2005: 47-51.

Diagnosis: Females, terminal cirri with four pairs with two-segmented caudal appendages without pedestals, opercular area with no posterior setose processes or lobes, posterior processes well-developed, orificial knob and lateral bars both present or absent. Dwarf males with no attachment stalk.

Remarks: Utinomi (1950) erected this genus and the species were described without caudal appendages. This genus only included *B. taiwanus* and *B. balanodytes* and subsequently no species were added to this genus. In 2013 Chan et al. discovered that a *B. taiwanus* specimen from Utinomi had caudal appendages. The diagnosis was corrected and was the same as that of *Armatoglyptes* Kolbasov and Newman, 2005, which consisted of nine species, but without a type species designated. Thus, all species of *Armatoglyptes* were moved to *Balanodytes* and *Armatoglyptes* was deemed to be a junior synonym and the name is no longer effective (Chan et al., 2013; Lin, Kolbasov and Chan, 2016). Currently there are 11 species in this genus. Two species are present in South Africa, of which one is still formally undescribed.

Balanodytes flexuosus (Chan, Kolbasov and Cheang, 2012)

Fig. 2.18: *Balanodytes flexuosus*, from *Charonia lampas* from Port Shepstone, female. Lateral view of a whole specimen.

Armatoglyptes flexuosus Chan, Kolbasov and Cheang, 2012: 10 – 15, Fig. 2, Fig. 3, Fig. 4, Fig. 5, Fig. 6.

Material examined: CLP14-4, Port Shepstone, Eastern Cape, August 2017, 1 specimen on *Charonia lampas* shell (specimen used for dissection).

Diagnosis*:* *Balanodytes* with opercular bars with bifid teeth, posterior processes L-shaped, strongly bent/ recurved at tip.

Description: Female, body oval-shaped, narrowing below to opercular bars (Fig. 2.18; 2.19A). length 1.65 mm, width 1.05 mm, opercular bars 500 µm in length, with row of bifid teeth and setae (Fig. 2.19B). Posterior processes hook-like (anteriorly bent/recurved), L-shaped, with bifid teeth and setae along the length (Fig. 2.18; 2.19B). Comb collar with long, feather-like projections, fused at bases (Chan, Kolbasov and Cheang, 2012). Orificial knob distinct with setae and simple or bifid teeth (Fig. 2.19B). Lateral area below opercular bar covered with sparse simple setae and rows of large multifid scales. Feeble lateral bars. Burrow opening narrow, oval-shaped (Chan, Kolbasov and Cheang, 2012).

Four pairs of terminal cirri and pair of two-segmented caudal appendages (Fig. 2.19C, D). Mouth cirri with both rami three-segmented, with anterior ramus shorter than posterior ramus, both rami with plumose setae (Fig. 2.19H). Labrum saddle-like, with small, blunt teeth on anterior margin (Fig. 2.19E). Mandible with three large teeth and two smaller ones close to lower margin, large notch between first and second teeth. Inferior angle with two sharp denticles and setae (Fig. 2.19F). Maxillule with two long, sharp upper and single, smaller lower cuspidate setae. Notch with short, sharp seta, lower 2/3 of cutting edge with numerous short, sharp setae (Fig. 2.19G). Maxilla triangular with setae on both exterior and interior margins. Mandibular palp trapezoidal, with simple setae along exterior margin (Chan, Kolbasov and Cheang, 2012).

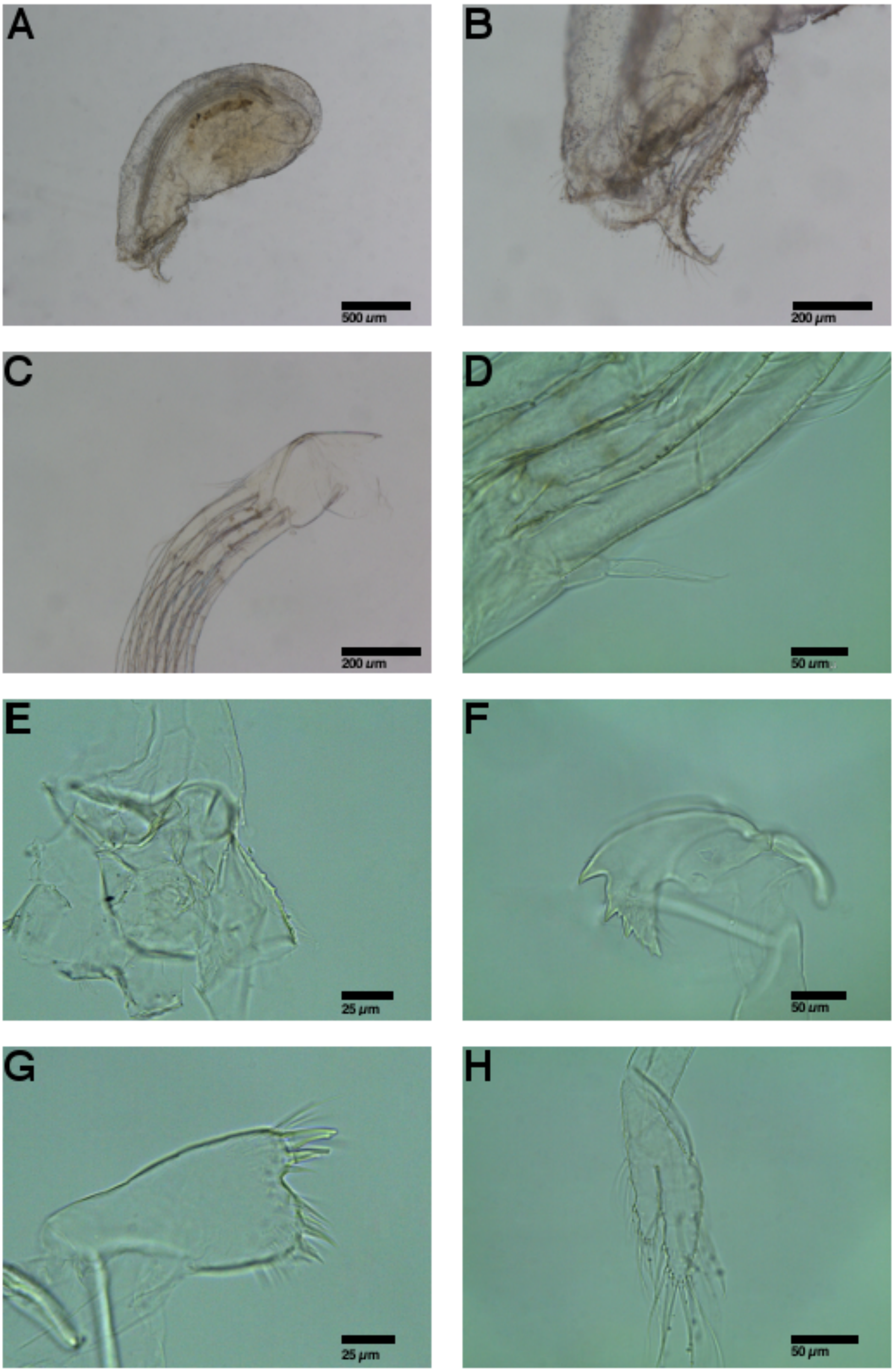

Fig. 2.19: *Balanodytes flexuosus,* collected from *Charonia lampas* from Port Shepstone. Light microscopy of external and internal structures, female. A – Lateral view of whole

specimen; B – Opercular area, lateral view; C – Terminal cirri; D – Caudal appendage; E – Labrum; F – Mandible; G – Maxillule; H – Mouth cirri.

Hosts: Previously in the coral *Pavona sp.* from Mozambique Channel (Chan, Kolbasov and Cheang, 2012). Collected in South Africa from a *Charonia lampas* shell.

Distribution: Originally described from Mozambique Channel (26°11’00”S, 35°01’00”E). Collected in South Africa at Port Shepstone (30°44'38.8"S, 30°27'28.7"E). In South Africa only in KwaZulu-Natal (Fig. 2.20).

Fig. 2.20: *Balanodytes flexuosus.* Distribution along South African coastline.

Remarks: Only 1 individual collected, found in association with *Balanodytes n. sp.*

Balanodytes n. sp.

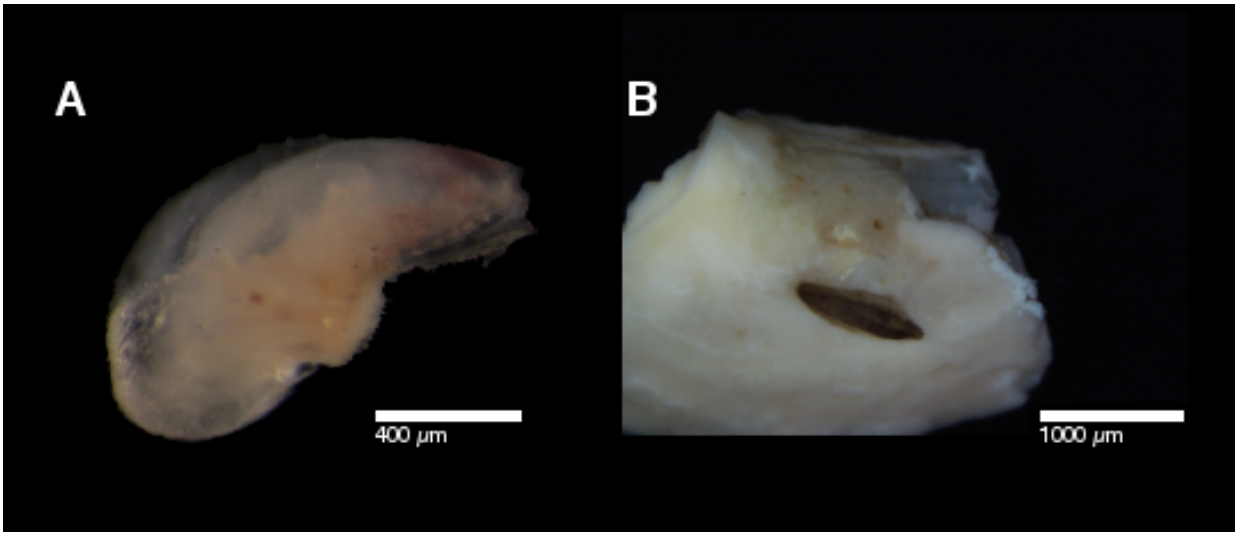

Fig. 2.21: *Balanodytes n. sp.* collected from *Charonia lampas* from Port Shepstone, female. A - Lateral view of whole specimen; B – Burrow opening.

Material examined: Holotype. SAMC-A091082, Port Shepstone, KwaZulu-Natal, August 2017, 1 specimen in *Charonia lampas* shell. Paratype. SAMC-A091083, one additional specimen, same data as holotype. Paratype. SAMC-A091084, one additional specimen, same data as holotype. SAMC-A091090, Port Shepstone, KwaZulu-Natal, South Africa, 19 September 2017, 2 specimens on *Mancinella capensis* shells (only 1 deposited, other specimen used for dissections). **Other material:** DV06, Port Shepstone, KwaZulu-Natal, South Africa, 19 September 2017, 1 specimen on *Dinoplax validifossus* Ashby, 1934 shell plate (not deposited, used for SEM's).

Diagnosis: *Balanodytes* with a well-developed, armed orificial knob, opercular bars with straight posterior processes with slightly anterior facing spine branching off at apex.

Description: Female, length 2.1 mm and width 1.05 mm. Opercular bars 500 um long. Lateral row of large bifid teeth on opercular bar that extends onto posterior processes, with several rows of smaller rosette nodules closer to opening along opercular bar (Fig. 2.22C, D, F). Rostral end of opercular bar with large bifid tooth on each opercular bar (Fig. 2.22C; 2.23B). Opercular bar with large posterior processes, with small spine branching off at tip that is slightly recurved (anterior facing) with several bifid teeth and simple spines (Fig. 2.22D). Pronounced comb collar that starts on inside of posterior processes of opercular bar and extends to anterior end of opercular bar (Fig. 2.22A, B). Several hook-like spines and setae present below opercular bar. Orificial knob well-developed with setae and simple teeth (Fig. 2.23A, B). Multifid scales and randomly distributed setae visible along operculum. Mantle with several bifid teeth randomly-distributed (Fig. 2.22D). Lateral bars absent. Area below opercular bars purple, rest of body reddish-brown. Turns light brown when preserved in alcohol (Fig. 2.21A). Burrow opening narrow, oval-shaped (Fig. 2.21B).

Terminal cirri consists of four pairs with two-segmented caudal appendages with three setae (Fig. 2.23C, D). Mouth cirri with four-segmented anterior ramus longer than four-segmented posterior ramus, both with long plumose setae (Fig. 2.23H). Mandible with three large teeth, first upper tooth separated from other lower teeth, lower margin below third tooth has three smaller teeth with setae (Fig. 2.23F). Maxillule with two long cuspidate setae, notch with short setae, with lower margin with numerous short, sharp setae (Fig. 2.23G). Maxilla triangular with long setae on exterior margin (Fig. 2.23E). No males observed.

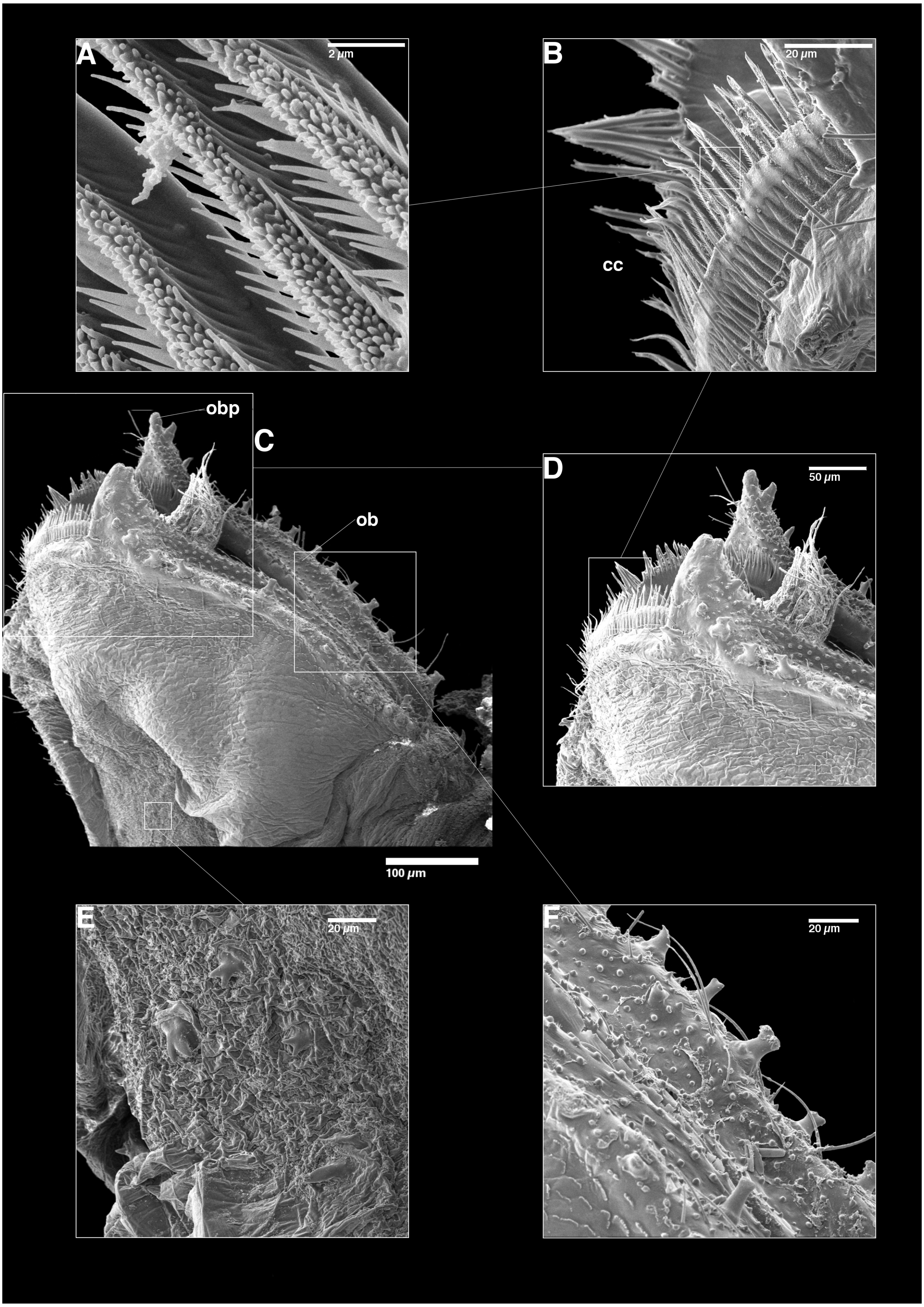
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Fig. 2.22: *Balanodytes n. sp.* from *Charonia lampas* from Port Shepstone. Scanning electron microscopy of external morphology of external structures, female. A – Magnified view of comb collar; B – Comb collar and setae on caudal end of opercular area; C – Opercular area; D – Posterior processes and spines on opercular bars; E – Bifid spines on mantle surface; F – Simple spines and nodules on opercular bar. Abbreviations: *cc* – comb collar, *ob* – opercular bar, *obp* – posterior process of opercular bar.

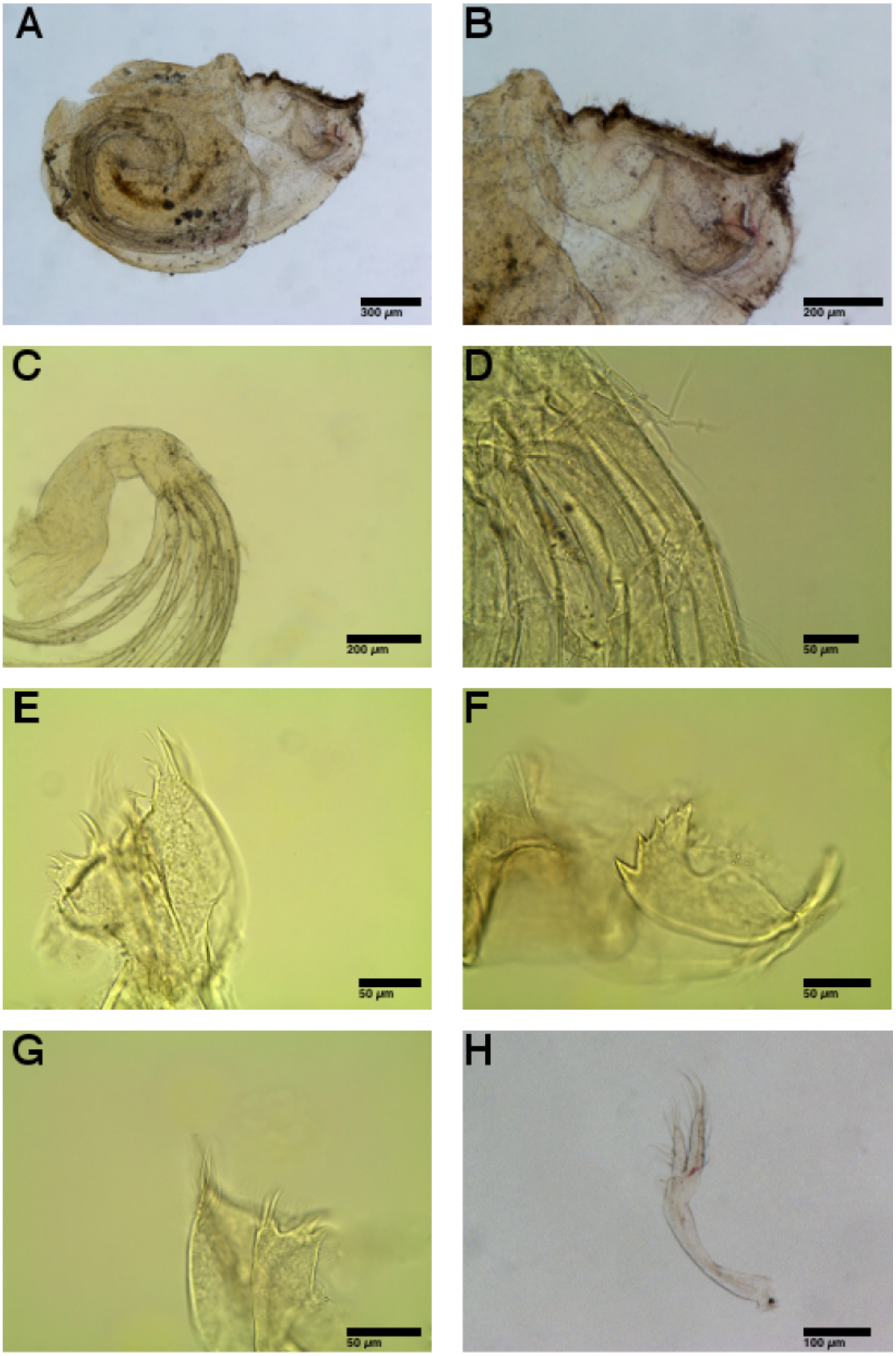


Fig. 2.23: *Balanodytes n. sp.* collected from *Charonia lampas* from Port Shepstone. Light microscopy of mantle and internal structures, female. A – Lateral view of whole specimen; B

– Lateral view of opercular area; C – Terminal cirri; D – Caudal appendage; E – Maxilla; F – Mandible; G – Maxillule; H – Mouth cirri.

Hosts: Type host is a hermit crab-occupied *Charonia lampas* from Port Shepstone. Also found in *Dinoplax validifossus* and *Mancinella capensis*.

Distribution: Known only from Port Shepstone (30°44'38.8"S, 30°27'28.7"E). Endemic to KwaZulu-Natal (Fig. 2.24).

Fig. 2.24: *Balanodytes n. sp.* Distribution along the South African coastline.

Variation: Other specimens ranged in length from 1.65 – 2.5 mm (mean = 1.98 mm) and width 0.95 – 1.3 mm (mean = 1.05 mm). Opercular bars on average 510 um long.

Remarks: Caudal appendages without basal pedestals, unlike *Auritoglyptes* Kolbasov and Newman, 2005 and *Lithoglyptes* Aurivillius, 1892. This genus has species with posterior processes that are either straight (as in *B. echinoideus*, *B. egorovi* and *B. mitis*), recurved (bent posteriorly) (as in *B. balanodytes, B. cornutus* and *B. scamborachis*) or decurved (bent anteriorly) (as in *B. flexuosus, B. habei, B. stirni, B. thomasi, B. wilsoni*) (Kolbasov and Newman, 2005; Chan, Kolbasov and Cheang, 2012; Chan, Hsieh and Kolbasov, 2014). Only *B. flexuosus*, *B. habei* and *B. mitis* (*taiwanus*) have a well-developed orificial knob (as does *Balanodytes n. sp.*). Lateral bars either feeble (*B. egorovi*, *B. flexuosus*, *B. habei*, *B. mitis*, and *B. scamborachis*) or absent (*B. balanodytes*, *B. cornutus*, *B. echinoideus*, *B. stirni*, *B. thomasi* and *B. wilsoni*). Based on this information *Balanodytes n. sp.* is most similar to *B. flexuosus* and *B. mitis*, but differs as it has simple spine that branches off the posterior processes of opercular bar (that makes it look bifid, unlike *B. flexuosus* where the whole posterior process is recurved), and not recurved teeth (or no teeth). Differences also exist between in the opercular knob, as it is more developed and pronounced in *Balanodytes* n. *sp.* Moreover, differences also exist in the mandible, teeth on the opercular bar and *Balanodytes n. sp.* is purple in colour around the opercular area, and not orange. No dwarf males observed.

Subfamily **KOCHLORININAE** Gruvel, 1905

Diagnosis: Females with three pairs of terminal cirri, two-segmented caudal appendages present.

Remarks: Consists of two genera; *Kochlorine* Noll, 1872 and *Kochlorinopsis* Stubbings 1967, with only the former present in South Africa. Globally these genera have 7 and 1 species respectively.

Genus ***Kochlorine*** Noll, 1872

Kochlorine Tomlinson, 1969: 65.

Diagnosis: Females with three pairs of terminal cirri, caudal appendages present (two-segmented), developed lateral bars and orificial knob. Dwarf males with elongated attachment stalk and lateral projections (Chan, Hsieh and Kolbasov, 2014).

Remarks: There are currently seven described species in this genus, one of which *K. bihamata*, was previously thought to occur in South Africa. Here it is suggested that report be discounted. However, two other species belonging to this genus are reported for the first time from the region, one of which is considered to be new to science.

Kochlorine bihamata **Noll, 1883 (deletion from fauna list)**

Kochlorine bihamata Barnard (1924): 99; Tomlinson, 1969: 72; Kolbasov, 2009: 193.

Diagnosis: Females with no anterior conical processes, mantle aperture with two posterior hooks and spiny teeth on rim; 5 mm in size (Tomlinson, 1969).

Hosts: Collected as dried specimens observed in a *Haliotis* shell. Although it is not explicitly stated which *Haliotis* shells they burrow into, it can be assumed that it is the common abalone species, *Haliotis midae*, which is known to host other Acrothoracicans.

Remarks: This species has never been observed again since its description by Noll in 1883 and there remains doubt regarding the validity of the species. This species was described from Cape Town. Noll (1883) mentioned that: “Should new specimens of *Kochlorine* arise from Cape Town, one can well label it *Kochlorine bihamata*. Therefore, it is safe to assume that the genus *Kochlorine* occurs from Cadiz, Spain to Cape Town, South Africa and burrows into shells of *Haliotis spp.*”. Although Tomlinson (1969) calls into question the validity of the species, he later adds that *K. bihamata* should be treated as a valid species. However, following our survey no trace of this species was found, despite the fact that the type host was collected at the type locality and several localities adjacent to that. Thus, it is safe to assume that this is a *nomen nudum*.

Kochlorine bocqueti **Turquier, 1977**

Kochlorine bocqueti Turquier, 1977a: 134; 1978: 107; Kolbasov, 1999: 139; Kolbasov, 2002a: 536, 540, Fig. 7 (u); Kolbasov, 2009: 193, Fig. 10 (*в*), Fig. 13 (*з*), Fig. 15 (*е*), Fig. 109.

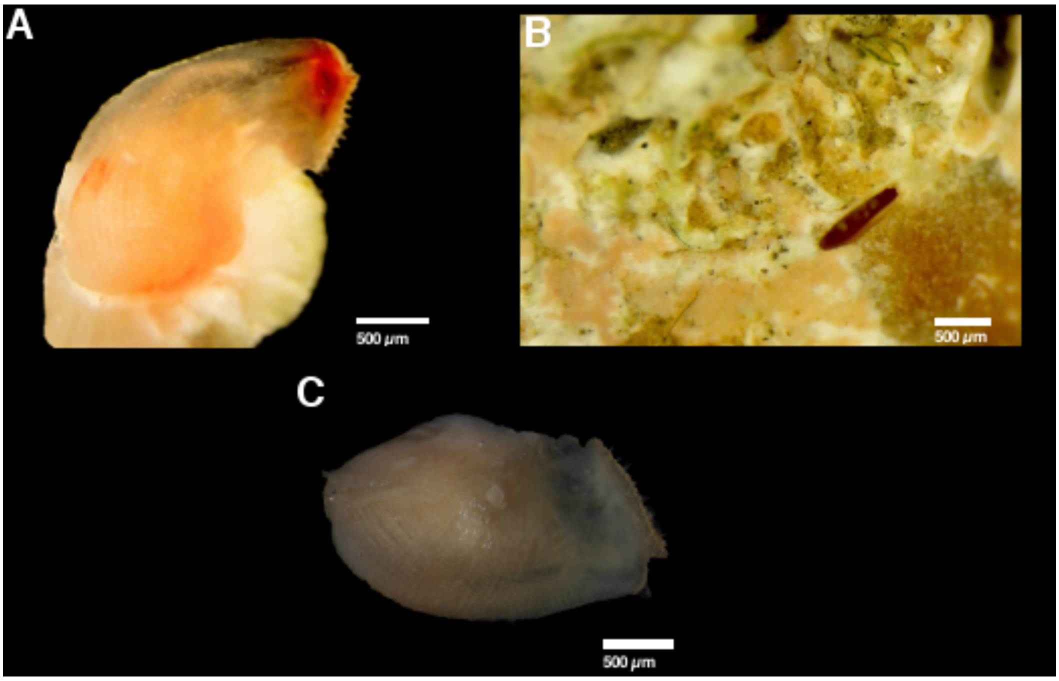


Fig. 2.25: *Kochlorine bocqueti*, female. A - Lateral view of a whole specimen showing natural colouration from *Mancinella capensis* from Gonubie; B – Burrow opening in *Mancinella capensis* from Gonubie; C – Lateral view of a whole specimen from *Charonia lampas* from Kwelera Bay.

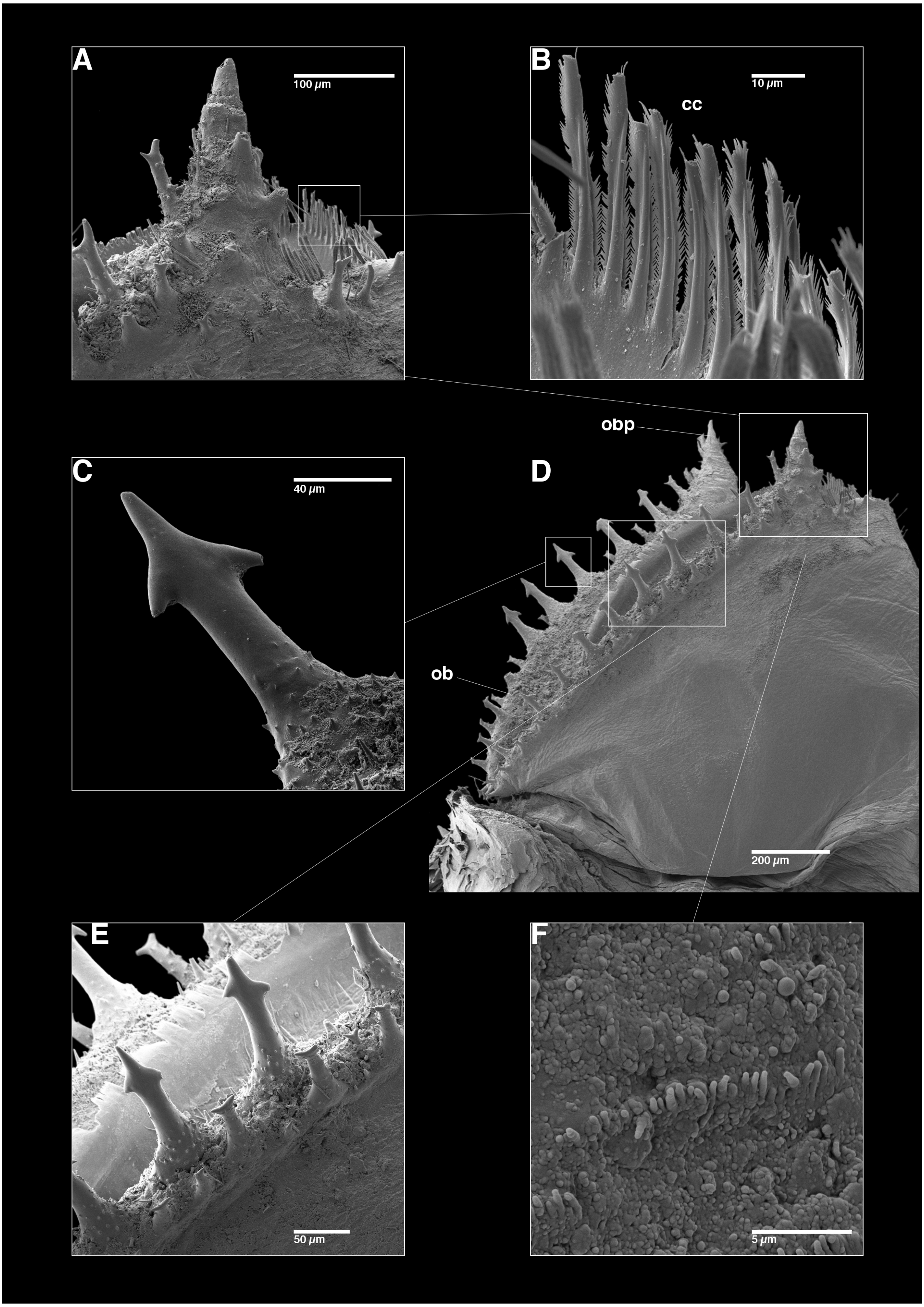
Material examined: ELMC 0420, Kwelera Bay, Eastern Cape, 7 January 1986, 21 specimens in *Charonia lampas* shell (7 specimens not deposited, used for SEM's, dissections and genetic analyses). SAMC-A091087, Gonubie, Eastern Cape, South Africa, 27 April 2017, 4 specimens in *Ranella gemmifera* shell (1 not deposited, used for genetic analyses). SAMC-A091086, Gonubie, Eastern Cape, South Africa, 27 April 2017, 2 specimens in 2 *Turbo sarmaticus* shells. SAMC-A091089, Gonubie, Eastern Cape, South Africa, 27 April 2017, 2 specimens in 2 *Haliotis midae* shells. SAMC-A091088, Chintsa West, Eastern Cape, South Africa, 26 April 2017, 1 specimen in *Dinoplax gigas*. **Other material:** TCC01, Gonubie, Eastern Cape, South Africa, 27 April 2017, 1 specimen on *Mancinella capensis* shell (specimen used for genetic analyses).

Diagnosis: Opercular bars with a pair of small posterior processes, and with bifid and 8 – 13 long, lance-shaped teeth.

Description: Female, length 1. 7 – 3.4 mm (mean = 2.69 mm) and width 0.85 – 1.85 mm (mean = 1.56 mm). Body oval-shaped (Fig. 2.25C; 2.27A). Opercular bars an average of 0.98 mm long and armed by medial row of 'arrowhead-shaped' spines and setae, also lined with lateral row of bifid teeth and more setae (Fig. 2.26D, E). Two posterior processes on opercular bar with several bifid and simple teeth (Fig. 2.26A). Comb collar feather-like, with small projections along entire edge (Fig. 2.26B). Orificial knob well developed (Fig. 2.27B).

Surface below opercular bars smooth and ‘plate-like’, completely different to surface of rest of the animal (Fig. 2.26A). Developed lateral bars present that runs from opercular bar downwards, as well as reinforcement bars that runs from dorsal side of opercular bar downwards. Female bright red below opercular area, rest of body brownish-red (Fig. 2.25A), becomes dark brown when preserved (Fig. 2.25C). Slit-like, elongated burrow opening (Fig. 2.25B).

Three pairs of terminal cirri with two-segmented caudal appendages (Fig. 2.27C). Mouth cirri with four-segmented posterior ramus shorter than six-segmented anterior ramus, both rami with long plumose setae on each segment. Both rami extend off two-segmented protopod (Fig. 2.27H). Mandible with three large teeth, first separated from rest by notch. Inferior angle with small teeth and setae (Fig. 2.27E). Maxillule with two cuspidate setae, above notch, with several setae, lower two-thirds of cutting edge with several sharp setae (Fig. 2.27F). Maxilla triangular, with long dense setae at tip (Fig. 2.27D). Mandibular palp trapezoid with long dense setae at tip (Fig. 2.27G). No males observed.


A
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B
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cc
C
40 µm
obp
D
ob
200 µm
E
50 µm
F
5 µm

Fig. 2.26: *Kochlorine bocqueti* from *Charonia lampas* from Kwelera Bay. Scanning electron microscopy of external features, female. A – Posterior process of opercular bar; B – Comb collar; C – Lance-shaped spine on opercular bar, magnified; D – Opercular area, lateral view with opercular bar showing lance-shaped spines; E – Two rows of spine on opercular bar, lateral row bifid, while medial row lance-shaped; F - Multifid scale. Abbreviations: *cc* – comb collar, *ob* – opercular bar, *obp* – posterior process of opercular bar.

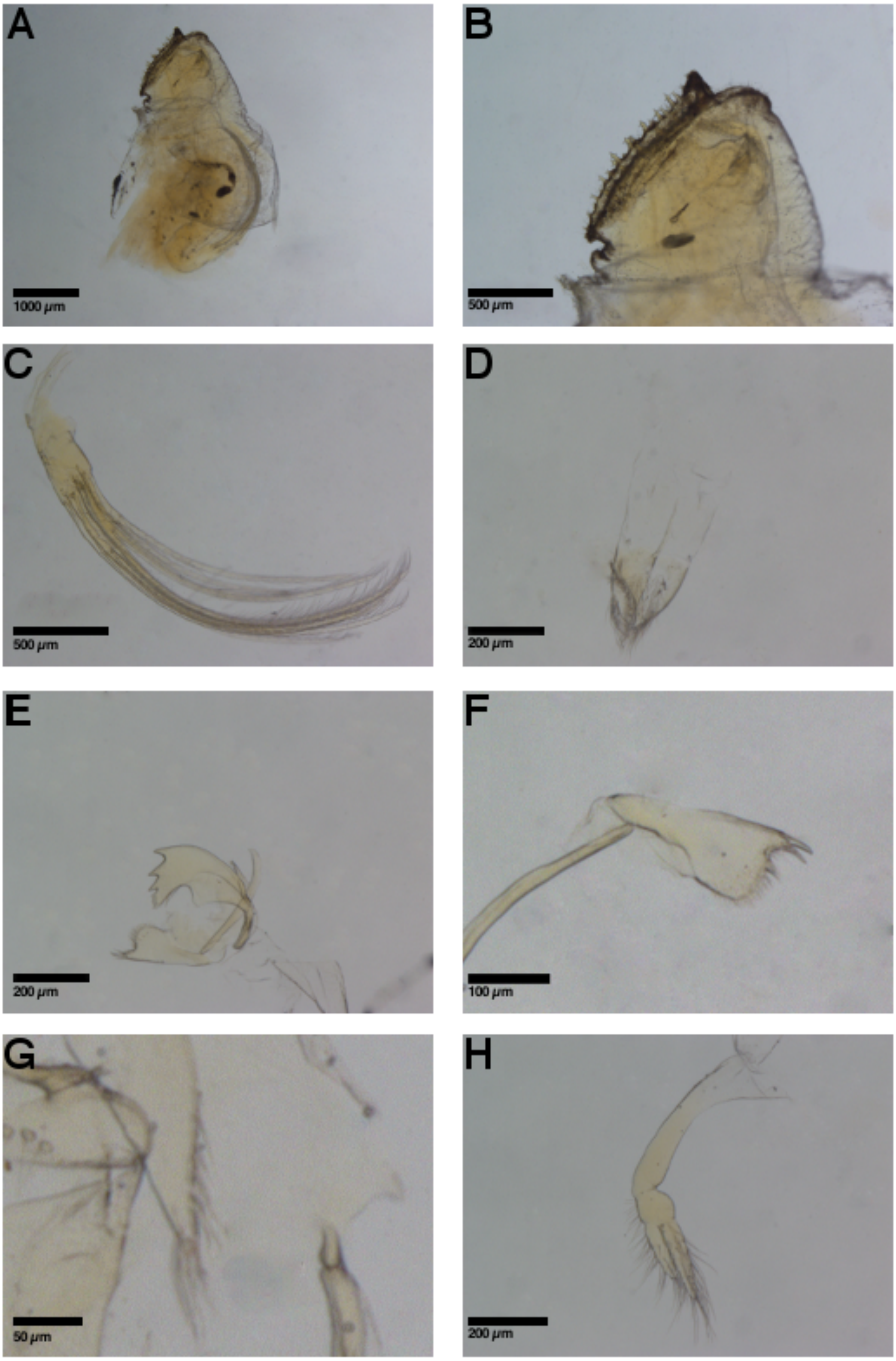

Fig. 2.27: *Kochlorine bocqueti* from *Charonia lampas* from Kwelera Bay. Light microscopy of opercular area and some internal structures, female. A – Lateral view of whole specimen;

B – Opercular area, lateral view showing opercular bar with orificial knob; C – Three pairs of terminal cirri; D - Maxilla; E – Mandible; F – Maxillule; G – Mandibular palp; H – Mouth cirri.

Hosts: Previously described from *Charonia tritonis* (Linnaeus, 1758) and *Conus terebra* Born, 1778. Collected in South Africa in the areas surrounding East London from *Charonia lampas, Dinoplax gigas, Haliotis midae, Mancinella capensis, Ranella gemmifera* and *Turbo sarmaticus*.

Distribution: Previously known from Madagascar and Socotra Island (Kolbasov, 2002a). In South Africa found intertidally and subtidally up to 30 m deep in the Eastern Cape (Fig. 2.28), ranging from Kwelera Bay (32°50'08.0"S, 28°07'09.5"E) to Gonubie (32°56'33.8"S, 28°02'00.9"E). In South Africa endemic to Eastern Cape.

Fig. 2.28: *Kochlorine bocqueti.* Distribution along the South African coastline.

Remarks: Differences were observed in number of segments on each ramus on mouth cirri. The posterior ramus had 6 segments, the anterior one 4 segments. There are currently 6 species (previously 7, but *K. bihamata* was determined to be a *nomen nudum*) in the genus, not including two undescribed species from Chan, Hsieh and Kolbasov (2014) and an undescribed species, *Kochlorine n. sp.* (see below). This South African acrothoracican is deemed to be *Kochlorine bocqueti,* firstly as these are similar in overall body shape, as well as length. *Kochlorine bocqueti* has length of 2.1 mm (Kolbasov, 2002a), and a maximum width of 1.2 mm (Kolbasov, 2002a), which are both within the ranges of South African specimens (1.7 – 3.4 mm and 0.85 – 1.85 mm respectively), albeit much lower than the maxima reported locally. Similarly, the reported opercular bar size (0.75 mm) is within the range found in South Africa (0.6 – 1.35 mm). More importantly, South African specimens fit the diagnosis reported for *K. bocqueti*, which is (as translated from Russian): "Opercular bars with a pair of small posterior processes armed with bifid and 8 - 13 long, sharp lance-shaped teeth". South African specimens had the same number of unique lance-shaped spines on the opercular bar. Lastly, *K. bocqueti* is reported from Madagascar and Socotra Island, while South African specimens were found in the East London area, which would represent a plausible range extension further down the east coast of Africa. Thus, it is safe to assume that this species is indeed *K. bocqueti,* but represents a range extension, and also adds several new hosts. This species was also found in association with *A. utinomii*, *W. hirsuta* and *W. spinosa*.

Kochlorine n. sp.

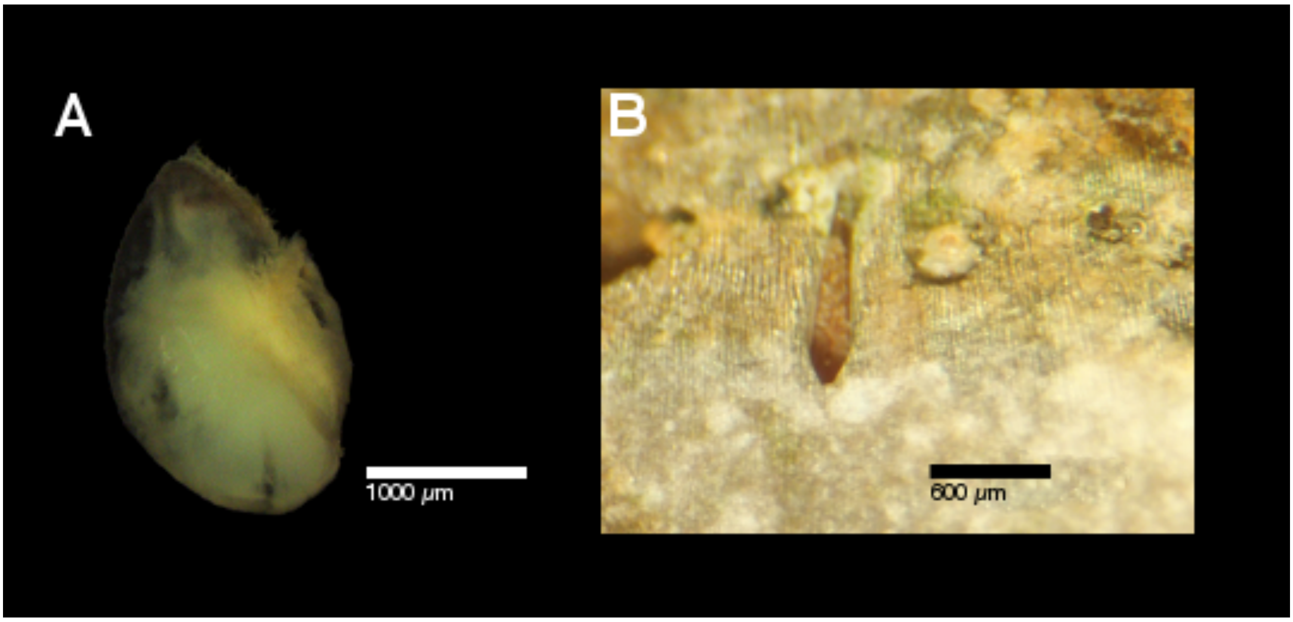

Fig. 2.29: *Kochlorine n. sp.* from *Purpura panama* from Isipingo, female. A - Lateral view of whole specimen; B – Burrow opening.

Material examined: Holotype, SAMC-A091085, Isipingo, KwaZulu-Natal, South Africa, 21 September 2017, 1 specimen collected from *Purpura panama* shell. Paratype, SAMC-A091137, Isipingo, KwaZulu-Natal, South Africa, 21 September 2017, 1 dissected specimen from *Purpura panama* shell. **Other material:** 1 specimen used for SEM's collected from *Purpura panama* shell.

Diagnosis: Similar to *K. bocqueti*, however teeth on opercular bar not lance-shaped, but shorter, broader, more arrowhead-shaped, ranges from 5 – 8 teeth; orificial knob not as well developed, less globular, with spines and setae.

Description: Female, length 2.15 mm and width 1.2 mm. Body oval-shaped (Fig. 2.29A; 2.31A). Opercular bar 0.75 mm with posterior processes with small simple teeth and setae and simple spine apically (Fig. 2.30D, E). Opercular bar with two rows of teeth, row of bifid teeth laterally and row of ‘arrowhead-shaped’ teeth (5 – 8), while some are bifid (Fig. 2.30A, C, D; 2.31B). Comb collar long, with feather-like cuticular projections, fused at their bases (Fig. 2.30F). Orificial knob not well-developed, with simple spines and setae (Fig. 2.31C). Lateral surface of opercular area with broad multifid scales (Fig. 2.30B). Colour red/purple below opercular bar when examined fresh, turns dull brown when preserved in ethanol (Fig. 2.29A). Burrow opening narrow, oval-shaped (Fig. 2.29B).

Terminal cirri with three pairs and two-segmented caudal appendages, with setae on terminal segment, pedestal absent (Fig. 2.31D, E). Mouth cirri with three-segmented posterior ramus, shorter than three-segmented anterior ramus, both rami have long plumose setae (Fig. 2.31H). Mandible with four teeth, with three more smaller teeth between third and fourth tooth. Large dent between first and second tooth, inferior angle with dense setae (Fig. 2.31F). Maxillule with two long upper cuspidate setae, notch with short, sharp setae, with several more setae on lower margin (Fig. 2.31G). No males observed.

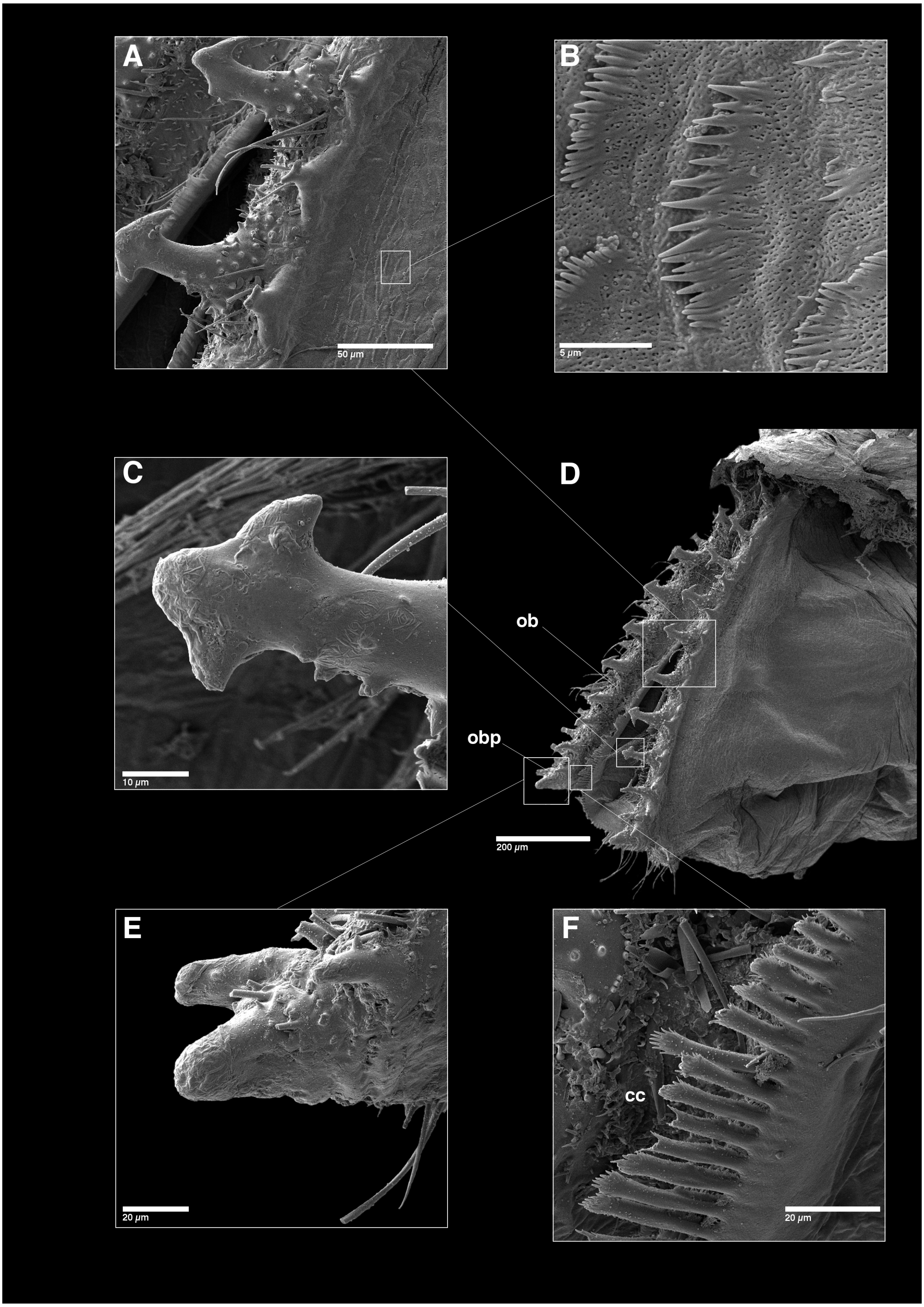
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Fig. 2.30: *Kochlorine n. sp.* from *Purpura panama* from Isipingo. Scanning electron microscopy of external morphology, female. A – Two rows of spines on opercular bar, lateral row small bifid, medial row with broad arrowhead-shaped spines; B – Multifid scales; C – Arrowhead-shaped spine; D – Opercular area showing opercular bars with arrowhead-shaped spines; E – posterior process of opercular bar with a simple spine on apex; F – Comb collar. Abbreviations: *cc* – comb collar, *ob* – opercular bar, *obp* – posterior process of opercular bar.

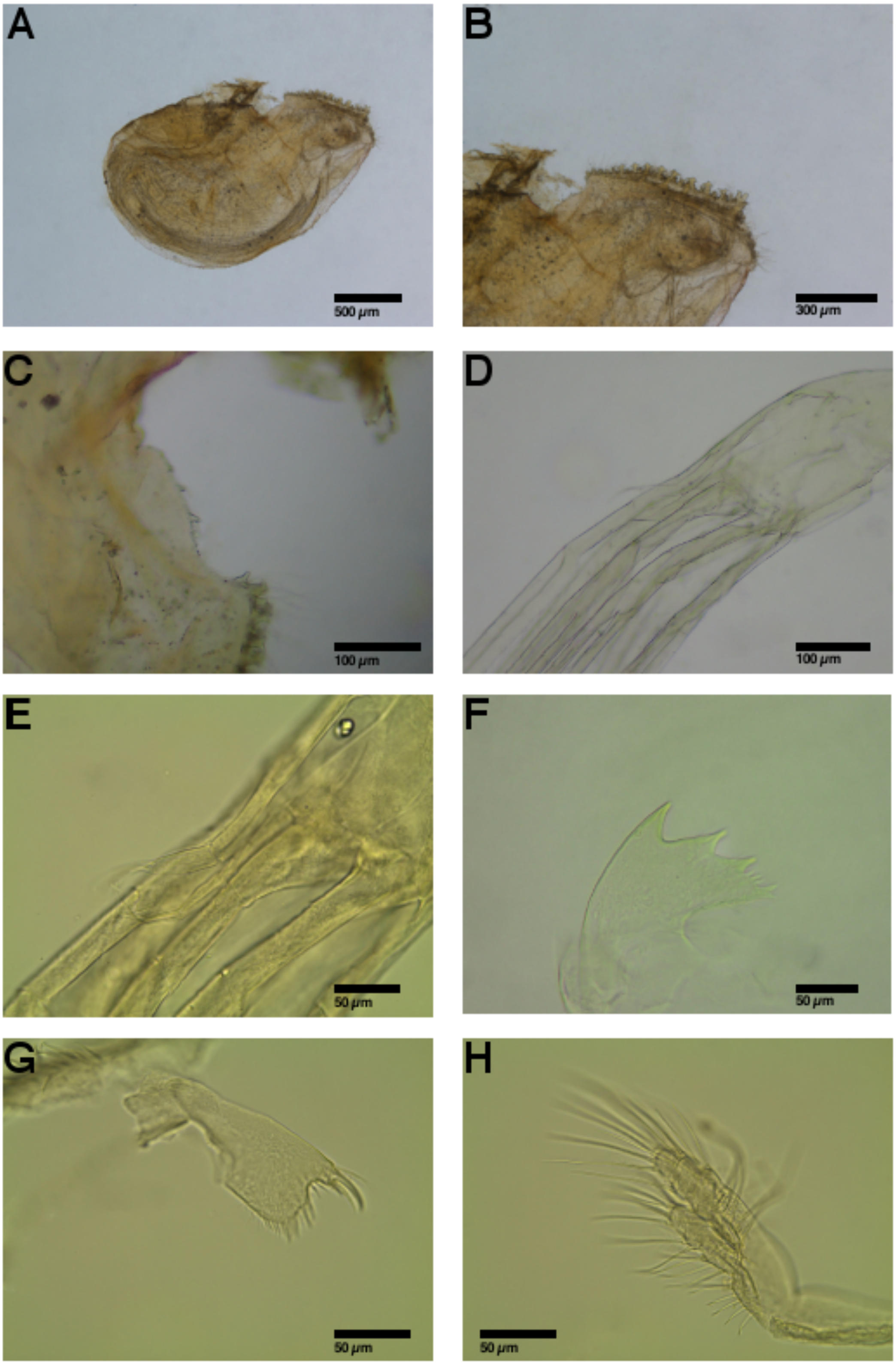

Fig. 2.31: *Kochlorine n. sp.* from *Purpura panama* from Isipingo. Light microscopy of external morphology and internal structures, female. A – Lateral view of a whole specimen;

B – Opercular area; C – Orificial knob; D – Terminal cirri; E – Caudal appendages; F – Mandible; G – Maxillule; H – Mouth cirri.

Hosts: To date found exclusively on *Purpura panama* shells.

Distribution: Found only at Isipingo (29°59'44.1"S, 30°57'00.8"E) in KwaZulu-Natal (Fig. 2.32).

Fig. 2.32: *Kochlorine n. sp.* Distribution along the South African coastline.

Variation: Females range in length from 2 – 2.6 mm (mean = 2.25 mm) and width 1.05 – 1.75 mm (mean = 1.33 mm). Opercular bar 0.75 mm

Remarks: Only three individuals were observed from three different shells. One was found in the same shell along with 44 *A. utinomii* specimens. Differs from most species in the genus as it has arrowhead-shaped teeth on the opercular bar. Only two species have similar-shaped teeth on the opercular bar, these are *K. bocqueti* and *K. anchorella*. This species differs from *K. bocqueti*, as it has an orificial knob that is less developed and is not as rounded or globular, also has fewer arrowhead-shaped teeth on the opercular bar, which is larger, more broad and shorter. Posterior process has a spine that branches off at the apex, unlike *K. bocqueti*. Differs from *K. anchorella* as the arrowhead-shaped teeth are a different shape and not as rounded as those of *K. anchorella*. Labrum and maxilla not observed.

Discussion

This study is the first of its kind in South Africa and raises the number of known acrothoracicans from four to eight species and of known cirripedes from 90 to 94 species. Five species are added to the acrothoracican fauna, of which three are new records to the region, and two are undescribed species new to science (although will only be formally described and named once published in a journal). One existing species is also removed from the fauna as it is a *nomen nudum*. Although this represents a doubling of the known acrothoracican fauna, much more remains to be explored, as no samples were collected from deeper waters, or from large sections of the coastline (notably the Northern Cape and north coast of KwaZulu-Natal). Further research on other hosts such as corals and hermit crabs might reveal genera such as *Berndtia* and *Trypetesa*, that are frequently found elsewhere in the world. As both the Acrothoracica and Thoracica have now been reviewed (Biccard, 2012), the Rhizocephala still remains very poorly studied. Certainly, this group is in desperate need to be reviewed and is an obvious target for future research.

Chapter 3: Diversity, Biogeography and Host Specificity of South African Acrothoracica

Introduction

The Acrothoracica have a global distribution, occurring in all the major oceans, although they are most diverse in the tropics (Kolbasov, 2009). They are mostly intertidal, but some deep-water species have been described (Kolbasov, 2009). Few publications have examined the diversity, distribution patterns and/or rates of endemicity of the acrothoracican fauna of specific countries. In one of few examples Chan, Hsieh and Kolbasov (2014) found that 23.08% of the acrothoracicans in Taiwan were endemic, although most species in their study were endemic to the wider region. Some species are exceptions to this and have cosmopolitan distributions, such as *Kochlorine hamata* Noll, 1872 and *Auritoglyptes bicornis* (Aurivillius, 1892).

Most acrothoracicans are generalists in terms of the hosts which they colonise and thus show no host specificity (Tomlinson, 1969; Smyth, 1990; Kolbasov, 2009), but this is not the case for all genera. Chan, Hsieh and Kolbasov (2014) noted that the genus *Berndtia* showed high host specificity to the corals they burrow into. This genus seems to be an exception, as most species are able to bore into multiple hosts, including organisms that are only distantly related (Tomlinson, 1969; Kolbasov, 2009; Chan, Hsieh and Kolbasov, 2014). *Kochlorine hamata*, for example, bores into bivalves (*Tridacna sp.*), corals, thoracican barnacles and gastropods (Kolbasov, 2009; Alvarez-Cerrillo, Valentich-Scott and Newman, 2017). Thus, any calcareous substrate may suffice, although specifically with regards to shells, certain criteria need to be met. For example, the periostracum needs to be somewhat eroded, and the shell needs to be thick enough for the animal to bury into it, without boring through it. The periostracum is a layer on the external surface of mollusc shells that is kept intact by the live mollusc and protects the shell against boring and fouling organisms (Bottjer, 1981). As the animal ages and after death, the periostracum becomes eroded and it is subsequently easier for acrothoracicans to colonise. With no animal living in the shell, the internal surface also becomes available to colonise (Tomlinson, 1969). Acrothoracicans can colonise both live and dead shells of molluscs and show no preference to the presence of a mollusc in the shell (Smyth, 1990).

Acrothoracicans are not classified as parasites, as most do not utilise a critical resource from their host, but rather as obligate commensals. However, members of the Trypetesidae (not observed in South Africa) exclusively inhabit gastropod shells occupied by hermit crabs and Williams, Gallardo and Murphy (2011) showed that *Trypetesa lampas* (Hancock, 1849) predates on hermit crab eggs. The authors argue that it might thus be more accurate to refer to these acrothoracicans as transient parasites of hermit crabs. Other acrothoracicans can also have negative impacts on their hosts, as their holes compromises shell strength (Kolbasov, 2009). These barnacles have been documented to occur in astonishing numbers, for example 3350 *Australophialus melampygos* (Berndt, 1907) individuals have been found in a single *Haliotis iris* Gmelin, 1970 shell (Tomlinson, 1969).

South Africa's marine invertebrate fauna is considered highly diverse, with more than 12900 described species, of which a third are endemic to the region (Griffiths et al., 2010). Of these species, over 3 300, or 18%, are Crustacea, which form the second most diverse group after Mollusca. These high levels of diversity are unsurprising and are a function of the exceptional variability in physical conditions around the coastline of South Africa, which is *c.* 3650 km in length (Griffiths et al., 2010; Teske et al., 2011) and is dominated by two major ocean currents that run along either side of the country. On the west coast the cold Benguela

Current runs from south to north and on the east coast the warm Agulhas Current runs from north to south, with the two currents meeting along the south coast. This results in an increase in temperature as one moves from west to east and the presence of several distinct bioregions existing along the South African coastline (Lombard et al., 2004; Branch and Branch, 2018). When moving from west to east three prominent biological patterns emerge: productivity declines, biomass decreases and diversity increases (Branch and Branch, 2018). The first two trends are due to upwelling occurring almost exclusively on the west coast, which brings cold, nutrient-rich water to the surface, which in turn stimulates productivity. There are several hypotheses as to why there is a higher species diversity to the east. Some suggest that the Indian Ocean is older and thus there has been more time for the evolution of new species, however other theories, such as the 'paradox of enrichment', suggests that such high productivity in fact causes high population growth, which results in intense competition and subsequently the dominance of few species (Rosenzweig, 1971).

At the start of this dissertation, there were 90 described species of cirripedes in South Africa, of which only four were acrothoracicans (Kolbasov, 2009), three were rhizocephalans (Day, 1939; Boschma, 1958a, b) and 83 were thoracicans (Biccard and Griffiths, 2016). Almost nothing is known about the distribution, abundance or ecology of the Acrothoracica of South Africa, apart from the original species descriptions (Berndt, 1907; Barnard, 1924; Tomlinson, 1969), of which the most recent was almost 50 years ago. In the previous chapter the number of South African acrothoracicans was increased from four species to eight (one was determined to be a *nomen nudum*, and five species were added, of which two were new to science). Nevertheless, much remains unknown about the biology of South African acrothoracicans. This chapter aims to partially fill this gap by describing aspects of the diversity, biogeography and host specificity of South African acrothoracicans.

Methods

Methods as in Chapter 2.

Statistical analyses

All tables were created using Microsoft Excel (2018).

Definition of terms:

Bush et al. (1997) clarifies and explains 27 population and community terms frequently used by parasitologists. Although most Acrothoracica are not considered parasites, this study employs some of the terminology designed to quantify parasites. Thus, slightly adjusted from Bush et al. (1997), the following terms are used:

- Prevalence is the number of hosts that are infected by one or more individuals of a particular species (acrothoracicans in this study), divided by the total number of hosts examined, and expressed as a percentage.
- Mean abundance is the total number of individuals of a particular acrothoracican species in a sample of a particular host species, divided by the total number of hosts for the species examined.
- Mean intensity is the total number of barnacles of a particular species found in a sample, divided by the number of hosts infected with that barnacle species.

Results

In total, 1992 acrothoracicans were collected during the course of this study and these were extracted from 15 mollusc species and four coralline algal species. Besides these, no acrothoracicans were found in other categories of hosts (bryozoans, scleractinian corals and thoracicans) or from limestone. Species from 11 different mollusc families were found to host acrothoracicans. Of these, 10 were Gastropoda, namely Buccinidae, Calyptraeidae, Charoniidae, Cymatiidae, Fasciolariidae, Haliotidae, Muricidae, Ranellidae, Patellidae, Turbinidae. Chaetopleuridae was the only family of the Polyplacophora recorded as a host and no bivalve hosts were recorded.

Diversity

Both orders of Acrothoracica, the Cryptophialida and Lithoglyptida, were found in South Africa, with two of the three known families represented, and only the Family Trypetesidae not represented. Moreover, two species of each of the subfamilies within the Lithoglyptidae were collected (Table 3.1).

Table 3.1: Table showing the number of species present in South Africa and the families and subfamilies of Acrothoracica to which they belong (global numbers of species after Kolbasov, Chan and Cheng, 2017; WoRMS, 2019).

Acrothoracica	**Number of species in SA**	**Number of species globally**
Family Cryptophialidae	**2**	**16**
Family Lithoglyptidae	**6**	**42**
Subfamily Berndtiinae	2	18
Subfamily Lithoglyptinae	2	16
Subfamily Kochlorininae	2	8
Family Trypetesidae	**0**	**7**
Total species	**8**	**65**

Biogeography

This collection included specimens from both acrothoracican orders, with 56.68% individuals collected being from the order Lithoglyptida (six species), and 43.32% from the Cryptophialida (two species). *Weltneria spinosa* Berndt, 1907 represented 53.87% of the sample. *Australophialus turbonis* (Barnard, 1925) made up 20.53% of the total sample, while *Australophialus utinomii* Tomlinson, 1969 represented 22.79%. The other five lithoglyptid species combined represented only 2.76% of the total sample. These species had less than 10 individuals in total, or were collected from a single sample and yielded no useful results regarding prevalence, abundance and intensity.

Both cryptophialids, *A. turbonis* and *A. utinomii* had the greatest mean prevalence and mean abundance, with the seond and third greatest and intensity, while *W. spinosa* had a high mean prevalence and mean abundance and the highest intensity (Table 3.2).

Eight acrothoracican species were recorded around the coast of South Africa, with two species found in the Western Cape, four in the Eastern Cape and four in KwaZulu-Natal. Only two of the species were present in more than one province (Table 3.2). *Weltneria spinosa* occurred in both the Western and Eastern Cape, while *A. utinomii* was found in both the Eastern Cape and KwaZulu-Natal.

Table 3.2: Mean prevalence, abundance, intensity and frequency for each acrothoracican species and in each province, with the number of host species each acrothoracican species was found inhabiting (WC – Western Cape, EC – Eastern Cape, KZN – KwaZulu-Natal).

Acrothoracican species	**Province**	**Mean Prevalence**	**Mean Abundance**	**Mean Intensity**	**Number of host species**	**Frequency**
Weltneria spinosa	WC	22.97%	5.75	30.12	8	511
	EC	28.57%	6.69	23.42	8	562
Australophialus turbonis	WC	33.93%	7.30	21.53	7	409
Australophialus utinomii	EC	44%	7.18	16.32	5	359
	KZN	20%	3.17	15.80	4	95
Kochlorine bocqueti	EC	15.69%	0.59	3.75	6	30
Weltneria hirsuta	EC	100%	14.00	14.00	1	14
Kochlorine n. sp.	KZN	37.50%	0.38	1.00	1	3
Balanodytes n. sp.	KZN	19.23%	0.27	1.40	3	7
Balanodytes flexuosus	KZN	100%	1.00	1.00	1	1

Ecology

Of the 27 potential host species collected, 19 were occupied by one or more acrothoracican species. Of the eight acrothoracican species, all were found occupying the same individual host with at least one other acrothoracican. *Australophialus utinomii, Kochlorine bocqueti* Turquier, 1977 and *W. spinosa* were found in the same individual host with up to three other acrothoracican species, while the other five species were only found with one other acrothoracican species in the same host species. Of these, eight different host species harboured one species of acrothoracican, while four had two species of acrothoracicans, four had three different barnacle species and three harboured four different barnacle species (Table 3.3). In the Western Cape, 62.50% of potential host species sampled were found to host acrothoracicans, while interestingly in the Eastern Cape, all 10 host species sampled had one or more species of acrothoracicans. Lastly, in KwaZulu-Natal 71.43% of potential host species sampled contained acrothoracicans.

Eight of the 27 species were found to host no acrothoracicans (Table 3.3). This included shells of various different species (mostly *Bullia spp.*) occupied by hermit crabs which were sampled, as members of the Trypetesidae are known to occur in the columella of hermit-occupied shells, but no such acrothoracicans were found.

Table 3.3: List of all host species sampled, with the number of acrothoracican species found in each host.

	Acrothoracican species								
Host species	***A. turbonis***	***A. utinomii***	***K. bocqueti***	***W. hirsuta***	***Kochlorine n. sp.***	***Balanodytes n. sp.***	***B. flexuosus***	***W. spinosa***	**None**
Algae									
Heydrichia woelkerlingii								✓	
Lithophyllum neoatalayense								✓	
Lithophyllum sp. (rhodolith)								✓	
Neogoniolithon brassica-florida								✓	
Bivalvia									
Atrina squamifera									✓
Cirripedia									
Austromegabalanus cylindricus									✓
Gastropoda									
Argobuccinum pustulosum	✓							✓	
Burnupena cincta	✓	✓						✓	
Burnupena lagenaria									✓
Burnupena papyracea									✓
Crepidula porcellana	✓								
Charonia lampas			✓	✓		✓	✓		
Fusinus ocelliferus	✓								
Haliotis midae	✓		✓					✓	
Mancinella capensis		✓	✓			✓		✓	
Mancinella echinulata									✓
Purpura bufo		✓							
Purpura panama		✓			✓				
Ranella gemmifera		✓	✓					✓	
Scutellastra argenvillei									✓
Scutellastra tabularis								✓	
Tenguella granulata									✓
Turbo cidaris	✓							✓	
Turbo sarmaticus	✓	✓	✓					✓	
Polyplacophora									
Dinoplax gigas		✓	✓					✓	
Dinoplax validifossus		✓				✓			
Other									
Hermit shells									✓

Discussion

Diversity

At the start of this study there were only four species of acrothoracicans (including one which has now been designated a *nomen nudum*) known from South Africa, with only two of these described from adequate material. However, following this study, the number of acrothoracican species known from South Africa has been raised to eight (Chapter 2). These eight species represented a broad range of the known acrothoracican taxa of the world, as all three subfamilies in the order Lithoglyptida were represented, with two species in each known subfamily. One of the two genera in the subfamily Berndtiinae is represented by two species in *Weltneria*, of which *W. spinosa* was found to be remarkably common. The large subfamily Lithoglyptinae, has two *Balanodytes spp.* present (no members of the *Auritoglyptes* or *Lithoglyptes* were collected), while two species in the subfamily Kochlorininae were found, both in the genus *Kochlorine* (no *Kochlorinopsis*). No species of the family Trypetesidae were found in South Africa, despite several samples of hermit crabs being examined. One of the two genera in the Family Cryptophialidae was represented in the form of two species in the genus *Australophialus.* Thus, most of the acrothoracican families and subfamilies are now represented in South Africa.

Weltneria spinosa dominated the sample, and of the 1992 acrothoracicans collected, almost 54% comprised this species (which was recorded from 13 different host species). This species is a member of the Lithoglyptida, which have cypris larvae that possess well-developed thoracopods and are swimming larvae able to disperse to different hosts and locations (Kolbasov, 2009). Therefore, it is unusual for a lithoglyptid to attain the high abundance and intensity reported in this study for *W. spinosa*. In one instance 235 individuals were collected from a single *Haliotis midae* Linnaeus, 1758 shell. Conversely, it is expected for both australophialids to have a high mean prevalence, abundance and intensity, as these species are part of the Cryptophialida. These barnacles have larvae that lack thoracopods (swimming appendages) and are thus often found in great densities, as the larvae are not able to actively disperse, but rather rely on other methods (Kolbasov, 2009). Tomlinson (1969) also found *W. spinosa* and *A. turbonis* to be common within their respective distributions.

Biogeography

Before the start of this dissertation both *A. turbonis* and *W. spinosa* were known to occur only in the Western Cape, while *A. utinomii* was only recorded in the Eastern Cape at Kwelera Bay (near East London). Following the survey, *A. turbonis* was the only species for which a range extension was not reported (though it was found at new localities and in new hosts within the known range). All other species are either new to science, or to the region, or were found to have larger ranges than previously described. Two of these, *W. spinosa* and *A. utinomii* had range extensions within South Africa of about 1000 km and 500 km respectively. Three species are new records for South Africa, these being *Balanodytes flexuosus* (Chan, Kolbasov and Cheang, 2012)*, K. bocqueti* and *Weltneria hirsuta* (Tomlinson, 1963). The first two represent relatively small range extensions, as *B. flexuosus* was previously known from the Mozambique Channel (Chan, Kolbasov and Cheang, 2012), while *K. bocqueti* was known from Madagascar and Socotra Island (Kolbasov, 2002). *Weltneria hirsuta,* however, was previously known only from Hawaii, Japan and Taiwan in the Pacific Ocean and finding this species in the Eastern Cape region of South Africa represents a major range extension. The two new species added to the acrothoracican fauna of South Africa, *Balanodytes n. sp.* and *Kochlorine n. sp.* are both known from single localities, Port Shepstone and Isipingo respectively.

Of the eight acrothoracican species found in South Africa, five are endemic to South Africa. Griffiths et al. (2010) found that 33% of the marine fauna of South Africa were endemic, while Biccard (2012) reported 24.7% of thoracicans were South African endemics. Both these percentages are substantially lower compared to 62.5% endemicity reported for the Acrothoracica in this study. This percentage is also much higher than found by Chan, Hsieh and Kolbasov (2014) in Taiwan (23.08%).

This high endemicity percentage could be due to several factors. Firstly, the absolute number of species in the group is very low, so percentage endemicity calculations are volatile and would be strongly swayed (by >10%) by the discovery of just one additional species. Secondly, besides the description of *B. flexuosus,* which was described from a cruise in the Mozambique Channel (Chan, Kolbasov and Cheang, 2012), no research has been undertaken on acrothoracicans elsewhere in the regions surrounding South Africa. As Griffiths and Robinson (2016) note, poor sampling in adjacent regions commonly inflates the endemicity percentage within a country, as species deemed to be endemic may also occur in these neighbouring countries, but have not been detected there. It should also be noted that acrothoracican research within South Africa remains limited, mostly due to lack of taxonomic expertise, and more intensive sampling will almost certainly reveal more new records within the region. This could increase the endemicity rate, if species new to science are discovered, or reduce it, if species known elsewhere are detected in the region for the first time.

Interestingly though, within South Africa, most species are endemic to specific provinces, and only two of the eight species reported here were found in more than one of the three provinces sampled. In the Western Cape, *A. turbonis* was an endemic, most likely as it is not adapted to the warm temperate region east of Cape Agulhas (Teske et al., 2011). *Weltneria* *spinosa* occurred both in the Western Cape and Eastern Cape, along with two endemics, *K. bocqueti* and *W. hirsuta* in the latter province. *Australophialus utinomii* was also present here and in KwaZulu-Natal along with three endemics, *Balanodytes n. sp., B. flexuosus* and *Kochlorine n. sp.* The rate of local endemicity thus increases as one moves from west to east and peaks in the KwaZulu-Natal (however, it is important to note that no samples were collected from the northern KwaZulu-Natal (Delagoa Bioregion) and sampling here will likely influence the rates of local endemicity). The reason for the high rates of local endemicity is unlikely to be host limitation, as hosts for a specific barnacle were often sampled in the adjacent province, but without detecting that barnacle (for example, *Mancinella capensis* (Petit de la Saussaye, 1852) was collected from both the Eastern Cape and KwaZulu-Natal, but *K. bocqueti* was only collected from this host in the Eastern Cape). This was the case for *B. flexuosus, Balanodytes n. sp, K. bocqueti* and *W. hirsuta.* Therefore, it is likely that physical conditions drive local endemicity, which is unsurprising, as South Africa is known to experience major climatic differences between its three coasts (Branch and Branch, 2018).

Species diversity also increases from west to east, as there are two species in the Western Cape, while the Eastern Cape and KwaZulu-Natal each have four species. This is similar to the described trend for marine organisms in South Africa as a whole (Awad, Griffiths and Turpie, 2002; Branch and Branch, 2018). Note also that this trend occurred despite the fact that more sampling occurred on the west coast, while the south and east coast were only visited during one dedicated trip each.

Ecology

Of all the species sampled, only *Kochlorine n. sp.* was found to be host specific (most likely due to limited sampling), while all other acrothoracicans were found occupying two or more host species, with *W. spinosa* having the maximum number of 13 host species. Thus, each of the six previously known acrothoracicans are less host specific than previously thought. For example, *A. turbonis* was found to have more than double the number of previously reported host species. Similarly, *A. utinomii* had nine times more hosts than previously thought, as it was previously known from five individuals collected from a single specimen of *Dinoplax gigas* (Gmelin, 1791). *Kochlorine bocqueti* was found to have four times more host species than previously known, while *W. spinosa* had more than four times more host species than previously recorded. Furthermore, the number of hosts were doubled for *B. flexuosus,* while an additional host was added for *W. hirsuta*, raising its known number of host species to five. Most specimens were found burrowing in the thickest and most eroded areas of the host shells, most often either at the apex of the shell or around the operculum (pers. obs.). As Kolbasov (2009) and Chan, Hsieh and Kolbasov (2014) noted, the acrothoracicans showed no preference to presence or absence of the live mollusc.

Some acrothoracican species were found occupying a variety of distantly-related hosts. Six of the eight acrothoracican species were found to occupy hosts that differed at least by class, all occurred in gastropods, while four barnacle species were collected from chiton species (*A. utinomii, Balanodytes n. sp., K. bocqueti* and *W. spinosa*). Both *B. flexuosus* and *W. hirsuta* were previously known from coral species, but in this study, both were also collected from *C. lampas* (*W. hirsuta* was previously known from another gastropod). *Weltneria spinosa* had the greatest diversity of host species, not only in terms of number of hosts, but also groups of hosts, as it was collected from gastropods, a chiton and from coralline red algae.

Interestingly, Chan et al. (2013) found that individual acrothoracican species showed no morphological or molecular differentiation, regardless of the substrate within which they were observed. Moreover, this study also describes two new host families, Patellidae and Calyptraeidae, as *W. spinosa* was collected from the giant limpet, *Scutellastra tabularis* (Krauss, 1848) and *A. turbonis* was collected from the slipper-limpet, *Crepidula porcellana* Lamarck, 1801. Thus, South African acrothoracicans are much less host specific than previously thought. This is consistent to observations by Tomlinson (1969), Kolbasov (2009) and Chan, Hsieh and Kolbasov (2014), who noted that most acrothoracicans occur in any calcareous substrate.

Before this study it was known that two species of acrothoracicans could occur on a single host specimen (Tomlinson, 1969), however in South Africa this was only the case for *A. turbonis* and *W. spinosa* (Fig. 3.1). In this study all barnacle species were found sharing a host specimen with at least one other barnacle species, with some hosts (*M. capensis, Ranella gemmifera* (Euthyme, 1889) and *Turbo sarmaticus* Linnaeus, 1758) having as many as three acrothoracican species in a single host specimen. Moreover, some host species hosted as many as three or even four acrothoracican species (on different individuals). These host species, which include *Burnupena cincta* (Röding, 1798)*, Charonia lampas* (Linnaeus, 1758)*, D. gigas, H. midae, M. capensis, R. gemmifera* and *T. sarmaticus,* were also found to have the greatest prevalence, abundance and intensity of acrothoracicans (Appendix A, B, C). These species had several key characteristics which make them frequent acrothoracican hosts. They are large species living on rocky shores that often have a large part of the periostracum eroded off. These hosts are then easier to burrow into by acrothoracican larvae, that can then settle in great abundance. *Turbo sarmaticus* and *H. midae* hosted exceptional numbers of acrothoracicans, often over 100 individuals on a single specimen, with as many as 235 *W. spinosa* found on a single *H. midae*, while 376 barnacles were found on one individual *T. sarmaticus* (178 *A. turbonis* and 198 *W. spinosa*).

Fig. 3.1: Female *Weltneria spinosa* (red) and *Australophialus turbonis* (white) feeding using terminal cirri burrowed in a *Turbo sarmaticus*.

In total, acrothoracicans had a high mean prevalence, as 39.8% of individual hosts collected (only considering mollusc families known to host acrothoracicans) were inhabited by acrothoracicans. This is much higher than reported by Kolbasov (2009), as he found that 13% of hosts to be occupied by acrothoracicans. Although South Africa has many large molluscs, the number reported for this study is probably inflated due to selective sampling targeting species deemed to be appropriate (thick enough for an acrothoracican to be able to burrow into it).

Of the potential host species collected in all three provinces, several species were found to host no acrothoracicans. These included the large bivalve, *Atrina squamifera* (G. B. Sowerby I, 1835), the barnacle *Austromegabalanus cylindricus* (Gmelin, 1780), and the gastropods *Burnupena lagenaria* (Lamarck, 1822), *Burnupena papyracea* (Bruguière, 1789), Hermit crab-occupied shells (mostly *Bullia spp.*), *Mancinella echinulata* (Lamarck, 1822)*,* *Scutellastra argenvillei* (Krauss, 1848) and *Tenguella granulata* (Duclos, 1832). The reasons these shells did not host any acrothoracicans could be because they were either too thin (*A. squamifera,* Hermit crab-occupied shells and *T. granulata)*, were undersampled (*M. echinulata*), had a bryozoan living on the shells (*B. papyracea*), or simply that by chance the individuals sampled were not infected. Although no live coral was investigated in this study, 300 photo transects taken by Camilla Floros of coral species in KwaZulu-Natal revealed no acrothoracicans. However, further analyses of live corals might reveal some acrothoracican species.

State of knowledge

The previous chapter raised the global number of acrothoracicans from 69 to 71 species (Chapter 2) with the addition of two new species. This study thus shows that 11.27% of the world's acrothoracicans are present in South Africa, which is substantially higher than the 5.79% known previously. Moreover, the new additions to the South African acrothoracican fauna raises the number of known cirripedes from 90 to 94 species.

This study does not represent a definitive survey of the Acrothoracica in South Africa, but rather a baseline that can be expanded on. Specifically, some biogeographic regions were not considered in this study, notably the Delagoa Bioregion in Northern KwaZulu-Natal and the Namaqua Bioregion North of Saldanha Bay on the west coast. Moreover, many potential host species were not sampled, or were undersampled in terms of numbers of specimens examined. Additional sampling of other host categories, especially corals and coralline red algae, will also probably yield additional records. Many acrothoracicans have been described from corals, while the potential for coralline red algae as a host is unknown, as this group was only recently discovered to host acrothoracicans (Chapter 1). Examining deep-water samples (which was outside the scope for this study) will also certainly add to the knowledge on the Acrothoracica, as some genera (*Balanodytes*, *Australophialus, Lithoglyptes* and *Weltneria*) have been recorded at depths below 200 m (Kolbasov, 2009).

In conclusion, South Africa was found to have more acrothoracican species, from a broader range of families, which occupy larger ranges and broader suites of host species than previously thought. This group also had higher rates of endemicity compared to other marine taxa in South Africa and acrothoracicans in Taiwan, although this percentage is likely inflated by the poor state of taxonomic research in countries adjoining South Africa. Certainly, more extensive sampling is required to capture the true extent of acrothoracican diversity, biogeography and host diversity within South Africa and this is a promising area for future research.

Appendix

Appendix A: Prevalence, mean abundance and mean intensity of acrothoracicans on individual host species in the Western Cape. N= number of host specimens sampled.

Western Cape

	Prevalence (%)		**Mean abundance**		**Mean intensity**	
Host species (N)	***W. spinosa***	***A. turbonis***	***W. spinosa***	***A. turbonis***	***W. spinosa***	***A. turbonis***
Argobuccinum pustulosum **(10)**	20.00	20.00	3.22	0.22	14.50	1.00
Burnupena cincta **(11)**	9.09	18.18	0.18	0.27	2.00	1.50
Crepidula porcellana **(3)**	-	100.00	-	5.67	-	5.67
Dinoplax gigas **(10)**	10.00	-	0.13	-	1.00	-
Fusinus ocelliferus **(5)**	-	20.00	-	0.20	-	1.00
Haliotis midae **(10)**	10.00	10.00	1.30	0.20	13.00	2.00
Heydrichia woelkerlingii **(13)**	7.69	-	0.08	-	1.00	-
Scutellastra tabularis **(13)**	7.69	-	0.30	-	4.00	-
Turbo cidaris **(19)**	10.53	21.05	1.84	2.37	17.50	15.00
Turbo sarmaticus **(11)**	81.82	45.45	38.73	30.90	47.33	56.67

Appendix B: Prevalence, mean abundance and mean intensity of acrothoracicans on individual host species in the Eastern Cape.

Eastern Cape

	Prevalence (%)					**Mean abundance**					**Mean intensity**				
Host species	***W. spinosa***	***A. utinomii***	***K. bocqueti***	***W. hirsuta***	***Unknown spp***	***W. spinosa***	***A. utinomii***	**K. bocqueti**	***W. hirsuta***	***Unknown spp***	***W. spinosa***	***A. utinomii***	**K. bocqueti**	***W. hirsuta***	***Unknown spp***
***Burnupena cincta* (13)**	-	76.9	-	-	-	-	0.15	-	-	-	-	1.8	-	-	-
***Charonia lampas* (1)**	-	-	100	100	-		-	21	14	-		-	21	14	-
***Dinoplax gigas* (11)**	9.09	18.2	9.09	-	-	0.27	0.55	0.09	-	-	3	3	1	-	-
***Haliotis midae* (13)**	23.08	-	15.38	-	7.69	18.38	-	0.15	-	0.15	79.67	-	1	-	2
***Lithophyllum neoatalayense* (1)**	100	-	-	-	-	12	-	-	-	-	12	-	-	-	-
***Mancinella capensis* (11)**	27.27	9.09	9.09	-	-	5.91	0.55	0.09	-	-	21.67	6	1	-	-
***Ranella gemmifera* (2)**	100	50	50	-	-	20.5	2	2	-	-	20.5	4	4	-	-
***Rhodolith* (*Lithophyllum sp.)* (2)**	10	-	-	-	-	1.9	-	-	-	-	19	-	-	-	-
Rhodolith **(Neogoniolithon**	5	-	-	-	-	0.05	-	-	-	-	1	-	-	-	-

brassica-florida*) (1)*															
***Turbo sarmaticus* (13)**	53.85	61.5	15.39	-	-	12.62	17.9	0.15	-	-	23.43	29.1	1	-	-

Appendix C: Prevalence, mean abundance and mean intensity of acrothoracicans on individual host species on the KwaZulu-Natal.

KwaZulu-Natal

	Prevalence (%)				**Mean abundance**				**Mean intensity**			
Host species	***Balanodytes flexuosus***	***A. utinomii***	***Kochlorine n.* sp.**	***Balanodytes n.* sp.**	***Balanodytes flexuosus***	***A. utinomii***	***Kochlorine n.* sp.**	***Balanodytes n.* sp.**	***Balanodytes flexuosus***	***A. utinomii***	***Kochlorine n.* sp.**	***Balanodytes n. sp.***
Charonia lampas (1)	100	-	-	100	1	-	-	3	1	-	-	3
Dinoplax validifossus (10)	-	10	-	20	-	0.1	-	0.2	-	1	-	1
Mancinella capensis (15)	-	-	-	13.33	-	-	-	0.133	-	-	-	1
Purpura bufo (5)	-	20	-	-	-	1.4	-	-	-	7	-	-
Purpura panama (8)	-	75	37.5	-	-	10.875	0.375	-	-	14.5	1	-

Synthesis

The aims of this thesis were to revise the ecology, taxonomy and biogeography of the Acrothoracica of South Africa.

Chapter 1 describes for the first time globally, the occurrence of live acrothoracicans in several species of coralline red algae. The implications of this finding are discussed and the need for future research is emphasized.

Chapter 2 summarises the history of research of the Acrothoracica globally, provides a key to South African acrothoracicans and for the first time gives a systematic account of the Acrothoracica of South Africa. In this account three known species from the region are re-described using modern techniques, three additional species are reported for the first time from the region, while two species new to science are described for the first time. Where possible, modern techniques (SEM's and light microscopy) are applied to the species in the account. This account elevates the known number of cirripedes in South Africa from 90 to 94.

In Chapter 3 the diversity, biogeography and host specificity of South African acrothoracicans are evaluated. Endemicity rates and the various different hosts of each acrothoracican species are discussed within the different provinces. This chapter shows that South Africa has more acrothoracican species, that occupy larger ranges and inhabit more host species than previously thought.

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