Curtin Medical School

Australian sponge barnacles: diversity, host dynamics and systematics

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Declaration

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Acknowledgement of Country

I would like to acknowledge the Whadjuk Noongar people as the traditional owners of the lands on which Curtin University and the Western Australian Museum are located. Specimens used in this thesis were collected from across Australia and I also acknowledge the many traditional owners of the sea country, or lands that are adjacent to the areas, where they were collected from. I pay my respects to them and their cultures; and to elders both past and present.

Abstract

A significant component of barnacle biodiversity is comprised of species that are symbiotic with other eukaryotes such as corals, marine mammals, other crustaceans and sponges. The transition from being free-living to symbiotic made available a new range of ecological niches to exploit, driving a range of evolutionarily novel adaptations to their hosts. In Australia the symbiotic species have received little attention, especially those associated with sponges. This thesis aims to determine the biodiversity of barnacles inhabiting sponges, explore patterns of host usage and to determine the evolutionary origins of sponge symbiosis. To fulfil these aims requires a modern integration of morphological and molecular methods to provide a phylogenetic framework that is coupled with the existing knowledge of barnacle systematics.

DNA barcoding is a powerful tool in identifying species and is an independent means for evaluating the constancy of phenotypic data sources such as morphology and ecology. Primary species hypotheses (PSH) were generated using a consensus approach to compare species delimitation analyses. The analyses consisted of the genetic distance-based method, Assemble Species by Automatic Partitioning (ASAP), that utilises a threshold method to delimit putative species based on the concept of a barcode-gap, and the three Poisson tree processes (PTP) model variants, which compare substitutions per site in the form of branch lengths to delimit species. A total of 638 *COI* sequences were partitioned into 99–178 species based on the top scoring results of the delimitation analyses. From the consensus approach a total of 115 species were inferred from the dataset, 101 of which were found in Australian waters. While only 55% of species were the result of unanimous support from the analyses, 90% were delimited by the majority of methods. The ASAP and multi-rate PTP methods were the most congruent.

Integrating the molecular delimitation analyses with morphological examinations of historical collections facilitated bridging the gap between data sources and allowed the undertaking of taxonomic actions. This included naming four new species: *Acasta caveata*, *Eucasta acutaflava*, *E. excoriatrix* and *Membranobalanus porphyrophilus*, as well as redescribing known species and assigning a lectotype to fix the identity of *Pectinoacasta cancellorum*.

Barnacles were found occupying a total of 179 host species and 85% were found in ≤2 host species. The order Dictyoceratida hosted the most barnacle species (42). A multilocus phylogeny was reconstructed using maximum likelihood and Bayesian inference analyses on a concatenated dataset of two mitochondrial genes, cytochrome oxidase subunit I and 12S ribosomal subunit, and two nuclear genes, Histone 3 and 28S ribosomal subunit, to examine the evolutionary relationships between barnacle species and host usage. Well-supported clades of barnacles were recovered with varying host usage and only three instances of host-sharing were identified. At one extreme, clades of four or five species were found to only inhabit species from a single host family. For example, the *A. flexuosa* complex only inhabited sponges of the family Dysideidae. Other clades were found to inhabit multiple families from within the host order, e.g. members of Clade A inhabited the Irciniidae, Spongiidae and Thorectidae. This group was morphologically more diverse than clades inhabiting a single family. An ancestral state reconstruction analysis suggested that the Thorectidae were the host of the barnacles' most recent common ancestor (MRCA) and that the subsequent radiation of barnacles occurred as the result of multiple host-shifts to different families of sponge.

Examination of the origins of sponge symbiosis involved expanding on this dataset to include 112 species symbiotic with sponges and cnidarians from across the Balanoidea. The concatenated alignment also included a partial sequence of the nuclear RNA polymerase subunit II locus resulting in a total of 3569 base pairs. The resulting phylogeny was incongruent with the current classification for the Acastinae and the broader Balanoidea. Some species have been simply misassigned to genera e.g. *Archiacasta tenuivalvata* should be transferred to *Membranobalanus*, while the placement of type species *Acasta spongites, Archiacasta membranacea* and *Neoacasta glans* within a single, well supported clade indicate that significant rearrangement of the generic classification within Acastinae is necessary. With some alteration, the Acastinae is largely monophyletic. The key disruption to this is that members of *Armatobalanus* and *Multatria* were recovered nested within the well supported clade of Acastinae, suggesting that the definition of Acastinae should be expanded to include the Brozobiinae. The Balanidae and Pyrgomatidae were not recovered as reciprocally monophyletic as members of *Conopea* were recovered within the broader clade of the Pyrgomatidae.

Balanoid barnacles evolved sponge symbiosis at least three times as inferred by the ancestral state reconstructions. These transitions from a free-living life history occurred at the MRCA for the clade containing *Membranobalanus*, again for the Acastinae and thirdly for the species *Acasta cyathus*. Two species of *Acasta* were found inhabiting octocorals, having evolved from within an otherwise sponge-inhabiting clade. Dating the evolution of symbiosis using molecular clock analyses indicate that the transition from free-living to sponge symbiosis occurred near the Cretaceous-Paleogene boundary and predates the emergence of other common shallow water groups such as the Megabalaninae and Amphibalaninae. The branching patterns for the Acastinae clade indicate that the diversity seen in Australia is the result of a radiation that occurred mostly from the Eocene through to the Miocene. The timings suggest that transition to sponge symbiosis occurred relatively early within the broader Balanoid radiation that occurred after the Cretaceous extinction event.

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Chapter 1. General introduction

1.1. Speciation and symbiosis

The factors driving speciation are a topic of much discussion and debate (Dieckmann et al., 2004; Mallet, 2001; Mallet et al., 2009; Margulis & Fester, 1991; Maynard Smith, 1966; Mayr, 1963, 1982; Potkamp & Fransen, 2019; Presgraves, 2010; Wiens, 2004). Some of the key elements in contention are what induces reproductive isolation between two or more populations, and what maintains the resulting divergence long enough for one species to become two. It was generally accepted that speciation could only occur in allopatry, in that a geographic or environmental barrier prevented gene flow and separated a species into diverging populations (Mayr, 1942, 1963). The phenomena of overlapping ranges of closely related species were considered to be a case of secondary contact after speciation. The mechanisms behind sympatric speciation were first put forward by Maynard Smith (1966). He argued that species can be divided by a shift in the ecological niche which then results in assortative mating that could lead to stable polymorphisms. Speciation via ecological shifts (expansions or contractions) can take many forms e.g. a shift in diet, habitat, or behaviour and has become a major principle behind speciation events (Nosil, 2012; Rice, 1987; Schluter, 2001; Via, 2001).

To some extent symbiosis between two organisms can be seen as a form of ecological specialisation for at least one of the partners (Mestre et al., 2020). In cases where a host and symbiont can be easily designated e.g. commensal barnacles attached to a biotic substrate, then the host can be treated as any other habitat or ecological resource required by the symbiont. The breadth of this ecological niche will vary from case to case depending on various biotic and abiotic factors resulting in a spectrum of relative specialisation between species, which may vary over time and space. A change in host availability or utility may cause an expansion or retraction of host usage resulting in isolation or subdivision of a population that, if maintained, may lead to eventual speciation (Mestre et al., 2020). While initially demonstrated among insects (see Coyne & Orr, 2004), examples in the marine environment are increasing in number (Duffy, 1996; Faucci et al., 2007; Layton et al., 2019; Munday et al., 2004; Schiaparelli et al., 2015).

Early theories on the importance of symbiosis in the evolution of life were met with scepticism and nearly forgotten (Margulis & Fester, 1991; Mereschkowsky, 1905; Wallin, 1927). However, examples of symbiotic relationships that impact on the physiological, morphological or behavioural traits of the organisms involved are now numerous, and symbiosis has become accepted for the important role it plays in evolutionary innovation (see Sapp, 2004 for an overview). Further to this, the study of symbiotic relationships has been revolutionised in the last few decades as molecular techniques continue to increase in their ability to answer a broad range of scientific questions (Brucker & Bordenstein, 2012; Oliver & Russell, 2016).

The definition of “symbiosis” has widely fluctuated since it was coined by De Bary (1879), sometimes referring strictly to mutualistic interactions between conjoined species, through to antagonistic interactions such as parasitism, and also to interactions between otherwise free-living organisms e.g. predator-prey relationships and reliance on ecosystem service providers (Lewin, 1982; Martin & Schwab, 2012, 2013). The simple definition of symbiosis being different organisms “living together”, whether it be as a mutualistic, commensal, or parasitic relationship (or a mixture of these) is generally accepted and followed here.

1.2. Modern taxonomy

1.2.1. Taxonomy in demand

The present era has been described as the Anthropocene where human impacts on the environment have become irreversible (Crutzen, 2002). There are approximately 1.2 million described species on Earth but estimates of the total number vary widely from 2 million to 1 trillion, with the larger estimates dominated by bacteria (Costello et al., 2012; Larsen et al., 2017; Locey & Lennon, 2016; Mora et al., 2011; Wilson, 1999). In the marine environment the estimate of described eukaryote species is ~226,000 with up to three times this still to be formally described (Appeltans et al., 2012). It is clear that taxonomic effort needs to be increased in order to describe and classify the organisms so that we can better understand, manage and protect the biosphere. Adding to the urgency is the prediction that we are facing the sixth great extinction event with estimates that extinction rates are presently 100–1000 times greater than normal pre-human rates (Barnosky et al., 2011; De Vos et al., 2015; Pimm et al., 2006; Stork, 2010).

Despite the clear demand for taxonomy, resources are declining, and the road ahead is hampered by what has been called the taxonomic impediment (Taylor, 1983). Although this concept is widely debated, it covers several aspects to the problem at hand (Wheeler, 2013). First, there is a declining number of dedicated taxonomists, and the field of taxonomy has been disappearing from university curricula as well as in positions within natural history collections (Bradford-Grieve, 2016; Hutchings, 2017). As such not only are there less researchers dedicated to actively describing species, there are less researchers who are able to use the outputs of taxonomic endeavours such as identifying species or understanding basic taxonomic concepts of description, revision and synonymy (Hutchings, 2020).

The second aspect relates to how species are described and how best to mobilise taxonomic data for broader biodiversity research and management (Agnarsson & Kuntner, 2007; Valdecasas et al., 2008). The last few decades have seen many advances and the taxonomic community is alive with debate on how to increase taxonomic activities. Calls to overhaul, or even completely reject, the existing Linnean classification system and nomenclatural codes have been proposed (Conix, 2019; Dayrat, 2005; De Queiroz, 1996). As with all branches of science, progress and refinement of techniques to improve the capacity for taxonomic research will be ongoing, but what has been demonstrated is that taxonomy, and taxonomists, are data hungry and look to innovate wherever possible (Goldstein & Desalle, 2011; Valdecasas et al., 2008).

1.2.2. Molecular revolution and integration

Theoretical and technological advancements throughout the second half of the 20th century enabled taxonomy and systematics to incorporate statistical analyses, transforming them from what had been perceived as qualitative and highly subjective fields (e.g. Felsenstein, 1978; Hennig, 1966; Nelson & Platnick, 1981). These cemented reciprocal monophyly as a central tenet for establishing classifications, and the uptake of phylogenetics integrated characters from all facets of an organism to analyse (Godfray & Knapp, 2004). Advancements in genetics, particularly the introduction of polymerase chain reactions (Mullis & Faloona, 1987) and Sanger sequencing (Sanger et al., 1977), made the genetic code accessible to researchers, opening up a vast data source to bring to bear on taxonomic problems.

These major innovations have altered the landscape of taxonomic research, in particular, the concept of the genetic barcode that could be used to identify species, which was formalised in 2003 (Hebert et al., 2003; Stoeckle, 2003). The core of this concept relied on the so-called barcode gap where in any given data set there would be a distinct break in the pairwise genetic distance between the intraspecific and interspecific variation that could be used as a threshold in identifying species (Hebert et al., 2003). The concept quickly gained traction, as well as detractors, and moved beyond the initially proposed application of simple species identifications without needing to be an expert in any given taxon, to being used to discover and provide backing for species descriptions (see Dasmahapatra & Mallet, 2006; Mitchell, 2008; Solé-Cava & Wörheide, 2007). Proponents of DNA sequences in taxonomy even suggested moving to a DNA based taxonomic classification system to the exclusion of morphology (Blaxter, 2004; Tautz et al., 2003). However, the concept of a universal barcode gap and related distance-based methods were quickly questioned as being potential artifacts of insufficient sampling (Wiemers & Fiedler, 2007; Will et al., 2005). Debate over how to use DNA barcoding for identification and discovery has been largely ongoing (Desalle & Goldstein, 2019; Krishnamurthy & Francis, 2012), particularly in light of perceived recent abuses (see Ahrens et al., 2021).

However, the debate has not stopped the use of cytochrome oxidase I (*COI*) as the dominant molecular marker in animal taxonomy and barcoding has become a standard procedure for many researchers. Barcoding has found many applications within biological sciences such as linking larval stages to adult phases an area that was reliant on rearing studies (Chen et al. 2013; Bracken-Grissom et al 2012) subsequently this allows for species-level studies of larval phases and communities and detection of potentially invasive species (Almeida et al., 2018; Webb et al., 2006; Valentini et al., 2009); verification of seafood products (Lamendin et al., 2015) and the aquarium trade (Steinke et al., 2009). The rise of metabarcoding of environmental DNA requires comprehensive reference libraries of sequence data for it to be an effective tool (Taberlet et al., 2012). As such *COI* is an important component to overcoming the taxonomic impediment when used with an understanding of its limitations (Desalle & Goldstein, 2019). The integration of genetic methods by the present cohort of taxonomists is just another example of how taxonomy has always sought out all available evidence to better describe and diagnose taxa (Davis, 1978; Valdecasas et al., 2008).

1.2.3. Impact on barnacle systematics

The higher classification and thus the reconstruction of evolutionary history via morphological phylogenetics is especially difficult when dealing with highly divergent groups where homologous structures are difficult to identify (Høeg, 1992). The use of larval and spermatozoan characters went someway to bridging these forms of data gaps seen in adults (Healy & Anderson, 1990; Newman & Ross, 2001). One of the early methods of comparing biochemical data was through comparing allozyme composition through the use of electrophoresis (see Thorpe & Solé-Cava, 1994). Use of allozyme electrophoresis allowed taxonomists to provide a line of evidence that was independent of morphology that could separate closely related groups (Achituv & Mizrahi, 1987; Chan et al., 2016; Dando & Crisp, 1979; Yamaguchi, 1987) and as a result refine morphological distinctions and describe new species (Dando & Southward, 1980) as well as link adults with larval phases (Miller et al., 1989).

Allozymes were displaced as the technology for genetic sequencing and analysis evolved. Early applications of sequence data were to infer evolutionary relationships between groups of high-level taxa (Abele et al., 1992; Spears et al., 1994), allopatric subspecies (Hasegawa et al., 1996) and intraspecific populations (Van Syoc, 1994, 1995). Early use of mitochondrial gene sequences were also utilised to demonstrate patterns of host specificity of symbiotic barnacles showing divergent groups associated with specific hosts (Mokady & Brickner, 2001; Mokady et al., 1999). Since the establishment of cytochrome oxidase I as the so-called DNA barcode of life (Hebert et al., 2003; Stoeckle, 2003) it has become a primary marker used in concert with morphological data to define species concepts (e.g. Brickner et al., 2010; Carrison-Stone et al., 2013; Chan et al., 2007; Chan et al., 2013; Chen et al., 2012; Pitombo & Burton, 2007).

As these methods became more prevalent so did the impact on the existing morphology-driven evolutionary hypotheses and the related classification systems. Much of the barnacle classification was not tied to the proposed phylogenies that were being presented and had largely been put in place in the absence of modern phylogenetic analyses using morphological data. Some of these were inherited from early workers prior to such methods (e.g. Darwin, 1852; Darwin, 1854; Hoek, 1913; Kruger, 1940; Pilsbry, 1907; Pilsbry, 1916), others more recently established utilising an evolutionary taxonomy approach (e.g. Anderson, 1992; Newman & Ross, 1976; Ross & Newman, 1973; Zevina, 1978). Modern phylogenetic analyses using morphological (Glenner et al., 1995; Pitombo, 2004; Young, 1999) and molecular (Linse et al., 2013; Pérez-Losada et al., 2008; Pérez-Losada et al., 2004; Tsang et al., 2015) data were incongruent with these traditional views of how taxa are to be classified.

However, aspects of the traditional classification have been shown to be founded on evolutionary history, just not on the concept of reciprocal monophyly. One example of this was the family Archaeobalanidae Newman and Ross, 1976, from which members of the Balanidae and Pyrgomatidae evolved. In particular, the genus *Armatobalanus* Hoek, 1913 was suggested to have given rise to genera within the Pyrgomatidae based on comparisons of wall structure, hosts (Scleractinia), opercular plate structure and spermatozoan ultrastructure (Healy & Anderson, 1990; Newman & Ross, 1976; Ross & Newman, 1973), and thus explicitly not considered to be monophyletic. Recent phylogenetic analyses have shown that some species of *Armatobalanus* are sister to the Pyrgomatidae (Malay & Michonneau, 2014; Simon-Blecher et al., 2007), thus proving the link with the proposed morphological evolutionary pathway and the perceived incongruence is a matter of classification methodology.

1.3. Barnacle symbiosis

The typical perception of barnacles is that of the rock-dwelling species common across the world's rocky shores. These species are certainly the most frequently encountered and as a result are the subject of most research with a long history of investigation across the various facets of their biology (e.g. Connell, 1961; Crisp & Barnes, 1954; Darwin, 1854; Newman & Ross, 1976; Rittschof et al., 1984; Southward, 1987). However, this perception is a rather limited view, as barnacles have adapted and radiated to fill almost all marine ecosystems and can be found attaching to many different abiotic and biotic substrates.

The most recent tallies put the number of described barnacles (Class Thecostraca) at 1413 extant species (Ahyong et al., 2011) or 2116 including fossil species (Chan et al., 2021). Examining the various families can provide an insight into how many species conform to the stereotype of barnacles being free-living species. A spectrum of life histories is seen with clear groups of free-living and highly specialised obligate symbionts at either end as well as species in between that may be difficult to categorise, particularly if the associations appear to be only facultative or simply epibiotic. In these species, the organisms to which they attach may simply be the nearest hard substrate inside the ecological niche within which they have evolved e.g. mangrove inhabitants, *Poecilasma* species attached to deep water decapods.

Groups such as the infraclasses Ascothoracida (110 species) and Rhizocephala (>250 species) are known to be highly specialised parasites (Høeg et al., 2019; Kolbasov & Petrunina, 2019). The largest group of barnacles, the Thoracicalcarea (~1100 species) contains species that range from free-living to highly specialised symbionts (Chan et al., 2021). Key symbiotic groups among the stalked barnacles include various genera of the Poecilasmatidae: *Octolasmis* (30 species) found attached around the mouthparts and gills of decapod crustaceans (Jeffries et al., 2005); *Oxynaspis* and *Minyaspis* (a total of 23 species), symbionts of antipatharians (Van Syoc & Dekelboum, 2011). Among the sessile barnacles are the families Coronulidae and Chelonibiidae (a total of 26 species), commensals on marine vertebrates; and the family Pyrgomatidae (~80 species), which are inhabitants of corals. Within the Archaeobalaninae are several groups such as *Conopea* (21 species) attached to the skeletal axis of octocorals and antipatharians (Kolbasov et al., 2016). Lastly, the Acastinae (77 species) found embedded in the tissues of sponges and Alcyonaceans (Kolbasov, 1993; Van Syoc et al., 2015). As a rough estimate, approximately half of the known barnacle species could be considered symbiotic, primarily as commensals and parasites, as no obligate mutualistic interactions with eukaryotes have been demonstrated to date.

The underlying hypothesis implicit in the classification of symbiotic barnacles is that the advent of symbiosis with particular host groups evolved once, followed by a subsequent radiation of species. However, only a few of the symbiotic groups of Thoracicalcarea have been subjected to rigorous phylogenetic studies. The Coronuloid families Coronulidae and Chelonibiidae form a monophyletic clade showing that symbiosis with marine reptiles and mammals has a single evolutionary origin (Hayashi et al., 2013). The Pyrgomatidae has also been shown to form a mostly monophyletic clade containing all scleractinian coral symbionts (Malay & Michonneau, 2014; Simon-Blecher et al., 2007; Tsang et al., 2014) once the genus *Wanella* was removed (Chan et al., 2021). However, further revision is required to include the species *Armatobalanus allium* (a scleractinian symbiont with characters typical of free-living balanids) within the Pyrgomatidae, as well as to test the phylogenetic position of the aberrant sponge-inhabiting pyrgomatid genus *Pyrgospongia*. In contrast, the genus *Conopea*, symbiotic with octocorals and antipatharians, was recently split using morphological phylogenetics with several species being transferred to the genus *Acasta* thus demonstrating at least two octocoral colonisation events within the Balanidae (Kolbasov et al., 2016). The recent decision to synonymise the Archaeobalanidae with the Balanidae by Chan et al. (2021) based on the results of previous molecular studies (e.g. Pérez-Losada et al., 2008; Pérez-Losada et al., 2014) has thrown together a diverse assemblage of barnacles from across the spectrum of symbiosis (see Table 1.1 for summary) that now need to come under renewed phylogenetic scrutiny.

Table 1.1. Summary of current classification of the Balanidae following Chan et al. (2021), indicating type species for extant genera and host usage within the genus. Number of species are as of 2017; groups are considered epibiotic if the association appears to be facultative rather than obligate.

Family	**Subfamily**	**Genus**	**Type species**	**# described extant species**	**Host groups**
Balanidae	Acastinae	*Acasta*	*Acasta spongites*	53	Porifera; Cnidaria
Balanidae	Acastinae	*Archiacasta*	*Archiacasta membranacea*	9	Porifera
Balanidae	Acastinae	*Euacasta*	*Euacasta dofleini*	10	Porifera; Cnidaria
Balanidae	Acastinae	*Neoacasta*	*Neoacasta glans*	6	Porifera
Balanidae	Acastinae	*Pectinoacasta*	*Pectinoacasta pectinipes*	6	Porifera; Cnidaria
Balanidae	Amphibalaninae	*Amphibalanus*	*Amphibalanus amphitrite*	15	Free-living; epibiotic
Balanidae	Amphibalaninae	*Fistulobalanus*	*Fistulobalanus pallidus*	9	Free-living; epibiotic; mangroves
Balanidae	Amphibalaninae	*Tetrabalanus*	*Tetrabalanus polygenus*	1	Free-living
Balanidae	Archaeobalaninae	*Armatobalanus*	*Armatobalanus quadrivittatus*	9	Free-living; Porifera; Cnidaria
Balanidae	Archaeobalaninae	*Bathybalanus*	*Bathybalanus pentacrini*	1	Echinodermata
Balanidae	Archaeobalaninae	*Chirona*	*Chirona hameri*	2	Free-living
Balanidae	Archaeobalaninae	*Conopea*	*Conopea galeatus*	20	Cnidaria
Balanidae	Archaeobalaninae	*Hesperibalanus*	*Hesperibalanus hesperius*	2	Free-living; epibiotic
Balanidae	Archaeobalaninae	*Membranobalanus*	*Membranobalanus declivis*	10	Porifera
Balanidae	Archaeobalaninae	*Notobalanus*	*Notobalanus flosculus*	2	Free-living
Balanidae	Archaeobalaninae	*Solidobalanus*	*Solidobalanus auricoma*	17	Free-living; Echinodermata; epibiotic
Balanidae	Archaeobalaninae	*Striatobalanus*	*Striatobalanus amaryllis*	8	Free-living
Balanidae	Balaninae	*Balanus*	*Balanus balanus*	13	Free-living
Balanidae	Bryozobiinae	*Bryozobia*	*Bryozobia synaptos*	2	Porifera
Balanidae	Bryozobiinae	*Eoatria*	*Eoatria goslineri*	3	Porifera
Balanidae	Bryozobiinae	*Microporatria*	*Microporatria loreleyae*	1	Porifera
Balanidae	Bryozobiinae	*Multatria*	*Multatria filigranus*	3	Porifera
Balanidae	Bryozobiinae	*Poratria*	*Poratria williamsi*	2	Porifera
Balanidae	Concavinae	*Arossia*	*Arossia panamensis*	3	Free-living
Balanidae	Concavinae	*Menesiniella*	*Menesiniella aquila*	2	Free-living

Family	Subfamily	Genus	Type species	# described extant species	Host groups
Balanidae	Concavinae	*Paraconcavus*	*Paraconcavus pacificus*	2	Free-living
Balanidae	Concavinae	*Perforatus*	*Perforatus perforatus*	1	Free-living
Balanidae	Hexacreusiinae	*Hexacreusia*	*Hexacreusia durhami*	2	Cnidaria
Balanidae	Hexacreusiinae	*Zulloana*	*Zulloana straeleni*	1	Cnidaria
Balanidae	Megabalaninae	*Austromegabalanus*	*Austromegabalanus psittacus*	6	Free-living
Balanidae	Megabalaninae	*Megabalanus*	*Megabalanus tintinnabulum*	25	Free-living; Cnidaria
Balanidae	Megabalaninae	*Notomegabalanus*	*Notomegabalanus decorus*	5	Free-living; epibiotic
Balanidae	Megabalaninae	*Pseudoacasta*	*Pseudoacasta libera*	1	Porifera?
Balanidae	Semibalaninae	*Semibalanus*	*Semibalanus balanoides*	2	Free-living
Balanidae	Wanellinae	*Wanella*	*Wanella millepora*	1	Cnidaria

1.4. Study group

The Acastinae show a variety of morphological characters that are presumed to have adaptive significance to their symbiotic lifestyles. They are generally thin walled and lacking the parietal tubes seen in some other Balanid subfamilies, in many species there are membranous gaps between the shell plates leaving large “windows” in contact with the sponge host. The function of these are unknown, and may simply reflect the lower structural requirement for the shell wall as they are supported by the host. Nonetheless, there has been speculation that they may facilitate chemical interactions between host and barnacle such as to inhibit an immune response or for the absorption of nutrients (Kolbasov, 1993; Van Syoc & Newman, 2010). Many species have calcareous projections that can be long and spinous and are considered to help anchor species within their host (Kolbasov, 1993; Yu et al., 2020b). In some members of the *Euacasta*, these are hollow and when broken leave perforations in the parietes that lead to the interior of the shell (Darwin, 1854; Nilsson-Cantell, 1921). The limbs are generally similar to other balanid barnacles, however the armament on the fourth cirrus is often comprised of heavy, hooked teeth, presumably to scrape away host tissue to prevent being smothered (Darwin, 1854; Kolbasov, 1993). These characters vary between and among species and have been used as key taxonomic characters when describing species. At one stage they were considered to be helpful characters in defining the subfamily, but as additional species were described from other groups such as *Membranobalanus*, Bryozobiinae (Van Syoc & Newman, 2010), *Armatobalanus* and *Conopea* (Kolbasov et al., 2016) these distinctions began to blur (Broch, 1931; Hiro, 1937; Kolbasov, 1993). The recent revision by Chan et al. (2021) left the phylogenetic position of the Acastinae within the Balanidae unresolved, particularly in relation to other symbiotic groups within the family e.g. *Membranobalanus*, *Armatobalanus*, *Conopea* and the Bryozobiinae.

The general biology of sponge-inhabiting barnacles does not appear to have diverged significantly from free-living species. The posterior cirri are still adapted for filtering the water column for food. Sponge spicules have been identified in only small quantities from the gut and therefore the host is so far not considered to be a primary food source but possibly incidentally from clearing the orifice of encroaching sponge (Tabachnik, 1986 cited in Kolbasov 1993). Detritus was identified as a major component of three species, potentially scraped from the surface of the host (Kolbasov, 1993). Sponge-inhabiting barnacles also follow the general pattern of barnacle reproduction: sperm is directly deposited inside the shell via copulation where the eggs are fertilised. The eggs are retained within the shell and the larval nauplii are expelled once they have hatched. A key consequence of this is that mating between barnacles will only occur between individuals embedded in the same host individual. This is an important factor in establishing assortative mating, the initial step in sympatric speciation (Rice, 1987; Schluter, 2001; Via, 2001).

All barnacles share a unique larval phase, known as the cyprid, which is responsible for selecting a substrate to settle upon and metamorphose. Settlement and metamorphosis of the cyprid larvae of free-living barnacle species has been well studied (see Aldred & Clare, 2009; Gebauer et al., 2020; Liang et al., 2019) particularly within the context of biofouling control (Christie & Dalley, 2018). The antennules of the cyprid larvae are equipped with sensory organs and are responsible for secreting the cement produced within the cement gland (Chan et al., 2014; Nott & Foster, 1969). The gross structure of the antennules are surprisingly uniform across the Cirripedia, regardless of substrate (Dreyer et al., 2020; Yu et al., 2020b). For symbiotic groups such as the coral dwelling Pyrgomatidae the attachment disc on the antennule is spear-shaped and used to pierce host tissues (Liu et al., 2016), compared to the bell-shaped disc of free-living species of balanomorph barnacles (Nott & Foster, 1969). For the most part, the sponge-inhabiting barnacles have an attachment disc described as shoe-shaped, with one known species where it is hook-shaped, but the specific function of these shapes are unknown (Yu et al., 2020b).

Adult sponge-barnacles are not cemented to the host (but see Van Syoc and Newman 2010 for discussion on Bryozobiinae) and the mechanism of larval settlement is poorly understood. The landmark publication by Yu et al. (2020b) demonstrated that *Euacasta dofleini* completely metamorphoses on the surface of the sponge host and will develop calcareous projections from the juvenile shell wall after ~six days and eventually be overgrown by sponge tissues. In contrast, they found that cyprids of *Membranobalanus brachialis* burrow into the host prior to metamorphosis but could not elucidate the burrowing mechanism. This burrowing is reminiscent of that exhibited by the coral-dwelling *Darwiniella angularis* (Liu et al., 2016). Further research in this area is vital for understanding the evolution of symbiotic relationships in barnacles as substrate choice will be driven by larval capability. Once a host has been colonised then further recruitment is likely driven by classic barnacle gregariousness (Clare, 2010; Clare & Matsumura, 2000).

1.4.1. Taxonomic history

Leach (1817) erected the genus *Acasta* for *A. montagui* (=*A. spongites* Poli, 1791) and Darwin (1854) with some hesitancy relegated *Acasta* and its then eight extant species, as a subgenus of *Balanus* Leach, 1817. However, all subsequent workers treated *Acasta* as a full genus when adding new species (Broch, 1916; Hoek, 1913; Krüger, 1911; Pilsbry, 1911, 1912; Pilsbry, 1916; Weltner, 1887). Meanwhile, *Membranobalanus* Hoek, 1913 remained a subgenus until the revision of the Balanomorpha by Newman and Ross (1976). The genus *Pseudoacasta* was established by Nilsson-Cantell (1930) for *P. libera* an enigmatic species that was presumed to have inhabited a sponge, but has not been reported on since. As the number of species assigned to the genus grew, Broch (1931) and Hiro (1937) arranged the species into groups based on armature of the fourth cirri and the details of the opercular plates, respectively. Neither author formalised their divisions into new genera or subgenera, citing difficulties separating the *Acasta* from other genera such as *Conopea*, *Membranobalanus* and *Armatobalanus*, which may also bear similar characters and are found in association with sessile invertebrates including sponges.

Newman and Ross (1976) split the Balanidae Leach, 1817 *sensu* Pilsbry (1916) and placed the Acasta within the newly established Archaeobalanidae along with the other sponge associated groups such as *Membranobalanus* and *Armatobalanus*. In the second half of the 20th century not much changed for the group beyond additional species being named and described (e.g. Kolbasov, 1991, 1992; Ren, 1984; Rosell, 1970; Rosell, 1991) until Kolbasov (1993) revised the group. He elevated *Acasta* to subfamily and divided it into five genera with diagnoses based on a mixture of shell and arthropodal characters. The combination of characters used in the generic diagnoses were often overlapping with the other genera and left some ambiguity about species placement. Synapomorphies are present in *Euacasta* (carinolateral reduced to an extremely narrow strip), *Neoacasta* (six marginal teeth on basis) and *Pectinoacasta* (heavily radial sculpture on the tergum). *Archiacasta* and *Acasta* were largely defined as not having these features, but lacked synapomorphies, to create a consistent character set found in all members. Kolbasov proposed that *Membranobalanus* was sister to this subfamily, but *Pseudoacasta* was not included in the revision, which has now been placed, without explanation, within the Megabalaninae by Chan et al. (2021). Up until 2017, the subfamily included 84 species across five genera: *Acasta* (53 species), *Archiacasta* (9 species), *Euacasta* (10 species), *Neoacasta* (6 species) and *Pectinoacasta* (6 species).

The Bryozobiinae was established by Van Syoc and Newman (2010) to accommodate newly described species as well as some poorly known sponge-associated members of *Armatobalanus*: *Eoatria funiculorum* (Annandale, 1906) *Eoatria quinquevittatus* (Hoek, 1913), *Mulatria filigranus* (Broch, 1916), *M. terebratus* (Darwin, 1854) and *M. perforata* (was *Acasta perforata* Rosell, 1991) based largely on adaptations of the shell wall. Ecologically, the Bryozobiinae were considered distinct in that the adults are still cemented to an underlying substrate beneath a sponge and not wholly embedded like the Acastinae or *Membranobalanus.* Their phylogeny suggested that the Acastinae was a sister clade and that the elaborate shell structures demonstrated that the Bryozobiinae represented a distinct lineage of sponge associated barnacles.

Recently the Archaeobalanidae was synonymised within the Balanidae as successive phylogenetic analyses have shown them to be paraphyletic and in need of taxonomic revisions at all levels below family (Chan et al., 2021; Pérez-Losada et al., 2008; Pérez-Losada et al., 2014). Chan et al. (2021) left all the existing subfamilies intact, and this new classification now needs phylogenetic research to provide a framework for the subfamily and generic-level arrangement. A key by-product of establishing a robust phylogenetic framework will be the ability to test hypotheses around the origins of symbiosis and host-driven adaptive radiations within the superfamily Balanoidea.

1.4.2. Host knowledge

Host usage by the Acastinae is very poorly understood and very few of the known species have hosts identified (Kolbasov, 1993; Van Syoc et al., 2015). Often the host was identified simply as a sponge followed by a descriptor such as the colour or texture (e.g. Broch, 1931; Broch, 1947; Hiro, 1937). As such it has been very difficult to draw any conclusions on the host diversity or specificity of the group. It also presents challenges with regards to identifications and assessments of barnacle biodiversity. Knowledge of host use is a first step in understanding the ecology of the species and can lead to a better understanding of a species ecological niche, distribution, and potential population size. Van Syoc (1988) and Kolbasov (1993) were the first to demonstrate the need to document the hosts used by sponge-inhabiting barnacles. For the smaller groups such as *Membranobalanus* and the Bryozobiinae, host usage is relatively well known with a clear preference for the sponge orders Clionaida and Poecilosclerida, respectively (Van Syoc, 1988; Van Syoc & Newman, 2010). For the much more diverse Acastinae, this is a much more difficult task, but one that recent authors are tackling (Pitriana et al., 2020; Sulistiono et al., 2014; Van Syoc et al., 2015; Van Syoc & Winther, 1999; Wibowo et al., 2011; Yu et al., 2017; Yu et al., 2020a).

While known to predominantly inhabit sponges, 18 species have been documented embedded in the tissues of octocorals and antipatharians (Kolbasov et al., 2016; Van Syoc et al., 2014). The cnidarian dwelling species have resulted in some confusion with the genus *Conopea* which has resulted in species being transferred between them (Kolbasov et al., 2016). The high diversity and multiple host phyla seen in the Acastinae make them an ideal candidate group for species discovery and testing hypotheses on host specificity. The morphologically and ecologically similar Bryozobiinae and *Membranobalanus* are curious outgroups that suggest multiple origins of sponge symbiosis.

1.4.3. Australian fauna

The Acastinae are found world-wide, but only three are found in Atlantic and Mediterranean waters, *Acasta cyathus* (Darwin, 1854), *Acasta spongites* (Poli, 1791) and *Neoacasta scuticosta* (Weltner, 1887), and only one is known from the Eastern Pacific, *Acasta newmani* (Van Syoc & Winther, 1999). The majority of species are found in the tropical Indo-West

Pacific, with the South China Sea region seen as the centre of biodiversity (Kolbasov, 1993). *Membranobalanus* is known from the Indo-West Pacific, as well as species on both coasts of the Americas, but absent from eastern Atlantic waters (Van Syoc, 1988). The Bryozobiinae are only known from the Indo-West Pacific (Van Syoc and Newman 2010).

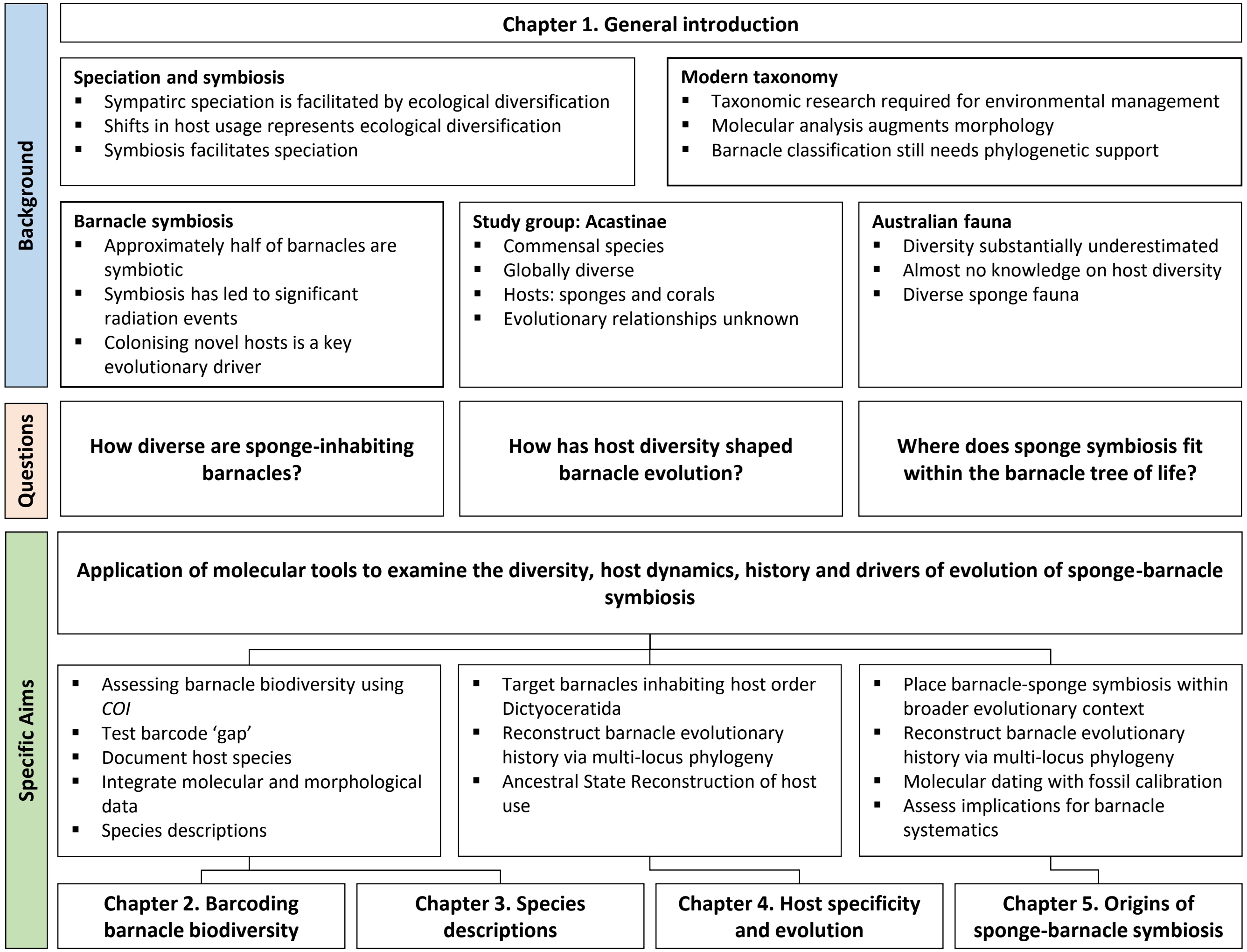
At the commencement of this project (2013) the Australian Acastinae were represented by 20 species, the Bryozobiinae by three species and only a single *Membranobalanus* species (Jones, 2012; Jones et al., 1990), all of which are predominantly distributed in shallow, tropical waters. Only a few publications have included detail on Australian species and very little is known about the hosts used (Jones, 1990a; Jones, 1990b). Most records are included in checklists (Hosie et al., 2015; Jones, 2012; Jones et al., 1990) rather than taxonomic treatments. Although not being treated in depth, the Acastinae were among the first barnacles documented in Australian waters beginning with specimens collected during the Baudin Expedition to Australia 1800–1803 (Lamarck, 1818).

1.5. Project aims

This project aims to explore and answer three key questions with respect to the sponge-inhabiting barnacles in Australia (Figure 1.1). Firstly, how many species are present in Australia? This will be addressed utilising genetic data to assess the alpha-diversity and underpin morphological characterisation to facilitate descriptions of species. As sponge barnacles are confined within a sponge it may be difficult to differentiate diagnostic or informative characters from variation caused by ontogenetic change or differing host morphology. In this context sequence data is an important tool to help demonstrate if the phenotypic characters have a genetic basis and are therefore inheritable and the result of selection rather than plasticity driven by environmental factors. Key goals are to discover undescribed species and determine geographic ranges of species. Species identification will involve molecular and morphological comparisons with published sequences and descriptions. Molecular data, initially *COI*, will be analysed using a range of distance-based and character-based delimitation analyses.

The second aim is identifying trends in host usage across this group of barnacles. This will be explored throughout this thesis and will range from simple metrics of total number of hosts per species to phylogenetic reconstructions investigating evolutionary relationships between barnacles and hosts. By determining host ranges, the relative specialisation between species and the evolutionary connections between groups of species, it will then be possible to assess aspects of the ecological requirements these barnacles have with respect to habitat.

The last question ties the first two together and asks how does the species diversity and host usage reflect on the present taxonomic classification of the group? To answer this, phylogenetic reconstruction of the evolutionary history of sponge barnacles will be integrated into a broader dataset including other groups of free-living and symbiotic barnacles from the superfamily Balanoidea. Through this it may be possible to uncover the origins of sponge symbiosis and re-assess the genus and subfamily relationships and where necessary, recommend an alternative classification that reflects this new data.



Background

Chapter 1. General introduction

Speciation and symbiosis
- Sympatirc speciation is facilitated by ecological diversification
- Shifts in host usage represents ecological diversification
- Symbiosis facilitates speciation

Modern taxonomy
- Taxonomic research required for environmental management
- Molecular analysis augments morphology
- Barnacle classification still needs phylogenetic support

Barnacle symbiosis
- Approximately half of barnacles are symbiotic
- Symbiosis has led to significant radiation events
- Colonising novel hosts is a key evolutionary driver

Study group: Acastinae
- Commensal species
- Globally diverse
- Hosts: sponges and corals
- Evolutionary relationships unknown

Australian fauna
- Diversity substantially underestimated
- Almost no knowledge on host diversity
- Diverse sponge fauna

Questions

How diverse are sponge-inhabiting barnacles?

How has host diversity shaped barnacle evolution?

Where does sponge symbiosis fit within the barnacle tree of life?

Specific Aims

Application of molecular tools to examine the diversity, host dynamics, history and drivers of evolution of sponge-barnacle symbiosis

- Assessing barnacle biodiversity using *COI*
- Test barcode ‘gap’
- Document host species
- Integrate molecular and morphological data
- Species descriptions

- Target barnacles inhabiting host order Dictyoceratida
- Reconstruct barnacle evolutionary history via multi-locus phylogeny
- Ancestral State Reconstruction of host use

- Place barnacle-sponge symbiosis within broader evolutionary context
- Reconstruct barnacle evolutionary history via multi-locus phylogeny
- Molecular dating with fossil calibration
- Assess implications for barnacle systematics

Chapter 2. Barcoding barnacle biodiversity

Chapter 3. Species descriptions

Chapter 4. Host specificity and evolution

Chapter 5. Origins of sponge-barnacle symbiosis

Figure 1.1. Conceptual diagram of thesis structure.

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Chapter 2. Barcoding Barnacle Biodiversity: Assessing Australia's Acastinae and Allies.

Synopsis

Australian waters are home to approximately 300 species of barnacles across all marine environments. While shallow water free-living species may be considered to be well known, the commensal species have only been the subject of cursory examination thus far. In this chapter the biodiversity of sponge-inhabiting barnacles is assessed using cytochrome oxidase I (*COI*), the so-called barcoding gene, as the primary measure of biodiversity from which to assess species boundaries and compare host usage. This will create a framework from which existing morphological concepts can be better defined and facilitate the naming and descriptions of novel species. Specimens were freshly collected from a series of field surveys from Western Australia or sourced from existing collections housed within the Western Australian, Queensland, and South Australian Museums. In total 592 specimens were successfully sequenced and analysed. A series of delimitation analyses were undertaken using Assemble Species by Automatic Partitioning (ASAP) and Poisson Tree Processes (PTP, bPTP and mPTP) to provide an estimate of the species diversity. Species designations were made via a combination of morphological and molecular analysis and comparison with published literature and sequences. An estimate of 115 species were sequenced in this chapter, of which 101 were collected from within Australian waters. Analysis of pairwise distances did not reveal the presence of a clear 'barcode gap' indicating that distance-based methods alone were unable to delimit closely related species. Estimates of novel diversity are uncertain, but potentially 57 species could be considered new to science. Sequenced barnacles were extracted from 179 host morphospecies. Host usage was largely restricted to single host species, with 62% of barnacle species found in a single host.

2.1. Introduction

Possibly the most significant innovation in biodiversity research in the last 50 years has been DNA sequencing for species identification and discovery. The concept of the genetic barcode to identify species was formalised in 2003 (Hebert et al., 2003; Stoeckle, 2003), but debate over its use is still ongoing (Ahrens et al., 2021; Desalle & Goldstein, 2019). Most of the debate is now directed to best practices and limitations rather than the validity of the barcoding concept and DNA based identifications. After almost 20 years, the mitochondrial gene cytochrome oxidase subunit I (*COI* or *COXI*) has remained the most common locus used in molecular taxonomy for animal groups. This dominance has been maintained because of how well *COI* diversity aligned with existing species concepts that were based on morphological data. As technology has advanced, genetic data has become more widely available, and its analysis has become more simplified, due to software becoming more user friendly. As such genetic barcoding, either direct from an organism or via environmental samples, has become a standard procedure for many researchers, particularly in biodiversity related fields such as community ecology and taxonomy, and is an important component to overcoming the taxonomic impediment (Daglio & Dawson, 2019; Desalle & Goldstein, 2019; Padial & De La Riva, 2010; Pires & Marinoni, 2010; Vinarski, 2020).

There are currently 8,991 species of crustaceans listed as present in Australian territories in the Australian Faunal Directory (ABRS, 2021) and it has been estimated that 30% of species are still to be described (Chapman, 2009). The barnacles make up a relatively small component of the total crustacean fauna, currently numbering just over 300 species (subclass Cirripedia). Globally they were considered to be one of the more 'complete' faunal groups by Appeltans et al. (2012) with an estimated 90% of the total number of species known leaving between 100 and 200 species to be named and described. Since this estimate was made 71 species have been described, averaging eight per year up until 2020 (Worms Editorial Board, 2021), indicating that the predicted number of species was an underestimate. Recent publications indicate that key areas for species discovery in barnacles are in the groups found in symbiosis with taxa such as corals, other crustacea and sponges (Chan et al., 2013; Frick et al., 2010; Høeg et al., 2019; Hosie et al., 2021; Jeffries et al., 1982; Kolbasov et al., 2016; Kolbasov & Petrunina, 2019; Ross & Newman, 1973; Van Syoc et al., 2014; Van Syoc & Dekelboum, 2011; Van Syoc et al., 2015; Yu et al., 2017a). The study of symbiotic barnacles in Australian waters has been sporadic, and few publications have been specifically focussed on their diversity (Monroe & Limpus, 1979), but they have instead been documented as part of regional studies (Jones, 2010; Jones, 1990; Krüger, 1914), incidental species descriptions (Achituv & Hosie, 2013; Ross & Pitombo, 2002) or checklists (Hosie et al., 2015; Jones, 2012; Jones et al., 1990).

Sponges in particular are proving to host a very diverse group of barnacles with a complex taxonomic history (Van Syoc et al., 2015). The majority of sponge-inhabiting barnacles belong to the Acastinae Kolbasov, 1993 (family Balanidae Leach, 1817), but approximately 20 members of this group are also found embedded in members of the Alcyonacea and Antipatharia (Kolbasov et al., 2016; Van Syoc et al., 2015). Other groups within the Balanidae also have sponge-inhabiting members, most notably the genus *Membranobalanus* Hoek, 1913 and the Bryozobiinae Van Syoc and Newman, 2010. The latter, while always found in association with sponges, are still attached to an underlying substrate (Van Syoc & Newman, 2010). Australia is known to have a high diversity of marine sponges with significant endemism (Fromont et al., 2016; Hooper et al., 2002), which could potentially harbour a high number of previously unknown symbiotic barnacles.

For this chapter, the aim is two-fold, to provide an estimate of the biodiversity of sponge-inhabiting barnacles in Australian waters and to document the diversity of hosts they inhabit. We utilised DNA barcodes to generate primary species hypotheses, to elucidate the potential number of species present and to assess the level of novel species to be described. These units may then form the basis of species descriptions (Chapter 3) and baseline data for the following chapters testing both host specificity (Chapter 4) and the evolution of sponge symbiosis within the Balanidae (Chapter 5).

2.2. Methods

2.2.1. Specimen collection and examination

Specimens of both the barnacles and the sponges were freshly collected during several diving and dredging expeditions to various regions of Western Australia (WA) including offshore atolls (Rowley Shoals, Ashmore Reef), 2013 and 2014; inshore Kimberley 2009–2016; Montebello Islands, 2015; Dampier Archipelago, 2017; Exmouth Gulf, 2016 and incidental collections around the Perth region during the study period. Additional specimens were sourced from existing collections held by the Western Australian Museum, Perth (WAM), Queensland Museum, Brisbane (QM) and South Australian Museum, Adelaide (SAMA). A complete table of the specimens sequenced in this study is presented in Appendix I at the end of this thesis. Specimens of *Striatobalanus amaryllis* (Darwin, 1854) from near Onslow, WA were selected to serve as an outgroup in the phylogenetic analyses. The use of an outgroup is primarily serving to root the resulting tree, and the free-living *S. amaryllis* is expected to be a near relative of sponge-inhabiting barnacles, but not fall within the same clade. For direct morphological examination of barnacle shell plates and arthropodal characters, the body and associated soft tissues were removed from the shell using forceps. The remnants of the barnacle tissue and host sponge on the surfaces of the parietes, scutum and tergum, were removed using a brush and forceps. The shell was then immersed in 2% bleach for <2 hours to completely digest the organic tissue and was subsequently rinsed in a water bath to remove bleach residue. Any remaining debris or contaminants were then removed by cleaning in a Vevor 2L ultrasonic cleaner for < 5 s. The specimens were examined under a Leica M205 C (Leica, Germany) stereomicroscope and digital photographs produced with a Leica DMC4500. All images were processed using GIMP 2.10 (www.gimp.org) or Inkscape 0.92 (www.inkscape.org). Barnacles were identified to genus using the morphological diagnoses given by Kolbasov (1993) and species level determinations were made where possible using relevant literature (e.g. Broch, 1931; Darwin, 1854; Hiro, 1931, 1937; Nilsson-Cantell, 1921; Yu et al., 2020a; Yu et al., 2017b), and genetically by comparison with previously published DNA sequences (see Appendix II).

Sponge identifications were partly facilitated by examining gross morphology, surface characteristics and microscopic skeletal characteristics of specimens (Figures 2.1 & 2.2). Subsamples of sponge tissue were sectioned at right angles to the surface of the sponge and processed for microscopic examination using a Shandon Elliott tissue processor. This included ethanol dehydration, histolene treatment to clear the tissue and subsequent paraffin impregnation. Thick sections (~90 µm) were cut with a Leitz slide microtome from wax blocks. Sections were de-waxed in histolene and mounted using Shandon EZ-Mountant. Skeletal slides were examined with an Olympus BX50. Spicules were obtained by dissolving sponge tissue in nitric acid or bleach, rinsing in water and ethanol and mounting with Shandon EZ-Mountant on microscope slides.

2.2.2. Molecular sequencing

Adductor or depressor muscle tissues of barnacles were subsampled from specimens, and genomic DNA was extracted using either a Bioline Isolate II or Qiagen DNeasy extraction kit following the manufacturer's instructions. Partial fragments of the cytochrome c oxidase I (*COI*) gene were amplified (using the primers detailed in Table 2.1) in a 25 µL reaction volume and consisting of 2 µL DNA extract, 1 unit MyTaq DNA polymerase, MyTaq PCR buffer and 0.1 µM of each primer. The following polymerase chain reaction (PCR) conditions were used: 2 min at 95 °C for initial denaturing, then 35 cycles of 30 s at 95 °C, 30 s at 46 °C, 45 s at 72 °C, and a final extension for 7 min at 72 °C. The resulting amplicons were sequenced at the Australian Genome Research Facility, Perth, using the same primers via Sanger (cycle) sequencing.

The sequence reads from both directions were assembled and trimmed using Geneious Prime 2020.2.5 (https://www.geneious.com). Quality control of sequences involved trimming low quality bases, inspecting for stop codons, verifying reading frame, checking for matches on BLAST and re-examination of original specimens to detect and remove potentially contaminated sequences. All *COI* sequences identified as belonging to sponge-inhabiting barnacles were downloaded from GenBank (www.ncbi.nlm.nih.gov/genbank; Appendix II). The combined dataset was aligned in Geneious Prime using Clustal Omega (Sievers & Higgins, 2014) on default settings and checked manually.

2.2.3. Biodiversity analyses

Species delimitation analyses were undertaken using the Assemble Species by Automatic Partitioning method (ASAP; https://bioinfo.mnhn.fr/abi/public/asap/#; Puillandre et al., 2020), both the Bayesian and maximum likelihood versions of the Poisson Tree Processes (bPTP and PTP, respectively; https://species.h-its.org/ptp/; Zhang et al., 2013) and multi-rate PTP (MPTP, https://mptp.h-its.org/#/; Kapli et al., 2017) online servers.

The ASAP analysis provides a genetic distance based method to delimit species based on the gene sequence data (Puillandre et al., 2020). The final *COI* alignment was uploaded to the ASAP server and analysed under three substitution models: Jukes-Cantor (JC69) (Jukes & Cantor, 1969), Kimura 2-parameter model (K2P) (Kimura, 1980) and uncorrected p-distance.

The bPTP and PTP was run using default parameters, 500,000 Markov chain Monte Carlo (MCMC) generations, checking that the chain had converged on the likelihood plots. The multi-rate mPTP was run using default parameters with cropped outgroups. These analyses delimit potential species based on the number of mutations determined from branch lengths and require a phylogenetic tree to analyse. A maximum likelihood (ML) phylogenetic tree was generated using the IQ-TREE webserver (Trifinopoulos et al., 2016) under default parameters. Substitution models were automatically assessed by IQ-Tree using ModelFinder (Kalyaanamoorthy et al., 2017) and different partitioning regimes (partitioned by each codon, by third codon or unpartitioned) were tested for best fit. Branch support was calculated by conducting 1000 ultra-fast bootstraps (Minh et al., 2013).

A final primary species hypothesis (PSH) was designated by the following process of checking the level of congruence between delimitation methods and mapping these to the phylogenetic tree. For specimens where all delimitation methods were in agreement, or when there was agreement with at least five methods then they were assigned to the corresponding PSH. In cases where four or fewer methods were in agreement then clades were checked for monophyly on the phylogenetic tree and specimen data checked to support splits e.g. long branches within clades, or where specimens were from the same host. In cases that were still ambiguous, then a more conserved approach was taken, and units were combined. The final PSH is denoted by a sequential number following an identification based on published morphological or genetic data e.g. *Acasta fenestrata* 80.

Genetic distances (number of base differences per site) within and between the putative species proposed by the delimitation analyses were calculated with uncorrected p-distance and Kimura-2-parameter (K2P) models using Taxi2 (Steinke et al., 2005; Vences et al., 2021).

Randomised sample rarefaction curves were calculated to plot species accumulation curves and examine species richness. Calculations were performed using EstimateS (Colwell, 2013) randomised 999 times. Accumulation curves were calculated once using samples defined as being sponge individuals and again defined as each sponge species.

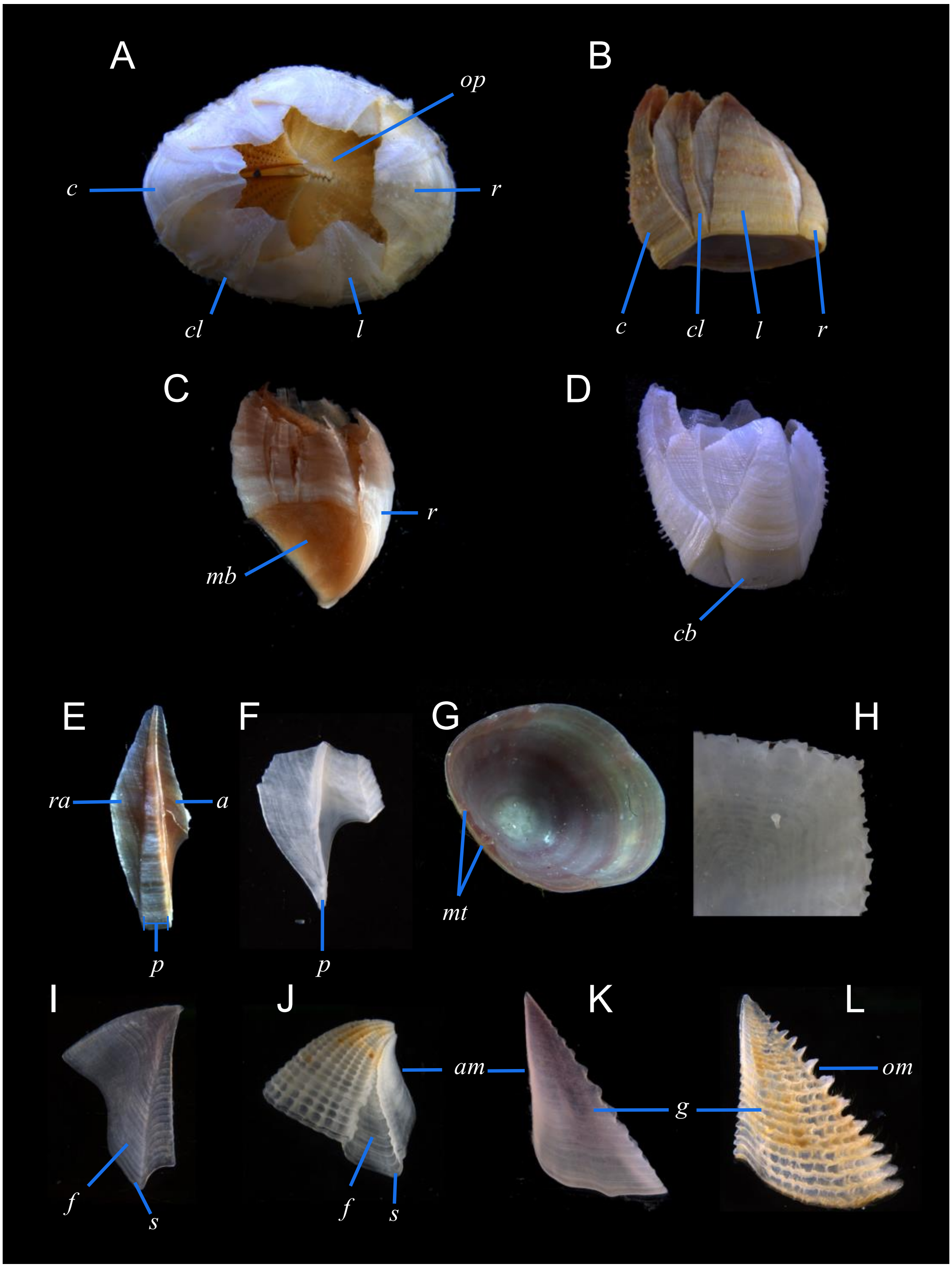

Figure 2.1. Shell morphology of sponge-inhabiting barnacles. **A**, ventral view of *Pectinoacasta sculpturata*; **B–D**, lateral views of *Archiacasta* sp., *Membranobalanus* 60 and *Euacasta excoriatrix* 49, respectively; **E**, **F**, carinolateral plate of *Neoacasta* 23 and *Euacasta excoriatrix* 49, respectively; **G**, cup-shaped basis of *Neoacasta* 23; **H**, crenulated basis rim of *Euacasta acutaflava* 43; **I**, **J**, terga of *Acasta flexuosa* 66 and *Pectinoacasta pecitinipes* 96, respectively; **K**, **L**, scuta of *Acasta flexuosa* 66 and *Archiacasta hainanensis* 20, respectively. *a*, ala; *am*, articular margin; *c*, carina; *cb*, calcareous basis; *cl*, carinolatus; *f*, spur furrow; *g*, growth lines; *l*, latus; *mb*, membranous basis; *mt*, marginal teeth; o*m*, occludent margin; *op*, operculum; *p*, paries (pl. parietes); *r*, rostrum; *ra*, radius; *s*, spur.

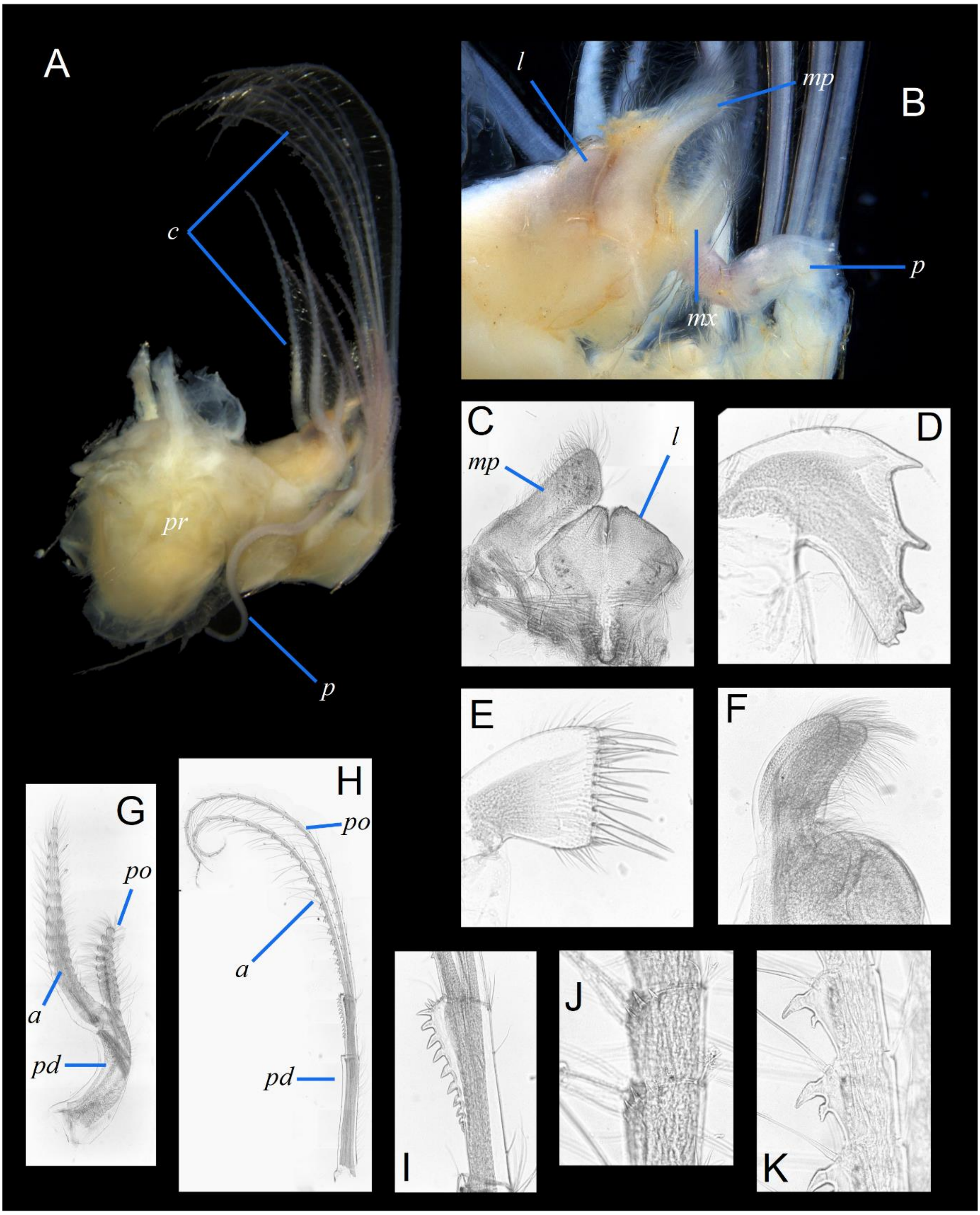

Figure 2.2. Limbs and mouthparts of sponge-inhabiting barnacles. **A**, body extracted from shell; **B**, close up of oral cone; **C**, labrum and mandible palp (right palp removed); **D**, mandible; **E**, maxillule; **F**, maxilla; **G**, cirrus I; **H**, cirrus IV; **I**, basis of cirrus IV protopod; **J**, example of erect spines on anterior ramus of cirrus III; **K**, example of hooked teeth on anterior ramus of cirrus IV. *a*, anterior ramus; *c*, cirrus (pl. cirri); *l*, labrum; *mp*, mandibular palp; *mx*, maxilla; *p*, penis; *pd*, protopod; *po*, posterior ramus; *pr*, prosoma.

Table 2.1. List of forward and reverse primers used in this study.

Primer	Reference
Forward	
LCO1490: 5'-GGTCAACAAATCATAAAGATATTGG-3'	(Folmer et al., 1994)
dgLCO1490 5'-GTCAACAAATCATAAAGAYATYGG-3'	(Meyer, 2003)
COI-F5: 5'-AAACCTATAGCCTTCAAAGCT-3’	(Chan et al., 2013)
COI-N: 5’-TGAGAAATTATTCCGAAGGCTGG-3’	(Van Syoc, 1994)
Reverse	
HC02198: 5'-TAAACTTCAGGGTGACCAAAAAATCA-3'	(Folmer et al., 1994)
dgHCO2198: 5'- TAAACTTCAGGGTGACCAAARAAYCA-3'	(Meyer, 2003)
COI-R4: 5’-GTATCHACRTCYATWCCTACHG-3’	(Chan et al., 2013)

2.3. Results

2.3.1. Specimens, hosts & genetic data acquisition

Over 360 sponge specimens representing over 200 sponge morphospecies were found to host barnacles. Of the almost 1000 extracted barnacles, *COI* was successfully sequenced from 592 specimens. These were combined with 42 sequences downloaded from GenBank (ranging from 336–794 bp) identified as representing 27 taxa. Only data pertaining to the sequenced specimens is considered in the remainder of this chapter.

2.3.2. Molecular results

Results from the delimitation analyses varied greatly, with the highest scoring estimates ranging from 98–178 predicted species. The top ten ranked partitions generated by the three substitution models used in the ASAP delimitation methods ranged from 89–455 putative species (JC90 and p-distance methods both gave 455 species ranked third, which is almost three times greater than the next highest estimate) with distance thresholds ranging between 0.025 and 0.074. The JC90 and p-distance models provided the same partitions and estimates of species in their top two ranked thresholds of 98 and 137. As these results were identical, they are treated as one method (as p-distance) for the remainder of the chapter except where specifically mentioned as separate. The K2P method estimated 137 and 140 at thresholds of 0.020 and 0.021, respectively (Table S2.1). Histograms showing the spread of the pairwise comparisons are given in Figure 2.1 (see also Appendix III). Both the p-distances and K2P methods show that there are three peaks in the pairwise distances at approximately 0–2%, 4–6% and >9%, however no clear break was demonstrated as small numbers of pairwise comparisons were found between these peaks. The thresholds given under the p-distances by ASAP were set on either side of the intermediate peak between 3% and 7%. The tree-based PTP methods estimated 178 (bPTP), 172 (PTP) and 107 (mPTP) species.

The stepwise process of determining a final estimate of species number resulted in 61 species (302 specimens) where all delimitation methods were in agreement, and 42 species (298 specimens) where at least five of the methods agreed. In this latter group it was mostly the least conservative bPTP and PTP methods that were in disagreement and that would routinely split these species hypotheses. The remaining specimens were split into a further nine species based on agreement of only a minority of the delimitation analyses. Not all specimens were easily assigned, such as those in *Euacasta* 89, a grouping that is genetically diverse, and the delimitation analyses estimated up to 20 species were present within this clade (Table S2.1, Figure S2.2). Some of these estimates resulted in polyphyletic groupings within the broader clade and as such *Euacasta* 89 is only supported by the two most conservative methods: p-distances (threshold of 7.1%) and mPTP. For the purposes of this chapter the dataset was divided into a total 115 PSH as an initial estimate of sponge-inhabiting barnacle species (Figure 2.2), accepting that there is a degree of uncertainty in a minority of cases.

The interspecific and intraspecific distances varied among the different PSHs and there is overlap between them (Table 2.2). A total of 29 PSHs had at least one nearest neighbour within the maximum interspecific distances of 0.76 p-distance or 0.81 K2P (Table 2.3). Conversely, the intraspecific distances of 13 PSHs was greater than the minimum intraspecific distances of 0.03 p-distance or 0.03 K2P distances (Table 2.4).

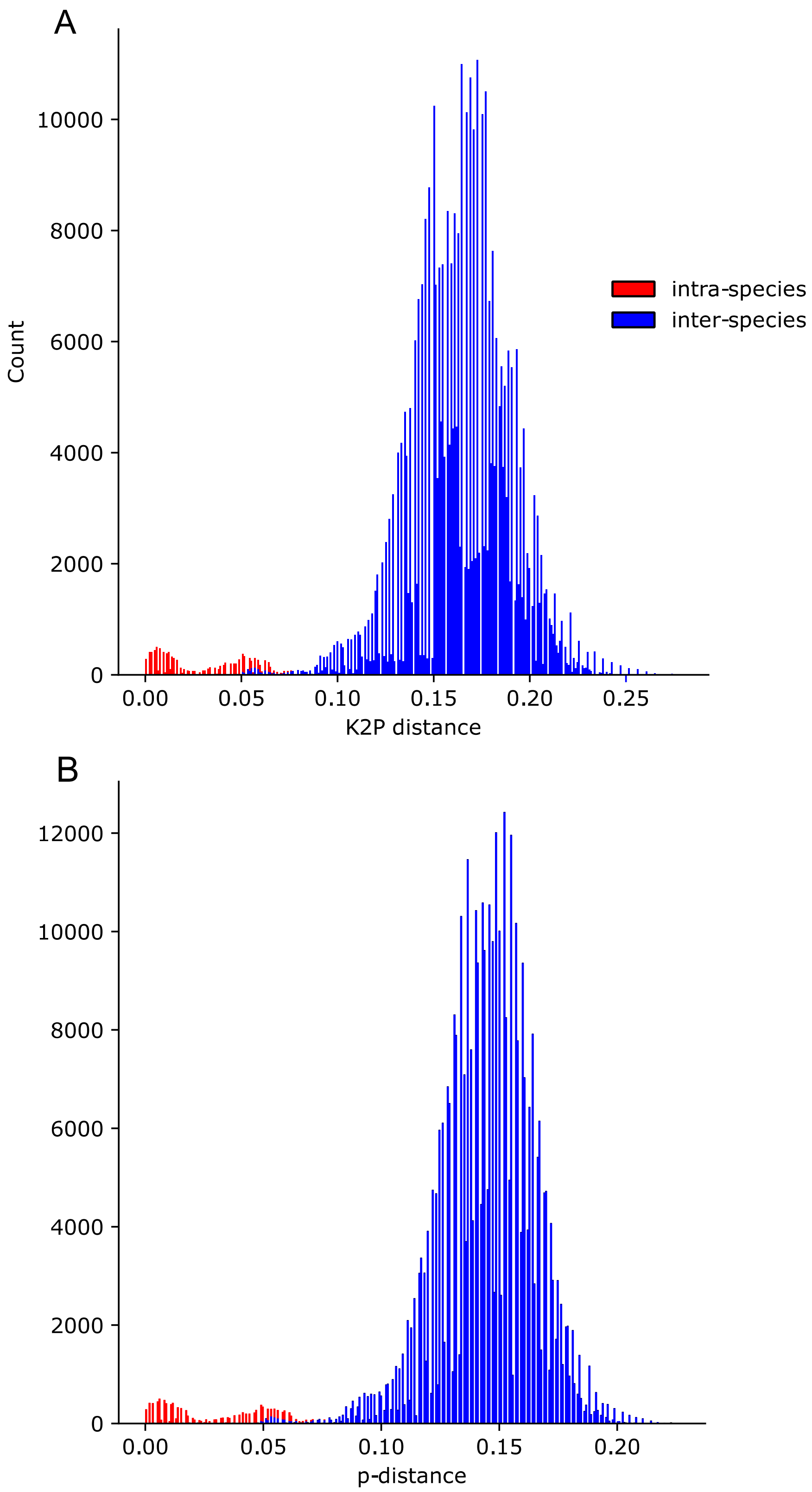

Figure 2.3. Histograms showing the distribution of pairwise distances of the COI dataset calculated using **A**, the Kimura 2-parameter (K2P) model and **B**, uncorrected p-distances. Colours indicate distributions of intra and inter specific distances as determined by the final primary species hypothesis designation.

Table 2.2. Summary statistics of genetic distances of the COI dataset comparing the uncorrected p-distances (p-d) and the Kimura 2-parameter (K2P) models for the complete alignment and separated into interspecific and intraspecific distances.

	Total		**Inter**		**Intra**	
	p-d	**K2P**	**p-d**	**K2P**	**p-d**	**K2P**
Mean	0.142	0.161	0.145	0.165	0.026	0.027
Std. Dev	0.027	0.033	0.02	0.025	0.02	0.021
Min	0	0	0.03	0.03	0	0
Max	0.226	0.279	0.226	0.279	0.076	0.081

Table 2.3. Pairs of species (PSH) with an interspecific genetic distance less than the determined maximum intraspecific distance.

PSH	PSH	p-distance	K2P distance
35	90	0.05927	0.06209
39	94	0.05319	0.05545
51	112	0.05488	0.05729
51	113	0.0562	0.05873
51	114	0.05785	0.06054
51	105	0.06551	0.06899
51	104	0.07438	0.07891
76	77	0.05015	0.05215
78	79	0.0625	0.06565
81	82	0.0506	0.05263
83	111	0.04915	0.05107
83	110	0.06383	0.06712
84	85	0.06612	0.06966
85	107	0.07585	0.08057
92	93	0.05927	0.06209
94	39	0.05319	0.05545
97	99	0.05927	0.06209
97	98	0.06088	0.06387
100	101	0.04711	0.04887
104	105	0.07186	0.07607
105	113	0.05988	0.06276
105	112	0.06358	0.06685
105	114	0.06387	0.06717
110	111	0.05763	0.06029
112	114	0.02975	0.03044
112	113	0.0595	0.06235
113	114	0.06777	0.0715

Table 2.4. Species (PSH) with intraspecific distances greater than the determined minimum interspecific distance.

PSH	K2P	p-d
63	0.05215	0.05015
64	0.04622	0.04464
80	0.05397	0.05183
87	0.04949	0.04769
88	0.04262	0.04128
89	0.08073	0.07599
90	0.03431	0.03343
96	0.03591	0.03495
105	0.04117	0.03992
106	0.06219	0.05936
107	0.0438	0.04239
108	0.0715	0.06777
109	0.03391	0.03306

2.3.3. Barnacle diversity

The 115 PSH were assigned to nine genera, all from the family Balanidae except *Pyrgospongia* Achituv & Simon-Blecher, 2006, which is currently assigned to the Pyrgomatidae Gray, 1825. The remaining eight genera are split between three subfamilies: Acastinae (5), Archaeobalaninae Newman and Ross, 1976 (2) and Bryozobiinae (1). The only genus recovered as monophyletic was the *Pyrgospongia*, the three putative species assigned to this genus were recovered with a clade of *Membranobalanus.* Examples of the barnacle diversity identified in this chapter are illustrated in Figure 2.3.

In this dataset 14 of the proposed species were not found in Australian waters, giving a final estimate of 101 species of sponge-inhabiting barnacles in Australian waters. The species accumulation curves show steep gradients when plotted against both sponge individuals and sponge species (Figure 2.4).

Of the 16 species of sponge-inhabiting barnacles already known in Australian waters prior to this study (pre-2013) only nine are definitely represented in the present data. The paucity of data from type material or localities for the other known species presented difficulties in identifications. The addition of morphologically similar or potentially cryptic species distinguished by the molecular delimitation also makes assigning specimens to known species difficult e.g. PSH 92 & 93 split the species morphologically identified as *Acasta* cf. *conica* Hoek, 1913*.* This pattern is common e.g. *Acasta* cf. *flexuosa* Nilsson-Cantell, 1931 was split into five PSH through the delimitation analyses and found in two different clades (Figure 2.2).

This uncertainty around species identities makes estimating the number of species new to science problematic. There are 10 known species considered to be new records for Australia (although in some cases there are multiple PSHs assigned to what was initially considered the same morphological species) and an estimated 57 putative species that are considered to be undescribed. This leaves 29 species where neither determination could be made.

2.3.4. Host usage

Typically, each barnacle species was found inhabiting only one or two host species with 62% identified from a single host, 22.5% from two hosts and 15.5% from three or more hosts. This corresponded with inhabiting one, two or three families (82%, 10% and 9%) and orders (90%, 4% and 6%). The most host species identified for a single barnacle species was 28 (11 families, 7 orders) for *Euacasta* 89 and the next most diverse, *Euacasta* 27 inhabited 12 sponge species (5 families, 3 orders).

The 179 sponge species identified as hosting barnacles belonged to 15 orders, with the Dictyoceratida, Haplosclerida and Poecilosclerida hosting the most barnacle species with 35, 27 and 17 species, respectively, identified in the current dataset. The families Thorectidae, Clionaidae and Petrosiidae were host to the most barnacle species with 13, 12 and 12 species inhabiting them (Table 2.5). The highest number of barnacle species found in any individual host species was three: *Phyllospongia foliascens* (Pallas, 1766), *Clathria* (*Thalysias*) *reinwardti* Vosmaer, 1880 and *Haliclona* sp.7 (Table S2.2).

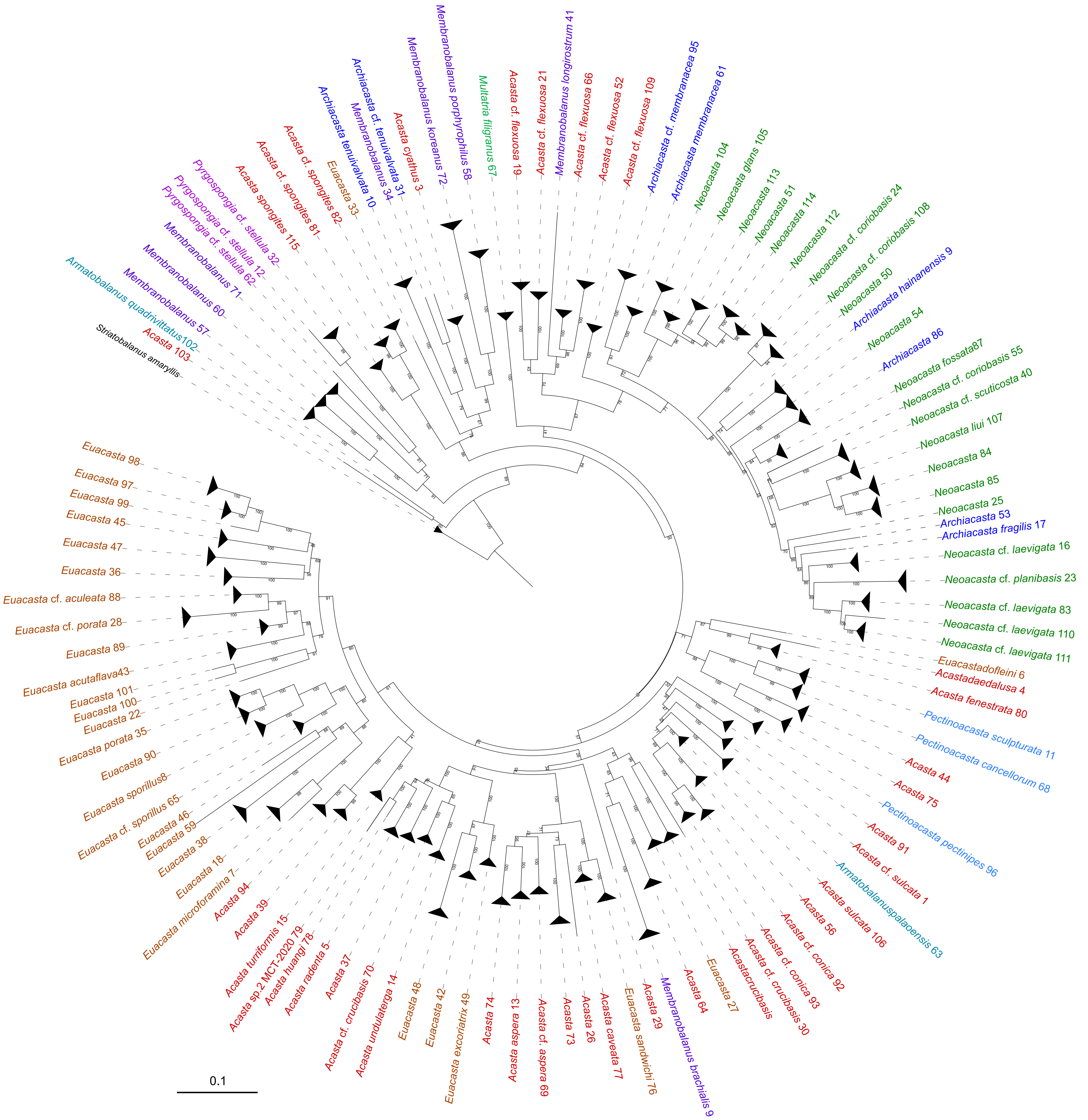

Figure 2.4. Maximum likelihood tree reconstructed from *COI* dataset showing the 115 sponge-inhabiting barnacle primary species hypotheses. Bootstrap support is given at the nodes and PSH clades are collapsed to simplify the tree. See Figure S2.1 for phylogenetic tree with uncollapsed clades. Scale bar indicates substitutions per site.

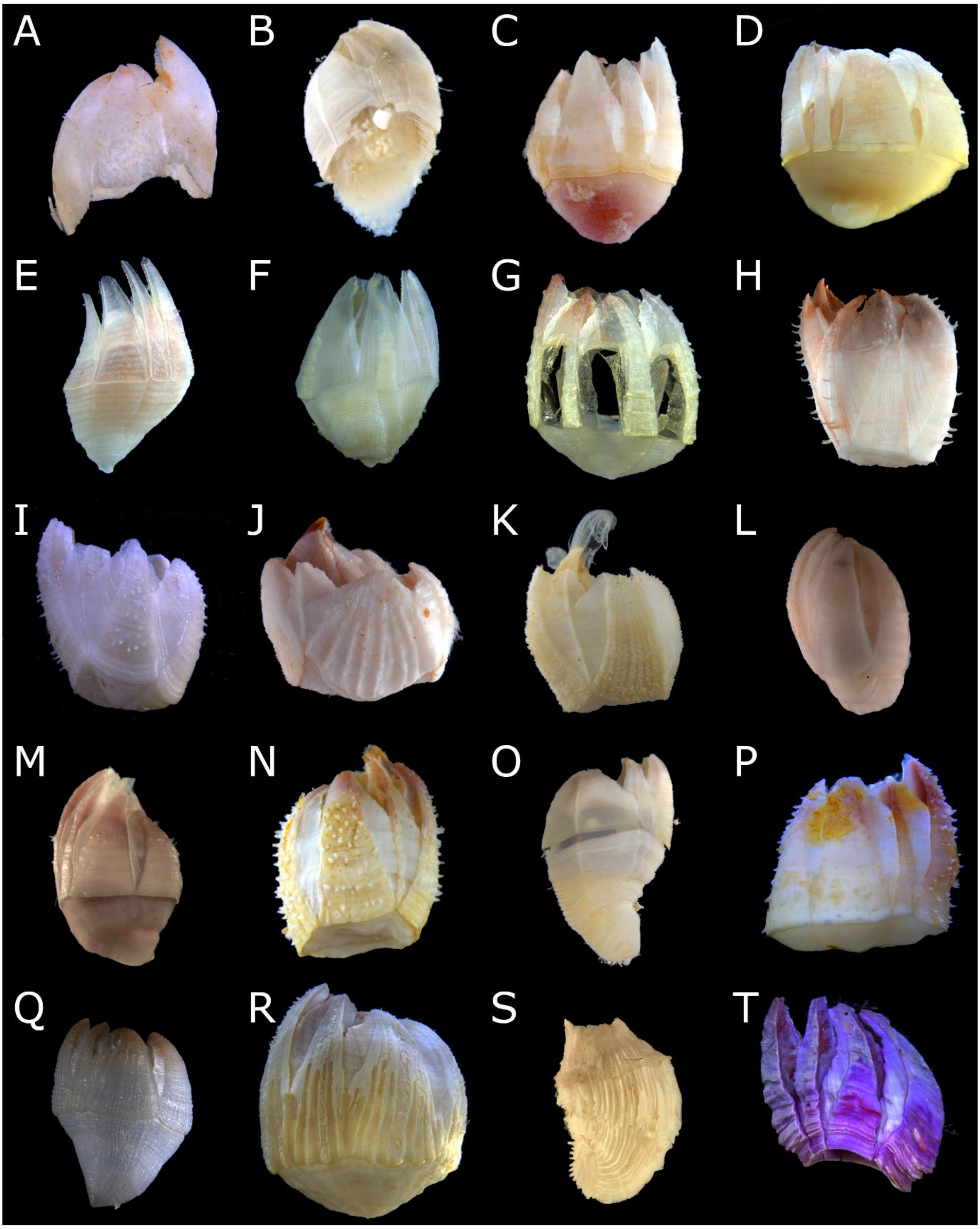

Figure 2.5. Examples of balanoid sponge-inhabiting barnacle species identified in this chapter, in lateral view. Acastinae: **A**, *Archiacasta* 86; **B**, Archiacasta *hainanensis* 20; **C**, *Acasta* cf. *conica* 93; **D**, *Acasta fenestrata* 80; **E**, *Acasta* cf. *flexuosa* 52; **F**, *Acasta* cf. *spongites* 82; **G**, *Acasta caveata* 77; **H**, *Acasta cyathus* 3; **I**, *Euacasta excoriatrix* 49; **J**, *Euacasta acutaflava* 43; **K**, *Euacasta* 89; **L**, *Euacasta* 90; **M**, *Neoacasta* cf. *laevigata* 16; **N**, *Neoacasta* 112; **O**, *Neoacasta* cf. *coriobasis* 24; **P**, *Neoacasta* 50; **Q**, *Pectinoacasta pectinipes* 96; **R**, *Pectinoacasta cancellorum* 68. Bryozobiinae: **S**, *Multatria filigranus* 67. Archaeobalaninae: **T**, *Membranobalanus porphyrophilus* 58.

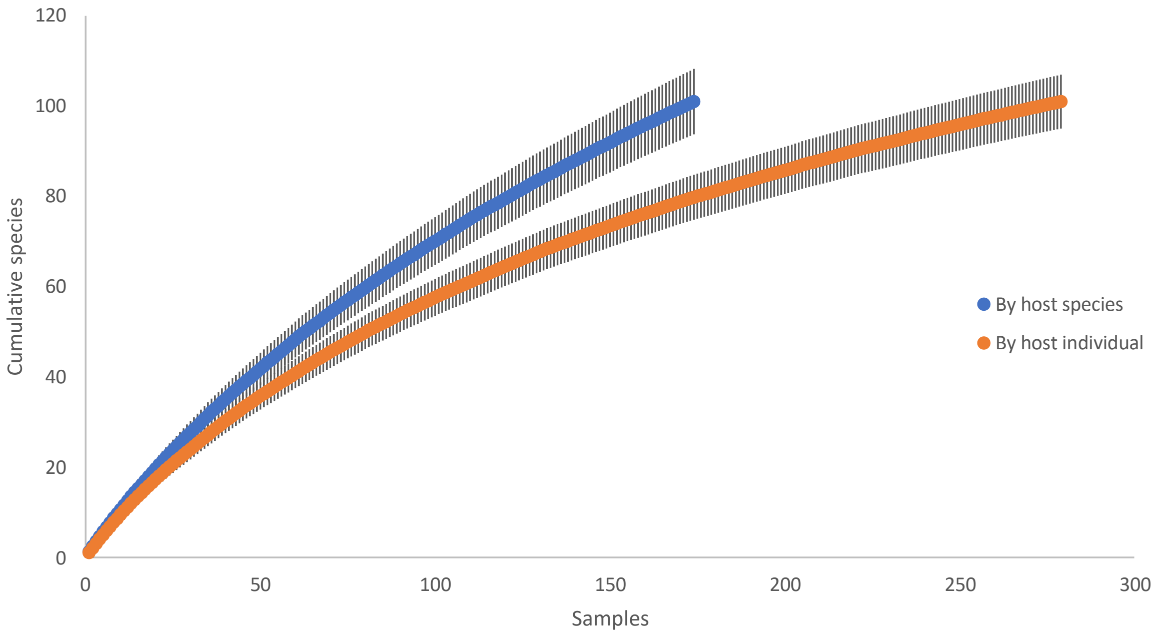

Figure 2.6. Randomised species accumulation curves of mean barnacle species (+/- 1 SD) against number of host species (n=174) or host individuals (n=280) sampled.

Table 2.5. Distribution of barnacle species by genus among host orders of sponge identified.

	Barnacle genera									
Host Order	***Acasta***	***Archiacasta***	***Armatobalanus***	***Euacasta***	***Membranobalanus***	***Multatria***	***Neoacasta***	***Pectinoacasta***	***Pyrgospongia***	**Total**
Agelasida								2		2
Axinellida	2			5						7
Biemnida		1								1
Bubarida				2						2
Clionaida		2		3	8				3	14
Dendroceratida				1						1
Dictyoceratida	7	4		2			22			35
Haplosclerida	18	1		6	1					26
Poecilosclerida	10		2	3		1		1		17
Polymastiida	1			1						2
Scopalinida	1			1						2
Suberitida	1	1		8						10
Tethyida				2			3			3
Tetractinellida	4	1		4			1			9
Verongiida				7						7

2.4. Discussion

2.4.1. Delimitation success

Despite the wide range of estimated species given by the species delimitation methods used in this study, most were congruent with 91% of the designated PSHs supported by five or more of the methods used. However only 55% of the designations were unanimous. All methods have limitations (Dellicour & Flot, 2018; Tang et al., 2014) and while many species will have been accurately delimited, there will be groups that may be further split e.g. *Acasta sulcata* 106, *Euacasta* 89, or lumped e.g. *Neoacasta* cf. *laevigata* 83, *N.* cf. *laevigata* 110 and *N.* cf. *laevigata* 111. The absence of an observable barcode gap in the present dataset left the distance-based methods vulnerable to error. This is caused by groupings of relatively recently diverged specimens, obscuring the needed distinction between interspecific and intraspecific distance to consistently delimit species. The reason distance-based methods can fail is that they only take into account how many mutations there have been, not specifically where these mutations have occurred (Carstens et al., 2013; Meier et al., 2008; Puillandre et al., 2020). In these cases, caution and additional data (e.g. molecular, morphological or ecological) need to be used when making definitive statements around species boundaries or undertaking nomenclatural acts such as establishing or synonymising species.

There are many published comparisons of the performance of the many molecular delimitation analyses that are available, and the general consensus is that using multiple methods is the only way forward (Carstens et al., 2013; Giarla et al., 2014; Larson et al., 2016; Luo et al., 2018; Miralles & Vences, 2013; Puillandre et al., 2020; Puillandre et al., 2012; Zhang et al., 2011). While it is beyond the scope of this chapter to go into a detailed evaluation of the methods used, some explanations and recommendations for future use are warranted. The distance-based ASAP provided a threshold of percentage difference under different substitution models. In all models the histograms showed an intermediate peak in pairwise distances between the peaks that could be more clearly defined as infraspecific and intraspecific. The top two thresholds for p-distance were placed either side of this peak (at ~3 and 7%), which is the reason why they were much more variable than the top two K2P estimates (2% and 2.1%). The apparent stability of K2P may be misleading, as the appropriateness of K2P as the primary model in barcoding studies has been questioned (Collins et al., 2012; Srivathsan & Meier, 2012). The ASAP distance method provided partitions intended to correlate with the biodiversity in question and is not driven by the relationship between characters i.e. mutations/site. As such the authors of that program recommend evaluating the results using independent data sources (morphological, ecological, behavioural, biochemical, etc) before making definitive statements or nomenclatural acts (Puillandre et al., 2020).

Previously, Chen et al. (2013) showed that their *COI* dataset, with broad taxonomic coverage (including stalked and acorn barnacles), a potential barcoding gap lay between 5% and 8 % under the K2P model. There were some exceptional outlying species with large intraspecific values such as *Wanella milleporae* (Darwin, 1854), a species known for having cryptic lineages (Tsang et al., 2009). The current dataset can be distinguished from Chen's (2013) from the fact that a group of closely related species were the primary target, and this is expected to decrease the probability of a functional barcode gap (Meyer & Paulay, 2005; Wiemers & Fiedler, 2007). Further comparison with published studies shows that the thresholds of ~2% (K2P) and 3% (uncorrected p-distance) determined here, are much lower than the minimum interspecific distances that are typically reported for barnacles. In the recent taxonomic literature, K2P and uncorrected distances of 10–20% or more between congeneric species are frequently encountered (Chan et al., 2007; Chen et al., 2012; Pitriana et al., 2020a; Simon-Blecher et al., 2021; Tsang et al., 2012). Although in symbiotic groups uncorrected p-distances of 8% and 4% have been reported (Carrison-Stone et al., 2013; Chan et al., 2017) and thus the potential thresholds calculated for delimiting the sponge-inhabiting barnacle species are not unprecedented and have a potential use in comparing datasets of a smaller scale.

The three PTP methods are based on substitution rates (mutations per site) as inferred from the phylogenetic tree used as the input file. The proposed outputs are therefore character based and consistent with the phylogenetic species concept (Kapli et al., 2017; Zhang et al., 2013) as opposed to the phenetic distance-based methods. The PTP and bPTP methods were the least conservative methods when estimating species richness and, after comparing with the other methods used in this chapter, were deemed to have over-split the dataset dramatically, proposing around 40 species more than the next highest estimate. The potential for these methods to seemingly over-split datasets has already been noted in a few publications (Blair & Bryson Jr, 2017; Dellicour & Flot, 2018). In part this was the reason for the development of mPTP to overcome some of the original methods' limitations by using the Akaike Information Criterion rather than a p-value test to decide the number of species based on the given data (Kapli et al., 2017).

Single-loci delimitation is not perfect, and it may not be possible for a single method to be 100% accurate (Carstens et al., 2013; Dellicour & Flot, 2018). The conclusion from this chapter would be that the bPTP and PTP methods for species level delimitation are unreliable. The mPTP provided a more conservative estimate and using this in conjunction with the distance-based ASAP method helped provide some confidence to the consensus-based framework of species put forward in this work. With the congruence-based approach using different delimitation methods there was a resulting overlap in interspecific and intraspecific distances. For future research involving *COI* barcoding, groups of species with distances ranging from 3–8% should be treated with some caution and should be corroborated with additional data (morphological, ecological, geographic etc) prior to undertaking any nomenclatural acts.

2.4.2. Barnacle diversity

The delimitation analyses revealed a diverse array of sponge-inhabiting barnacles, with even the most conservative estimates of 84 and 93 species being over five times the currently known diversity in Australian waters (16 species). Given that the vast majority of specimens are from northern WA (Appendix II), it would be expected that this number will be even higher once more comprehensive work on the eastern and southern coasts is undertaken. This is corroborated by the steep gradients seen in the species accumulation curves, indicating that additional species will be found as additional host species and individuals are surveyed. Should the estimate of 101 species be accurate, then it represents an increase in Australia's barnacle fauna of ~33%, with sponge inhabiting barnacles accounting for a quarter of all known species. Presently, the Pyrgomatidae, associated with corals, is the most speciose group of symbiotic barnacles with 23 described species reported in Australia (ABRS, 2021; Jones, 2012) and 95 species globally, being second place to the parasitic Rhizocephala with 290 (Worms Editorial Board, 2021). Van Syoc et al. (2015) estimated an additional 83 species of sponge inhabiting barnacles across the Indo-West Pacific in their study based on morphological data collated from various museum collection. Although direct comparison with the results in this chapter is not possible, their estimate appears to be corroborated by the molecular data reported here, suggesting that the Acastinae will overtake the Pyrgomatidae in terms of total number of species. The results also indicate that the estimate by Appeltans et al. (2012) of the numbers of barnacle species still to be described needs to be reassessed.

The estimated 57 undescribed species is substantial and raises the expectation of even more species waiting to be discovered in other geographic jurisdictions and host groups. Of particular note are the genera *Euacasta* and *Neoacasta* where the number of species reported here (29 and 22 species, respectively) are around three times more than the number of known species.

Reconstructing a robust phylogeny was not the aim for this chapter, and the polyphyletic genera and low support values were expected with the methods used here. The degree of intermixing of species from different genera suggests that elements of the present classification need revision, and not just the individual species. The need for revising the classification has already been noted as there is a degree of overlap in the purportedly diagnostic characters of the genera present in the dataset (Van Syoc & Winther, 1999). This is a potential source of confusion for the generic identity of species assigned to *Membranobalanus* and *Archiacasta* Kolbasov, 1993 as members of both genera may have a membranous basis. The putative species identified in this chapter will form the base units for testing evolutionary hypotheses in the following chapters.

Prior to this study, there were five species of sponge-inhabiting barnacle that had been first discovered and described in Australia waters: *Acasta sulcata* Lamarck, 1818 (Shark Bay, Western Australia), *Euacasta antipathidis* (Broch, 1916; near Broome, Western Australia), *E. zuiho* (Hiro, 1936; Arafura Sea, near the Northern Territory), *Neoacasta glans* (Lamarck, 1818; from King Island, Bass Strait), *Membranobalanus cuneiformis* (Hiro, 1936; Arafura Sea, near the Northern Territory) and *Multatria filigranus* (Broch, 1916; near Broome, Western Australia). Based on the morphological identifications, *E. antipathidis*, *E. zuiho* and *M. cuneiformis* have not been collected or sequenced during this study, but the sequenced *M. filigranus* specimens have been compared with the type specimens and are herein confidently assigned to this species. The specimens identified as *A. sulcata* and *N. glans* in this chapter are based on previous published sequences and associated morphology (Yu et al., 2017b; Yu et al., 2020c). Both of these species present complexes of species that have been reported across the Indo-West Pacific (e.g. Darwin, 1854; Hoek, 1913; Kolbasov, 1993; Ren, 1984; Yu et al., 2017b; Yu et al., 2020c). The key issue is that Lamarck, (1818) did not provide illustrations and the descriptions are very brief. Thus, the basis of many records are based on Darwin's (1854) accounts where he provided a detailed comparative account accompanied with some figures. However, Darwin described different varieties of both species, which are likely to be distinct species in light of the genetic results of this chapter. For specimens identified as *A. sulcata* 106, these most probably represent the smoother shelled var. b (see Yu et al., 2017b) and not the ribbed var. a that Darwin (1854, p.312) states is the same as that described by Lamarck (1818). Both species will likely require dedicated collecting around the reported type localities and other reported locations to compare across the published distribution to disentangle the taxonomic record.

2.4.3. Host diversity

The class Demospongiae is well known to be the main host for barnacles, with only a small number of records from the classes Calcarea or Hexactinellida (Kolbasov, 1993). An unknown species of barnacle was extracted from a member of the Calcarea, but sequencing was unsuccessful, and no symbiotic species were found on any hexactinellids during this study. Within the Demospongiae, barnacles were found in 46 families representing 15 of the 20 orders found in Australian waters demonstrating the ubiquitous nature of sponge-inhabiting barnacles.

The broad range of host use is not a function of the barnacle species being generalists. Overall, host usage per barnacle species is relatively restricted with most barnacles found inhabiting a small number of congeneric or confamilial hosts (Table S2.2). Future research should focus on examining the remaining host orders and families as it can be expected that more species will be discovered. There are also indications of niche conservatism across the tree, where closely related barnacle species inhabit closely related, but discrete, host sets. As an example, the sponges *Ianthella basta* (Pallas, 1766)*, I. reticulata* Bergquist & Kelly-Borges, 1995 and *I. flabelliformis* (Linnaeus, 1759) each host a separate barnacle species, which form a well-supported clade (*Euacasta* 97–99). At higher classifications barnacles inhabiting orders such as the Dictyoceratida appear to be forming loose clades (Figure 2.2, Table S2.2) and this will be investigated in Chapter 4.

From the dataset, it would appear that generalist species are relatively rare. Some examples include *Acasta aspera* Yu at al. 2017 which is documented to inhabit four families from the order Poecilosclerida with little evidence of genetic structuring within the clade. *Euacasta* 89 was found to occupy seven host orders, although genetic structuring within this clade is indicative of assortative mating that could lead to divergence. If this is correlated with, or possibly driven by, host usage then it is likely that with further study this PSH will be split further.

The current knowledge on host usage is poor and few trends have so far been elucidated, but the *Membranobalanus* have been considered to be specialists on sponges of the order Clionaida (Hosie et al., 2019; Van Syoc, 1988; Van Syoc et al., 2015). However, this is beginning to be challenged with specimens identified from the Suberitida and *Agelas*ida (Pitriana et al., 2020b; Wibowo et al., 2011). In this chapter specimens have also been found inhabiting the order Haplosclerida. More data is required to investigate whether *Membranobalanus* inhabits a more diverse range of hosts or if this is an artefact of the potential for morphological confusion with *Archiacasta* mentioned previously.

2.5. Conclusions

Despite that there was no observable barcode gap the utility of *COI* for assessing the diversity of sponge-inhabiting barnacles is here demonstrated, although it does have limitations. Strict reliance on threshold methods may misidentify closely related, or recently diverged, species of barnacles. The use of an interspecific threshold >7% divergence (p-distance) when comparing sequences will limit scenarios where specimens are incorrectly assigned to the same species. Likewise, an intraspecific threshold <3% will limit the risk of conspecific individuals being incorrectly assigned to multiple species. For specimens that fall between these, then judgements still need to be made through additional analytical methods such as mPTP, and data from other sources (e.g. from other molecular markers, morphology, ecology and geography) will be required to assess these more closely related groups.

The sponge-inhabiting fauna of Australia is clearly much more diverse than previously reported. The number of species delimited in this study is considered an estimate that requires further analysis utilising additional data e.g. nuclear loci, morphological, geographical and ecological data prior to describing new species. However, it is clear that the sponge-inhabiting barnacle fauna in Australia is seriously understudied and that sponges are the single biggest source of habitat for barnacles, even with the most conservative estimates of species.

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2.7. Chapter 2 Supplementary material

Table S2.1. Results of species delimitation analyses based on COI dataset, sorted by primary species hypothesis. Numbers represent species designation by each individual method: 1st and 2nd ranked partitions using p-distance (p-d 1st, p-d 2nd) and the Kimura 2-parameter model (K2P 1st, K2P 2nd), and the three implementations of the Poisson Tree Processes (bPTP, PTP and mPTP). Congruence indicates the number of methods that were in agreement with the final PSH: unanimous = all, majority = >5, conservative = <5. NB: WAMC55372 and WAMC55374 are the outgroup (OG) and were excluded from the PTP analyses but were included in the ASAP analyses.

SequenceID	**PSH**	**p-d 1st**	**p-d 2nd**	**K2P 1st**	**K2P 2nd**	**bPTP**	**PTP**	**mPTP**	**Congruence**
MN842020	1	2	2	2	2	4	4	1	Unanimous
WAMC55271	1	2	2	2	2	4	4	1	Unanimous
WAMC55393	1	2	2	2	2	4	4	1	Unanimous
WAMC55394	1	2	2	2	2	4	4	1	Unanimous
WAMC55396	1	2	2	2	2	4	4	1	Unanimous
WAMC58559	1	2	2	2	2	4	4	1	Unanimous
WAMC66714	1	2	2	2	2	4	4	1	Unanimous
MF796673	2	3	3	3	3	36	39	9	Unanimous
MF796674	2	3	3	3	3	36	39	9	Unanimous
MN842021	2	3	3	3	3	36	39	9	Unanimous
MN842022	3	4	4	4	4	8	7	92	Unanimous
WAMC46029	3	4	4	4	4	8	7	92	Unanimous
WAMC46073	3	4	4	4	4	8	7	92	Unanimous
WAMC46101	3	4	4	4	4	8	7	92	Unanimous
WAMC55298	3	4	4	4	4	8	7	92	Unanimous
WAMC55299	3	4	4	4	4	8	7	92	Unanimous
WAMC58878	3	4	4	4	4	8	7	92	Unanimous
WAMC61366	3	4	4	4	4	8	7	92	Unanimous
WAMC66644	3	4	4	4	4	8	7	92	Unanimous
WAMC67696	3	4	4	4	4	8	7	92	Unanimous

SequenceID	PSH	p-d 1st	p-d 2nd	K2P 1st	K2P 2nd	bPTP	PTP	mPTP	Congruence
WAMC67723	3	4	4	4	4	8	7	92	Unanimous
WAMC74374	3	4	4	4	4	8	7	92	Unanimous
MN842023	4	5	5	5	5	20	21	53	Unanimous
KY581619	5	6	6	6	6	70	74	14	Unanimous
MN842024	5	6	6	6	6	70	74	14	Unanimous
MN842036	6	13	13	13	14	15	15	56	Unanimous
MN842037	7	14	14	14	15	60	64	30	Unanimous
MN842038	8	15	15	15	16	68	71	34	Unanimous
WAMC58291	8	15	15	15	16	68	71	34	Unanimous
WAMC61392	8	15	15	15	16	68	71	34	Unanimous
WAMC61393	8	15	15	15	16	68	71	34	Unanimous
WAMC61415	8	15	15	15	16	68	71	34	Unanimous
WAMC61416	8	15	15	15	16	68	71	34	Unanimous
WAMC71763	8	15	15	15	16	68	71	34	Unanimous
WAMC71764	8	15	15	15	16	68	71	34	Unanimous
WAMC71765	8	15	15	15	16	68	71	34	Unanimous
WAMC71802	8	15	15	15	16	68	71	34	Unanimous
WAMC71803	8	15	15	15	16	68	71	34	Unanimous
MN842040	9	16	16	16	17	16	16	12	Unanimous
WAMC71847	9	16	16	16	17	16	16	12	Unanimous
WAMC71848	9	16	16	16	17	16	16	12	Unanimous
WAMC71861	9	16	16	16	17	16	16	12	Unanimous
WAMC71930	9	16	16	16	17	16	16	12	Unanimous
KC138493	10	17	17	17	18	14	14	95	Unanimous
MN842041	10	17	17	17	18	14	14	95	Unanimous
WAMC48735	10	17	17	17	18	14	14	95	Unanimous
WAMC48914	10	17	17	17	18	14	14	95	Unanimous
WAMC55408	10	17	17	17	18	14	14	95	Unanimous

SequenceID	PSH	p-d 1st	p-d 2nd	K2P 1st	K2P 2nd	bPTP	PTP	mPTP	Congruence
WAMC61381	10	17	17	17	18	14	14	95	Unanimous
WAMC61382	10	17	17	17	18	14	14	95	Unanimous
WAMC61383	10	17	17	17	18	14	14	95	Unanimous
WAMC61384	10	17	17	17	18	14	14	95	Unanimous
WAMC61385	10	17	17	17	18	14	14	95	Unanimous
WAMC61399	10	17	17	17	18	14	14	95	Unanimous
WAMC61400	10	17	17	17	18	14	14	95	Unanimous
WAMC61401	10	17	17	17	18	14	14	95	Unanimous
WAMC67773	10	17	17	17	18	14	14	95	Unanimous
MN842042	11	18	18	18	19	65	69	57	Unanimous
WAMC61394	11	18	18	18	19	65	69	57	Unanimous
WAMC61395	11	18	18	18	19	65	69	57	Unanimous
WAMC61396	11	18	18	18	19	65	69	57	Unanimous
MN842043	12	19	19	19	20	62	66	101	Unanimous
KY581614	13	20	21	21	22	58	62	24	Unanimous
KY581615	13	20	21	21	22	58	62	24	Unanimous
KY581616	13	20	21	21	22	58	62	24	Unanimous
WAMC55057	13	20	21	21	22	58	62	24	Unanimous
WAMC58741	13	20	21	21	22	58	62	24	Unanimous
WAMC58742	13	20	21	21	22	58	62	24	Unanimous
WAMC58743	13	20	21	21	22	58	62	24	Unanimous
WAMC58812	13	20	21	21	22	58	62	24	Unanimous
WAMC58813	13	20	21	21	22	58	62	24	Unanimous
WAMC58815	13	20	21	21	22	58	62	24	Unanimous
WAMC58835	13	20	21	21	22	58	62	24	Unanimous
WAMC58837	13	20	21	21	22	58	62	24	Unanimous
WAMC58838	13	20	21	21	22	58	62	24	Unanimous
WAMC71837	13	20	21	21	22	58	62	24	Unanimous

SequenceID	PSH	p-d 1st	p-d 2nd	K2P 1st	K2P 2nd	bPTP	PTP	mPTP	Congruence
WAMC71838	13	20	21	21	22	58	62	24	Unanimous
KY581620	14	24	27	26	28	64	68	17	Unanimous
KY581622	14	24	27	26	28	64	68	17	Unanimous
MF796671	15	27	31	30	32	19	20	50	Unanimous
MF796672	15	27	31	30	32	19	20	50	Unanimous
WAMC55286	16	29	33	32	34	30	33	74	Unanimous
WAMC58344	16	29	33	32	34	30	33	74	Unanimous
WAMC58797	16	29	33	32	34	30	33	74	Unanimous
WAMC58798	16	29	33	32	34	30	33	74	Unanimous
WAMC58799	16	29	33	32	34	30	33	74	Unanimous
WAMC58800	16	29	33	32	34	30	33	74	Unanimous
WAMC58801	16	29	33	32	34	30	33	74	Unanimous
WAMC58886	16	29	33	32	34	30	33	74	Unanimous
WAMC58887	16	29	33	32	34	30	33	74	Unanimous
WAMC58888	16	29	33	32	34	30	33	74	Unanimous
WAMC58889	16	29	33	32	34	30	33	74	Unanimous
WAMC61433	16	29	33	32	34	30	33	74	Unanimous
WAMC61500	16	29	33	32	34	30	33	74	Unanimous
WAMC61501	16	29	33	32	34	30	33	74	Unanimous
WAMC61502	16	29	33	32	34	30	33	74	Unanimous
WAMC61517	16	29	33	32	34	30	33	74	Unanimous
WAMC71746	16	29	33	32	34	30	33	74	Unanimous
WAMC71747	16	29	33	32	34	30	33	74	Unanimous
WAMC71748	16	29	33	32	34	30	33	74	Unanimous
WAMC71749	16	29	33	32	34	30	33	74	Unanimous
WAMC71750	16	29	33	32	34	30	33	74	Unanimous
WAMC71756	16	29	33	32	34	30	33	74	Unanimous
WAMC71935	16	29	33	32	34	30	33	74	Unanimous

SequenceID	PSH	p-d 1st	p-d 2nd	K2P 1st	K2P 2nd	bPTP	PTP	mPTP	Congruence
WAMC74449	16	29	33	32	34	30	33	74	Unanimous
WAMC67686	17	30	112	110	112	31	34	75	Unanimous
WAMC55406	18	31	35	33	35	61	65	31	Unanimous
WAMC55407	18	31	35	33	35	61	65	31	Unanimous
WAMC58803	18	31	35	33	35	61	65	31	Unanimous
WAMC58855	18	31	35	33	35	61	65	31	Unanimous
WAMC61351	18	31	35	33	35	61	65	31	Unanimous
WAMC61352	18	31	35	33	35	61	65	31	Unanimous
WAMC61367	18	31	35	33	35	61	65	31	Unanimous
WAMC71760	18	31	35	33	35	61	65	31	Unanimous
WAMC71815	18	31	35	33	35	61	65	31	Unanimous
WAMC71816	18	31	35	33	35	61	65	31	Unanimous
WAMC71933	18	31	35	33	35	61	65	31	Unanimous
WAMC71936	18	31	35	33	35	61	65	31	Unanimous
WAMC72907	18	31	35	33	35	61	65	31	Unanimous
WAMC55358	19	33	38	36	38	50	54	89	Unanimous
WAMC61421	19	33	38	36	38	50	54	89	Unanimous
WAMC61422	19	33	38	36	38	50	54	89	Unanimous
WAMC61423	19	33	38	36	38	50	54	89	Unanimous
WAMC58850	20	34	39	37	39	33	36	81	Unanimous
WAMC61496	20	34	39	37	39	33	36	81	Unanimous
WAMC61522	20	34	39	37	39	33	36	81	Unanimous
WAMC61523	20	34	39	37	39	33	36	81	Unanimous
WAMC61497	21	35	40	38	40	53	57	90	Unanimous
WAMC61498	21	35	40	38	40	53	57	90	Unanimous
WAMC61499	21	35	40	38	40	53	57	90	Unanimous
WAMC61527	22	37	43	41	43	45	49	39	Unanimous
WAMC61513	23	39	46	43	45	29	32	73	Unanimous

SequenceID	PSH	p-d 1st	p-d 2nd	K2P 1st	K2P 2nd	bPTP	PTP	mPTP	Congruence
WAMC61534	23	39	46	43	45	29	32	73	Unanimous
WAMC61535	23	39	46	43	45	29	32	73	Unanimous
WAMC67635	23	39	46	43	45	29	32	73	Unanimous
WAMC67643	23	39	46	43	45	29	32	73	Unanimous
WAMC67644	23	39	46	43	45	29	32	73	Unanimous
WAMC67673	24	40	48	45	47	77	81	83	Unanimous
WAMC67675	24	40	48	45	47	77	81	83	Unanimous
WAMC67679	24	40	48	45	47	77	81	83	Unanimous
WAMC67692	24	40	48	45	47	77	81	83	Unanimous
WAMC67693	24	40	48	45	47	77	81	83	Unanimous
WAMC67694	24	40	48	45	47	77	81	83	Unanimous
WAMC71751	24	40	48	45	47	77	81	83	Unanimous
WAMC72922	25	41	51	48	50	48	52	77	Unanimous
SAMAC8689	26	44	54	51	53	18	18	27	Unanimous
WAMC55051	27	45	55	52	54	17	17	13	Unanimous
WAMC55054	27	45	55	52	54	17	17	13	Unanimous
WAMC55055	27	45	55	52	54	17	17	13	Unanimous
WAMC55058	27	45	55	52	54	17	17	13	Unanimous
WAMC58241	27	45	55	52	54	17	17	13	Unanimous
WAMC58839	27	45	55	52	54	17	17	13	Unanimous
WAMC58841	27	45	55	52	54	17	17	13	Unanimous
WAMC58842	27	45	55	52	54	17	17	13	Unanimous
WAMC58843	27	45	55	52	54	17	17	13	Unanimous
WAMC58856	27	45	55	52	54	17	17	13	Unanimous
WAMC58858	27	45	55	52	54	17	17	13	Unanimous
WAMC61386	27	45	55	52	54	17	17	13	Unanimous
WAMC61387	27	45	55	52	54	17	17	13	Unanimous
WAMC61410	27	45	55	52	54	17	17	13	Unanimous

SequenceID	PSH	p-d 1st	p-d 2nd	K2P 1st	K2P 2nd	bPTP	PTP	mPTP	Congruence
WAMC61411	27	45	55	52	54	17	17	13	Unanimous
WAMC61412	27	45	55	52	54	17	17	13	Unanimous
WAMC61424	27	45	55	52	54	17	17	13	Unanimous
WAMC61425	27	45	55	52	54	17	17	13	Unanimous
WAMC67726	27	45	55	52	54	17	17	13	Unanimous
WAMC67742	27	45	55	52	54	17	17	13	Unanimous
WAMC67743	27	45	55	52	54	17	17	13	Unanimous
WAMC67774	27	45	55	52	54	17	17	13	Unanimous
WAMC67822	27	45	55	52	54	17	17	13	Unanimous
WAMC67823	27	45	55	52	54	17	17	13	Unanimous
WAMC71761	27	45	55	52	54	17	17	13	Unanimous
WAMC71762	27	45	55	52	54	17	17	13	Unanimous
WAMC71770	27	45	55	52	54	17	17	13	Unanimous
WAMC71831	27	45	55	52	54	17	17	13	Unanimous
WAMC71878	27	45	55	52	54	17	17	13	Unanimous
WAMC71879	27	45	55	52	54	17	17	13	Unanimous
WAMC71882	27	45	55	52	54	17	17	13	Unanimous
WAMC71883	27	45	55	52	54	17	17	13	Unanimous
WAMC74375	27	45	55	52	54	17	17	13	Unanimous
WAMC46102	28	46	57	53	55	27	30	40	Unanimous
WAMC53901	28	46	57	53	55	27	30	40	Unanimous
WAMC55277	28	46	57	53	55	27	30	40	Unanimous
WAMC61362	28	46	57	53	55	27	30	40	Unanimous
WAMC61389	28	46	57	53	55	27	30	40	Unanimous
WAMC61390	28	46	57	53	55	27	30	40	Unanimous
WAMC61413	28	46	57	53	55	27	30	40	Unanimous
WAMC71797	28	46	57	53	55	27	30	40	Unanimous
WAMC71798	28	46	57	53	55	27	30	40	Unanimous

SequenceID	**PSH**	**p-d 1st**	**p-d 2nd**	**K2P 1st**	**K2P 2nd**	**bPTP**	**PTP**	**mPTP**	**Congruence**
WAMC71818	28	46	57	53	55	27	30	40	Unanimous
WAMC71819	28	46	57	53	55	27	30	40	Unanimous
WAMC72908	28	46	57	53	55	27	30	40	Unanimous
WAMC48912	29	49	60	56	58	9	8	29	Unanimous
WAMC48913	30	50	61	57	59	37	40	10	Unanimous
WAMC48917	31	51	62	58	60	55	59	96	Unanimous
WAMC52691	32	53	64	60	62	63	67	102	Unanimous
WAMC55365	32	53	64	60	62	63	67	102	Unanimous
WAMC55366	32	53	64	60	62	63	67	102	Unanimous
WAMC61380	32	53	64	60	62	63	67	102	Unanimous
WAMC71856	32	53	64	60	62	63	67	102	Unanimous
WAMC71931	32	53	64	60	62	63	67	102	Unanimous
WAMC55061	33	56	69	64	66	2	2	97	Unanimous
WAMC55158	34	58	71	66	68	56	60	96	Unanimous
WAMC55059	35	54	68	63	65	101	106	37	Majority
WAMC55064	35	54	68	63	65	101	106	37	Majority
WAMC55337	35	54	68	63	65	101	106	37	Majority
WAMC55348	35	54	68	63	65	101	106	37	Majority
WAMC58788	35	54	68	63	65	101	106	37	Majority
WAMC66687	35	54	68	63	65	101	106	37	Majority
WAMC55293	36	61	75	72	73	25	28	44	Unanimous
WAMC55294	36	61	75	72	73	25	28	44	Unanimous
WAMC55326	37	62	76	73	75	57	61	16	Unanimous
WAMC55328	37	62	76	73	75	57	61	16	Unanimous
WAMC55329	37	62	76	73	75	57	61	16	Unanimous
WAMC55390	37	62	76	73	75	57	61	16	Unanimous
WAMC55391	37	62	76	73	75	57	61	16	Unanimous
WAMC55334	38	63	77	74	76	12	11	32	Unanimous

SequenceID	PSH	p-d 1st	p-d 2nd	K2P 1st	K2P 2nd	bPTP	PTP	mPTP	Congruence
WAMC55335	38	63	77	74	76	12	11	32	Unanimous
WAMC55359	38	63	77	74	76	12	11	32	Unanimous
WAMC55360	38	63	77	74	76	12	11	32	Unanimous
WAMC55361	38	63	77	74	76	12	11	32	Unanimous
WAMC55362	38	63	77	74	76	12	11	32	Unanimous
WAMC55363	38	63	77	74	76	12	11	32	Unanimous
WAMC55364	38	63	77	74	76	12	11	32	Unanimous
WAMC67762	38	63	77	74	76	12	11	32	Unanimous
WAMC67763	38	63	77	74	76	12	11	32	Unanimous
WAMC55346	39	65	81	78	80	91	96	51	Unanimous
WAMC61363	39	65	81	78	80	91	96	51	Unanimous
WAMC61364	39	65	81	78	80	91	96	51	Unanimous
WAMC61365	39	65	81	78	80	91	96	51	Unanimous
WAMC61428	39	65	81	78	80	91	96	51	Unanimous
WAMC61429	39	65	81	78	80	91	96	51	Unanimous
WAMC61430	39	65	81	78	80	91	96	51	Unanimous
WAMC71740	39	65	81	78	80	91	96	51	Unanimous
WAMC55347	40	67	82	79	81	49	53	68	Unanimous
WAMC55375	40	67	82	79	81	49	53	68	Unanimous
WAMC55376	40	67	82	79	81	49	53	68	Unanimous
WAMC55377	40	67	82	79	81	49	53	68	Unanimous
WAMC58875	40	67	82	79	81	49	53	68	Unanimous
WAMC61460	40	67	82	79	81	49	53	68	Unanimous
WAMC61461	40	67	82	79	81	49	53	68	Unanimous
WAMC61467	40	67	82	79	81	49	53	68	Unanimous
WAMC56664	41	70	88	85	87	3	3	88	Unanimous
WAMC58519	42	71	91	88	90	38	42	19	Unanimous
WAMC61479	42	71	91	88	90	38	42	19	Unanimous

SequenceID	PSH	p-d 1st	p-d 2nd	K2P 1st	K2P 2nd	bPTP	PTP	mPTP	Congruence
WAMC61480	42	71	91	88	90	38	42	19	Unanimous
WAMC71780	42	71	91	88	90	38	42	19	Unanimous
WAMC58744	43	72	92	89	91	28	31	43	Unanimous
WAMC58745	43	72	92	89	91	28	31	43	Unanimous
WAMC58746	43	72	92	89	91	28	31	43	Unanimous
WAMC61434	43	72	92	89	91	28	31	43	Unanimous
WAMC61435	43	72	92	89	91	28	31	43	Unanimous
WAMC58859	44	75	96	93	95	51	55	59	Unanimous
WAMC67755	44	75	96	93	95	51	55	59	Unanimous
WAMC61370	45	79	100	97	99	41	45	46	Unanimous
WAMC61371	45	79	100	97	99	41	45	46	Unanimous
WAMC61372	45	79	100	97	99	41	45	46	Unanimous
WAMC61406	45	79	100	97	99	41	45	46	Unanimous
WAMC61378	46	80	101	98	100	11	10	33	Unanimous
WAMC61407	47	81	102	99	101	26	29	45	Unanimous
WAMC67759	47	81	102	99	101	26	29	45	Unanimous
WAMC67760	47	81	102	99	101	26	29	45	Unanimous
WAMC67761	47	81	102	99	101	26	29	45	Unanimous
WAMC71744	47	81	102	99	101	26	29	45	Unanimous
WAMC71745	47	81	102	99	101	26	29	45	Unanimous
WAMC61426	48	82	104	101	103	39	43	20	Unanimous
WAMC61427	48	82	104	101	103	39	43	20	Unanimous
WAMC61475	49	83	105	103	105	40	44	21	Unanimous
WAMC71800	49	83	105	103	105	40	44	21	Unanimous
WAMC71801	49	83	105	103	105	40	44	21	Unanimous
WAMC61505	50	84	106	104	106	34	37	82	Unanimous
WAMC67640	51	21	108	106	108	98	103	61	Conservative
WAMC67636	52	85	107	105	107	52	56	87	Unanimous

SequenceID	**PSH**	**p-d 1st**	**p-d 2nd**	**K2P 1st**	**K2P 2nd**	**bPTP**	**PTP**	**mPTP**	**Congruence**
WAMC67638	52	85	107	105	107	52	56	87	Unanimous
WAMC67639	52	85	107	105	107	52	56	87	Unanimous
WAMC67678	53	87	110	108	110	32	35	76	Unanimous
WAMC67683	54	88	111	109	111	35	38	80	Unanimous
WAMC67685	54	88	111	109	111	35	38	80	Unanimous
WAMC67691	55	89	113	111	113	42	46	69	Unanimous
WAMC67769	56	91	120	118	120	67	70	6	Unanimous
WAMC67770	56	91	120	118	120	67	70	6	Unanimous
WAMC71875	56	91	120	118	120	67	70	6	Unanimous
WAMC71876	56	91	120	118	120	67	70	6	Unanimous
WAMC71877	56	91	120	118	120	67	70	6	Unanimous
WAMC71775	57	92	123	122	124	46	50	105	Unanimous
WAMC71777	57	92	123	122	124	46	50	105	Unanimous
WAMC71778	57	92	123	122	124	46	50	105	Unanimous
WAMC71787	57	92	123	122	124	46	50	105	Unanimous
WAMC71886	57	92	123	122	124	46	50	105	Unanimous
WAMC71853	58	93	128	127	129	7	6	94	Unanimous
WAMC71881	58	93	128	127	129	7	6	94	Unanimous
WAMC71859	59	94	129	128	131	10	9	33	Unanimous
WAMC71866	60	95	130	129	132	47	51	106	Unanimous
WAMC71867	60	95	130	129	132	47	51	106	Unanimous
WAMC71868	60	95	130	129	132	47	51	106	Unanimous
WAMC71902	61	97	133	132	135	44	48	64	Unanimous
WAMC71903	61	97	133	132	135	44	48	64	Unanimous
WAMC71904	61	97	133	132	135	44	48	64	Unanimous
WAMC71906	61	97	133	132	135	44	48	64	Unanimous
WAMC71909	61	97	133	132	135	44	48	64	Unanimous
WAMC71914	61	97	133	132	135	44	48	64	Unanimous

SequenceID	PSH	p-d 1st	p-d 2nd	K2P 1st	K2P 2nd	bPTP	PTP	mPTP	Congruence
WAMC71920	61	97	133	132	135	44	48	64	Unanimous
WAMC71922	61	97	133	132	135	44	48	64	Unanimous
WAMC71923	61	97	133	132	135	44	48	64	Unanimous
WAMC71925	61	97	133	132	135	44	48	64	Unanimous
WAMC71926	61	97	133	132	135	44	48	64	Unanimous
WAMC71932	62	98	134	134	137	13	12	103	Unanimous
MN842026	63	8	8	8	8	162	117	2	Majority
WAMC54220	63	8	66	8	8	105	118	2	Majority
WAMC55242	63	8	66	8	8	105	118	2	Majority
WAMC55246	63	8	66	8	8	105	118	2	Majority
WAMC67828	63	8	8	8	8	163	117	2	Majority
MN842028	64	10	10	10	10	122	110	11	Majority
WAMC46001	64	10	56	10	10	123	111	11	Majority
WAMC55367	64	10	56	10	10	123	111	11	Majority
WAMC55368	64	10	56	10	10	123	111	11	Majority
WAMC58346	64	10	56	10	10	123	111	11	Majority
WAMC58808	64	10	56	10	10	123	111	11	Majority
WAMC58809	64	10	56	10	10	123	111	11	Majority
WAMC58810	64	10	56	10	10	123	111	11	Majority
WAMC58811	64	10	56	10	10	123	111	11	Majority
WAMC61342	64	10	56	10	10	123	111	11	Majority
WAMC61343	64	10	56	10	10	123	111	11	Majority
WAMC61344	64	10	56	10	10	123	111	11	Majority
WAMC61345	64	10	56	10	10	123	111	11	Majority
WAMC71805	64	10	56	10	10	123	111	11	Majority
KU986749	65	26	29	28	30	173	72	38	Majority
WAMC67722	65	26	29	28	30	173	72	38	Majority
WAMC67727	65	26	29	28	30	174	72	38	Majority

SequenceID	**PSH**	**p-d 1st**	**p-d 2nd**	**K2P 1st**	**K2P 2nd**	**bPTP**	**PTP**	**mPTP**	**Congruence**
WAMC67744	65	26	29	28	30	173	72	38	Majority
WAMC67810	65	26	29	28	30	173	72	38	Majority
WAMC71752	65	26	29	28	30	173	72	38	Majority
WAMC71753	65	26	29	28	30	173	72	38	Majority
WAMC71869	65	26	29	28	30	173	72	38	Majority
WAMC71871	65	26	29	28	30	173	72	38	Majority
WAMC71934	65	26	29	28	30	173	72	38	Majority
WAMC58844	66	32	37	35	37	125	141	86	Majority
WAMC58846	66	32	37	35	37	126	142	86	Majority
WAMC48563	67	48	59	55	57	138	156	91	Majority
WAMC71865	67	48	59	55	57	139	157	91	Majority
WAMC50791	68	52	63	59	61	66	162	58	Majority
WAMC55302	68	52	63	59	61	66	162	58	Majority
WAMC55303	68	52	63	59	61	66	162	58	Majority
WAMC55304	68	52	63	59	61	66	162	58	Majority
WAMC55305	68	52	63	59	61	66	162	58	Majority
WAMC55306	68	52	63	59	61	66	162	58	Majority
WAMC55307	68	52	63	59	61	66	162	58	Majority
WAMC55308	68	52	63	59	61	66	163	58	Majority
WAMC55066	69	57	70	65	67	59	152	26	Majority
WAMC55067	69	57	70	65	67	59	153	26	Majority
WAMC55338	70	64	78	75	77	156	131	18	Majority
WAMC55339	70	64	78	75	77	157	132	18	Majority
WAMC55378	71	68	85	82	84	150	13	104	Majority
WAMC55379	71	68	85	82	84	151	13	104	Majority
WAMC55380	71	68	85	82	84	151	13	104	Majority
WAMC55381	71	68	85	82	84	151	13	104	Majority
WAMC58783	72	73	93	90	92	6	167	93	Majority

SequenceID	PSH	p-d 1st	p-d 2nd	K2P 1st	K2P 2nd	bPTP	PTP	mPTP	Congruence
WAMC58785	72	73	93	90	92	6	168	93	Majority
WAMC71832	72	73	93	90	92	6	168	93	Majority
WAMC71833	72	73	93	90	92	6	168	93	Majority
WAMC58789	73	74	94	91	93	146	19	28	Majority
WAMC58790	73	74	94	91	93	146	19	28	Majority
WAMC58791	73	74	94	91	93	147	19	28	Majority
WAMC61358	74	77	98	95	97	175	63	25	Majority
WAMC61403	74	77	98	95	97	176	63	25	Majority
WAMC71820	74	77	98	95	97	175	63	25	Majority
WAMC71897	75	96	132	131	134	140	148	60	Majority
WAMC71917	75	96	132	131	134	141	149	60	Majority
MF796675	76	7	7	7	7	80	84	22	Majority
MF796676	76	7	7	7	7	80	84	22	Majority
MN842025	76	7	7	7	7	80	84	22	Majority
WAMC47383	76	7	7	7	7	80	84	22	Majority
WAMC53344	76	7	7	7	7	80	84	22	Majority
WAMC67716	77	7	115	113	115	81	85	23	Majority
WAMC67717	77	7	115	113	115	81	85	23	Majority
KY581621	78	9	20	20	21	72	76	15	Majority
MN842027	79	9	9	9	9	71	75	15	Majority
MN842029	80	11	11	11	11	23	24	54	Majority
WAMC46096	80	11	11	11	11	23	24	54	Majority
WAMC46669	80	11	11	11	11	23	24	54	Majority
WAMC55251	80	11	11	11	11	22	23	54	Majority
WAMC55319	80	11	11	11	11	171	26	54	Majority
WAMC55320	80	11	11	11	11	23	24	54	Majority
WAMC55321	80	11	11	11	11	23	24	54	Majority
WAMC55322	80	11	11	11	11	23	24	54	Majority

SequenceID	PSH	p-d 1st	p-d 2nd	K2P 1st	K2P 2nd	bPTP	PTP	mPTP	Congruence
WAMC55323	80	11	11	11	11	160	27	54	Majority
WAMC55324	80	11	11	11	11	161	27	54	Majority
WAMC55325	80	11	11	11	11	171	26	54	Majority
WAMC58748	80	11	11	11	11	23	24	54	Majority
WAMC58749	80	11	11	11	11	172	26	54	Majority
WAMC67829	80	11	11	11	11	23	24	54	Majority
WAMC71738	80	11	11	11	11	24	25	54	Majority
WAMC71739	80	11	11	11	11	23	24	54	Majority
WAMC72909	80	11	11	11	11	23	24	54	Majority
WAMC72914	80	11	11	11	11	23	24	54	Majority
WAMC74419	80	11	11	11	11	21	22	55	Majority
MN842030	81	12	12	12	12	127	137	98	Majority
SAMAC12790	81	12	12	12	12	128	138	98	Majority
WAMC55403	82	12	34	12	13	97	102	99	Majority
WAMC55404	82	12	34	12	13	97	102	99	Majority
WAMC67811	82	12	34	12	13	97	102	99	Majority
WAMC67812	82	12	34	12	13	97	102	99	Majority
WAMC67813	82	12	34	12	13	97	102	99	Majority
WAMC50622	83	25	28	27	29	75	79	70	Majority
WAMC55429	83	25	28	27	29	75	79	70	Majority
WAMC55431	83	25	28	27	29	75	79	70	Majority
WAMC55432	83	25	28	27	29	75	79	70	Majority
WAMC58881	83	25	28	27	29	75	79	70	Majority
WAMC58893	83	25	28	27	29	75	79	70	Majority
WAMC58894	83	25	28	27	29	75	79	70	Majority
WAMC58895	83	25	28	27	29	75	79	70	Majority
WAMC58909	83	25	28	27	29	75	79	70	Majority
WAMC58910	83	25	28	27	29	75	79	70	Majority

SequenceID	PSH	p-d 1st	p-d 2nd	K2P 1st	K2P 2nd	bPTP	PTP	mPTP	Congruence
WAMC58911	83	25	28	27	29	75	79	70	Majority
WAMC61493	83	25	28	27	29	75	79	70	Majority
WAMC61494	83	25	28	27	29	75	79	70	Majority
WAMC61507	84	36	41	39	41	88	92	66	Majority
WAMC61508	84	36	41	39	41	88	92	66	Majority
WAMC61509	84	36	41	39	41	88	92	66	Majority
WAMC75729	84	36	41	39	41	88	92	66	Majority
WAMC72920	85	36	50	47	49	167	93	67	Majority
WAMC72927	85	36	50	47	49	168	93	67	Majority
WAMC61529	86	38	44	42	44	54	58	78	Majority
WAMC61531	86	38	44	42	44	54	58	78	Majority
WAMC66631	86	38	44	42	44	54	58	78	Majority
WAMC67745	86	38	44	42	44	54	58	78	Majority
WAMC67746	86	38	44	42	44	54	58	78	Majority
WAMC67747	86	38	44	42	44	54	58	78	Majority
WAMC67788	86	38	44	42	44	54	58	78	Majority
WAMC71893	87	38	131	130	133	111	150	79	Majority
WAMC71912	87	38	131	130	133	111	151	79	Majority
WAMC71916	87	38	131	133	136	112	123	79	Majority
WAMC71919	87	38	131	130	133	111	151	79	Majority
WAMC71921	87	38	131	130	133	110	122	79	Majority
WAMC71928	87	38	131	130	133	110	122	79	Majority
WAMC71929	87	38	131	130	133	110	122	79	Majority
WAMC46111	88	47	58	54	56	158	154	41	Majority
WAMC58252	88	47	58	54	56	158	154	41	Majority
WAMC58384	88	47	58	54	56	158	154	41	Majority
WAMC58727	88	47	58	54	56	158	154	41	Majority
WAMC61436	88	47	58	54	56	158	154	41	Majority

SequenceID	PSH	p-d 1st	p-d 2nd	K2P 1st	K2P 2nd	bPTP	PTP	mPTP	Congruence
WAMC61437	88	47	58	54	56	158	154	41	Majority
WAMC61438	88	47	58	54	56	158	154	41	Majority
WAMC71799	88	47	58	54	56	159	155	41	Majority
WAMC55188	89	47	73	69	70	120	115	42	Conservative
WAMC55261	89	47	73	70	71	152	119	42	Conservative
WAMC55296	89	47	73	69	74	113	112	42	Conservative
WAMC55297	89	47	73	69	74	113	112	42	Conservative
WAMC55341	89	47	79	76	78	89	94	42	Conservative
WAMC55342	89	47	80	77	79	153	120	42	Conservative
WAMC55349	89	47	73	69	74	113	112	42	Conservative
WAMC55350	89	47	73	69	74	113	112	42	Conservative
WAMC55351	89	47	73	69	74	113	112	42	Conservative
WAMC55353	89	47	83	80	82	102	107	42	Conservative
WAMC55354	89	47	83	80	82	102	107	42	Conservative
WAMC55355	89	47	83	80	82	102	107	42	Conservative
WAMC55356	89	47	83	80	82	102	107	42	Conservative
WAMC55357	89	47	83	80	82	102	107	42	Conservative
WAMC55382	89	47	86	83	85	103	108	42	Conservative
WAMC55383	89	47	73	69	74	113	112	42	Conservative
WAMC55384	89	47	73	69	74	113	112	42	Conservative
WAMC55401	89	47	73	69	74	113	112	42	Conservative
WAMC55402	89	47	73	69	74	113	112	42	Conservative
WAMC58242	89	47	89	86	88	86	90	42	Conservative
WAMC58600	89	47	73	69	74	113	112	42	Conservative
WAMC58682	89	47	80	77	79	153	120	42	Conservative
WAMC61355	89	47	89	86	88	86	90	42	Conservative
WAMC61356	89	47	89	86	88	86	90	42	Conservative
WAMC61357	89	47	89	86	88	86	90	42	Conservative

SequenceID	**PSH**	**p-d 1st**	**p-d 2nd**	**K2P 1st**	**K2P 2nd**	**bPTP**	**PTP**	**mPTP**	**Congruence**
WAMC61419	89	47	73	69	70	120	115	42	Conservative
WAMC61420	89	47	103	100	102	143	128	42	Conservative
WAMC61457	89	47	103	102	104	104	109	42	Conservative
WAMC61477	89	47	103	102	104	104	109	42	Conservative
WAMC61539	89	47	103	100	102	148	129	42	Conservative
WAMC61540	89	47	103	100	102	149	129	42	Conservative
WAMC66761	89	47	103	100	102	148	129	42	Conservative
WAMC67733	89	47	73	69	74	113	112	42	Conservative
WAMC67734	89	47	73	69	74	113	112	42	Conservative
WAMC67737	89	47	117	115	117	99	104	42	Conservative
WAMC67738	89	47	117	115	117	99	104	42	Conservative
WAMC67739	89	47	117	115	117	99	104	42	Conservative
WAMC67771	89	47	73	69	74	113	112	42	Conservative
WAMC67824	89	47	73	69	70	120	115	42	Conservative
WAMC67826	89	47	73	119	121	114	113	42	Conservative
WAMC71742	89	47	122	121	123	87	91	42	Conservative
WAMC71743	89	47	122	121	123	87	91	42	Conservative
WAMC71766	89	47	73	119	121	114	113	42	Conservative
WAMC71768	89	47	122	121	123	87	91	42	Conservative
WAMC71769	89	47	83	80	82	102	107	42	Conservative
WAMC71779	89	47	124	123	125	115	114	42	Conservative
WAMC71782	89	47	125	124	126	121	116	42	Conservative
WAMC71783	89	47	125	124	126	121	116	42	Conservative
WAMC71789	89	47	73	70	71	152	119	42	Conservative
WAMC71790	89	47	73	70	71	152	119	42	Conservative
WAMC71791	89	47	127	126	128	100	105	42	Conservative
WAMC71794	89	47	73	69	74	113	112	42	Conservative
WAMC71795	89	47	73	69	74	113	112	42	Conservative

SequenceID	**PSH**	**p-d 1st**	**p-d 2nd**	**K2P 1st**	**K2P 2nd**	**bPTP**	**PTP**	**mPTP**	**Congruence**
WAMC71796	89	47	73	69	70	120	115	42	Conservative
WAMC71804	89	47	122	121	123	87	91	42	Conservative
WAMC71821	89	47	83	80	82	102	107	42	Conservative
WAMC71826	89	47	73	69	70	120	115	42	Conservative
WAMC71827	89	47	73	69	70	120	115	42	Conservative
WAMC71839	89	47	79	76	78	89	94	42	Conservative
WAMC71843	89	47	73	69	70	120	115	42	Conservative
WAMC71872	89	47	103	100	102	143	128	42	Conservative
WAMC71873	89	47	103	100	102	143	128	42	Conservative
WAMC74371	89	47	137	137	140	136	143	42	Conservative
WAMC74372	89	47	137	137	140	137	144	42	Conservative
WAMC74373	89	47	137	137	140	136	143	42	Conservative
WAMC74376	89	47	103	100	102	143	128	42	Conservative
WAMC74377	89	47	103	100	102	143	128	42	Conservative
WAMC53978	90	54	65	61	63	169	139	35	Majority
WAMC58820	90	54	65	61	63	170	140	36	Majority
WAMC58823	90	54	65	61	63	170	140	36	Majority
WAMC61348	90	54	65	61	63	170	140	36	Majority
WAMC61349	90	54	65	61	63	170	140	36	Majority
WAMC61350	90	54	65	61	63	170	140	36	Majority
WAMC61397	90	54	65	61	63	170	140	36	Majority
WAMC61398	90	54	65	61	63	170	140	36	Majority
WAMC61404	90	54	65	61	63	170	140	36	Majority
WAMC61405	90	54	65	61	63	170	140	36	Majority
WAMC61417	90	54	65	61	63	169	139	35	Majority
WAMC61418	90	54	65	61	63	169	139	35	Majority
WAMC66622	90	54	65	61	63	170	140	36	Majority
WAMC66652	90	54	65	61	63	170	140	36	Majority

SequenceID	PSH	p-d 1st	p-d 2nd	K2P 1st	K2P 2nd	bPTP	PTP	mPTP	Congruence
WAMC67740	90	54	65	61	63	170	140	36	Majority
WAMC67741	90	54	65	61	63	170	140	36	Majority
WAMC67753	90	54	65	61	63	170	140	36	Majority
WAMC67754	90	54	65	61	63	170	140	36	Majority
WAMC55186	91	59	72	67	69	133	124	7	Majority
WAMC55187	91	59	72	67	69	134	125	7	Majority
WAMC71854	91	59	72	68	130	135	126	7	Majority
WAMC55280	92	60	74	71	72	84	88	4	Majority
WAMC58829	92	60	74	71	72	84	88	4	Majority
WAMC58830	92	60	74	71	72	84	88	4	Majority
WAMC58831	92	60	74	71	72	84	88	4	Majority
WAMC58832	92	60	74	71	72	84	88	4	Majority
WAMC58833	92	60	74	71	72	84	88	4	Majority
WAMC58834	92	60	74	71	72	84	88	4	Majority
WAMC61359	92	60	74	71	72	84	88	4	Majority
WAMC61360	92	60	74	71	72	84	88	4	Majority
WAMC61361	92	60	74	71	72	84	88	4	Majority
WAMC61373	92	60	74	71	72	84	88	4	Majority
WAMC61374	92	60	74	71	72	84	88	4	Majority
WAMC61375	92	60	74	71	72	84	88	4	Majority
WAMC67757	92	60	74	71	72	84	88	4	Majority
WAMC67758	92	60	74	71	72	84	88	4	Majority
WAMC67785	92	60	74	71	72	84	88	4	Majority
WAMC71829	92	60	74	71	72	84	88	4	Majority
WAMC58804	93	60	95	92	94	85	89	5	Majority
WAMC58805	93	60	95	92	94	85	89	5	Majority
WAMC58806	93	60	95	92	94	85	89	5	Majority
WAMC58807	93	60	95	92	94	85	89	5	Majority

SequenceID	PSH	p-d 1st	p-d 2nd	K2P 1st	K2P 2nd	bPTP	PTP	mPTP	Congruence
WAMC58816	93	60	95	92	94	85	89	5	Majority
WAMC58817	93	60	95	92	94	85	89	5	Majority
WAMC58818	93	60	95	92	94	85	89	5	Majority
WAMC58825	93	60	95	92	94	85	89	5	Majority
WAMC58826	93	60	95	92	94	85	89	5	Majority
WAMC58827	93	60	95	92	94	85	89	5	Majority
WAMC58828	93	60	95	92	94	85	89	5	Majority
WAMC55369	94	66	84	81	83	177	158	52	Majority
WAMC55370	94	66	84	81	83	164	147	52	Majority
WAMC71741	94	66	84	81	83	178	159	52	Majority
WAMC55385	95	69	87	84	86	43	47	63	Majority
WAMC61353	95	69	87	84	86	43	47	63	Majority
WAMC58873	96	76	97	94	96	108	41	8	Majority
WAMC67748	96	76	118	116	118	107	41	8	Majority
WAMC67749	96	76	118	116	118	106	41	8	Majority
WAMC67750	96	76	118	116	118	106	41	8	Majority
WAMC67772	96	76	118	116	118	109	41	8	Majority
WAMC67728	97	90	116	114	116	129	130	47	Majority
WAMC67751	97	90	116	114	116	144	171	47	Majority
WAMC67752	97	90	116	114	116	131	134	47	Majority
WAMC67766	97	90	116	114	116	142	146	47	Majority
WAMC67767	97	90	116	114	116	145	172	47	Majority
WAMC67768	97	90	116	114	116	130	133	47	Majority
WAMC71773	97	90	116	114	116	130	133	47	Majority
WAMC71774	97	90	116	114	116	132	145	47	Majority
WAMC67764	98	90	119	117	119	82	86	48	Majority
WAMC67765	98	90	119	117	119	82	86	48	Majority
WAMC71841	98	90	119	117	119	82	86	48	Majority

SequenceID	PSH	p-d 1st	p-d 2nd	K2P 1st	K2P 2nd	bPTP	PTP	mPTP	Congruence
WAMC71784	99	90	126	125	127	83	87	49	Majority
WAMC72912	100	78	135	135	138	96	101	39	Conservative
WAMC61369	101	78	99	96	98	95	100	39	Conservative
KU986738	102	28	32	31	33	1	1	107	Majority
WAMC54239	103	55	67	62	64	5	5	107	Majority
WAMC55426	104	21	36	34	36	69	73	62	Majority
WAMC55428	104	21	36	34	36	69	73	62	Majority
MN653641	105	21	22	22	23	124	169	61	Conservative
MN653642	105	21	22	22	23	124	169	61	Conservative
MN653645	105	21	22	22	23	124	170	61	Conservative
WAMC67630	105	21	45	22	23	165	127	61	Conservative
WAMC67631	105	21	45	22	23	166	127	61	Conservative
KY581617	106	23	25	25	26	118	161	3	Conservative
KY581618	106	23	25	25	26	118	160	3	Conservative
SAMAC8686	106	23	26	25	27	119	121	3	Conservative
WAMC67827	106	23	121	120	122	92	97	3	Conservative
MN653643	107	22	23	23	24	93	98	65	Conservative
MN653644	107	22	24	24	25	94	99	65	Conservative
WAMC67695	108	42	114	112	114	78	82	84	Conservative
WAMC72925	108	42	52	49	51	79	83	84	Conservative
WAMC58342	109	43	90	87	89	117	136	85	Conservative
WAMC72928	109	43	53	50	52	116	135	85	Conservative
WAMC72913	110	25	136	136	139	74	78	72	Majority
KU986746	111	25	30	29	31	73	77	71	Majority
WAMC54067	111	25	30	29	31	73	77	71	Majority
WAMC54301	111	25	30	29	31	73	77	71	Majority
WAMC55249	111	25	30	29	31	73	77	71	Majority
WAMC55250	111	25	30	29	31	73	77	71	Majority

SequenceID	PSH	p-d 1st	p-d 2nd	K2P 1st	K2P 2nd	bPTP	PTP	mPTP	Congruence
WAMC55265	111	25	30	29	31	73	77	71	Majority
WAMC55266	111	25	30	29	31	73	77	71	Majority
WAMC55267	111	25	30	29	31	73	77	71	Majority
WAMC55268	111	25	30	29	31	73	77	71	Majority
WAMC55269	111	25	30	29	31	73	77	71	Majority
WAMC61514	112	21	49	46	48	155	166	61	Conservative
WAMC61515	112	21	49	46	48	155	166	61	Conservative
WAMC72917	112	21	49	46	48	155	165	61	Conservative
WAMC67665	113	21	47	44	46	90	95	61	Majority
WAMC67666	113	21	47	44	46	90	95	61	Majority
WAMC67667	113	21	47	44	46	90	95	61	Majority
WAMC67731	113	21	47	44	46	90	95	61	Majority
WAMC67732	113	21	47	44	46	90	95	61	Majority
WAMC61519	114	21	42	40	42	154	164	61	Majority
WAMC61520	114	21	42	40	42	154	164	61	Majority
WAMC61521	114	21	42	40	42	154	164	61	Majority
WAMC71811	114	21	42	40	42	154	164	61	Majority
WAMC71812	114	21	42	40	42	154	164	61	Majority
WAMC67649	115	86	109	107	109	76	80	100	Unanimous
WAMC67711	115	86	109	107	109	76	80	100	Unanimous
WAMC67712	115	86	109	107	109	76	80	100	Unanimous
WAMC55372	OG	1	1	1	1	OG	OG	OG	Unanimous
WAMC55374	OG	1	1	1	1	OG	OG	OG	Unanimous

Table S2.2. Summary table of host identifications sorted by primary species hypothesis (PSH). Where there is more than one barnacle ID attributed to a PSH, these indicate incongruent identifications drawn from a GenBank record. Citations indicate previously published host identification.

PSH	barnacle ID	Host ID	Host Family	Host Order	Remarks
1	*Acasta* cf. *sulcata* 1	*Axinella* sp.	Axinellidae	Axinellida	(Yu et al., 2020b)
1	*Acasta* cf. *sulicata* 1	*Clathria* (Thalysias) cf. reinwardti	Microcionidae	Poecilosclerida	
2	*Acasta crucibasis* 2	*Xestospongia vansoesti*	Petrosiidae	Haplosclerida	(Yu et al., 2020a)
3	*Acasta cyathus* 3	*Halichondria* sp.	Halichondriidae	Suberitida	
3	*Acasta cyathus* 3	*Petrosia* sp.	Petrosiidae	Haplosclerida	
3	*Acasta cyathus* 3	*Petrosia* (*Petrosia*) SS2	Petrosiidae	Haplosclerida	
3	*Acasta cyathus* 3	*Petrosia* SS2	Petrosiidae	Haplosclerida	
3	*Acasta cyathus* 3	*Thorectandra* NG1	Thorectidae	Dictyoceratida	
3	*Acasta cyathus* 3	*Xestospongia* NG3	Petrosiidae	Haplosclerida	
3	*Acasta cyathus* 3	*Xestospongia testudinaria*	Petrosiidae	Haplosclerida	(Yu et al., 2020b)
4	*Acasta daedalusa* 4	*Petrosia* (*Petrosia*) sp.	Petrosiidae	Haplosclerida	(Yu et al., 2020b)
5	*Acasta radenta* 5	*Jaspis splendens*	Ancorinidae	Tetractinellida	(Yu et al., 2020b; Yu et al., 2017b)
6	*Euacasta dofleini* 6	*Haliclona* sp.	Chalinidae	Haplosclerida	(Yu et al., 2020b)
7	*Euacasta microforamina* 7	*Haliclona* sp.	Chalinidae	Haplosclerida	(Yu et al., 2020b)
8	*Euacasta sporillus* 8	Aaptos suberitoides	Suberitidae	Suberitida	(Yu et al., 2020b)
8	*Euacasta sporillus* 8	*Hymeniacidon* sp.	Halichondriidae	Suberitida	
9	*Membranobalanus brachialis* 9	*Spheciospongia* sp.	Clionaidae	Clionaida	
9	*Membranobalanus brachialis* 9	*Spheciospongia* confoederata	Clionaidae	Clionaida	(Yu et al., 2020b)
10	*Archiacasta tenuivalvata* 10	*Neofibularia* KMB1	Biemnidae	Biemnida	
10	*Archiacasta tenuivalvata* 10	*Petrosia* sp.	Petrosiidae	Haplosclerida	
10	*Membranobalanus orcutti* 10	*Petrosia* (*Petrosia*)	Petrosiidae	Haplosclerida	(Yu et al., 2020b)
10	*Archiacasta tenuivalvata* 10	*Petrosia* SS5	Petrosiidae	Haplosclerida	
10	*Membranobalanus longirostrum* 10	Unknown	Unknown	Unkown	(Chen et al., 2013)
11	*Pectinoacasta sculpturata* 11	*Agelas nemoechinata*	*Agelas*idae	*Agelas*ida	(Yu et al., 2020b)

PSH	barnacle ID	Host ID	Host Family	Host Order	Remarks
11	*Pectinoacasta sculpturata* 11	*Amphinomia* sulphurea	*Agelas*idae	*Agelas*ida	
12	*Pyrgospongia stellular* 12	*Spheciospongia vagabunda*	Clionaidae	Clionaida	(Yu et al., 2020b)
13	*Acasta aspera* 13	*Crella* (*Yvesia*) *spinulata*	Crellidae	Poecilosclerida	
13	*Acasta aspera* 13	*Hamigera* PB1	Hymedesmiidae	Poecilosclerida	
13	*Acasta aspera* 13	*Iotroata* sp.	Iotrochotidae	Poecilosclerida	(Yu et al., 2017b)
13	*Acasta aspera* 13	*Lissodendoryx* (*Acanthodoryx*) KMB1	Coelosphaeridae	Poecilosclerida	
14	*Acasta undulaterga* 14	*Jaspis splendens*	Ancorinidae	Tetractinellida	(Yu et al., 2017b)
15	*Acasta turriformis* 15	*Lissodendoryx* (*Lissodendoryx*)	Coelosphaeridae	Poecilosclerida	(Yu et al., 2017a)
16	*Neoacasta* cf. *laevigata* 16	*Polyfibrospongia flabellifera*	Thorectidae	Dictyoceratida	
16	*Neoacasta* cf. *laevigata* 16	*Polyfibrospongia kulit*	Thorectidae	Dictyoceratida	
17	*Archiacasta fragilis* 17	*Sarcotragus* cf. 2	Irciniidae	Dictyoceratida	
18	*Euacasta* 18	*Aegropila* PB1	Mycalidae	Poecilosclerida	
18	*Euacasta* 18	*Callyspongia* (*Toxochalina*)	Callyspongiidae	Haplosclerida	
18	*Euacasta* 18	*Dysidea* cf. *granulosa*	Dysideidae	Dictyoceratida	
18	*Euacasta* 18	*Halichondria* NW1	Halichondriidae	Suberitida	
18	*Euacasta* 18	*Hymeniacidon* KMB1	Halichondriidae	Suberitida	
18	*Euacasta* 18	*Spheciospongia* sp.	Clionaidae	Clionaida	
18	*Euacasta* 18	*Tedania* (*Trachytedania*) sp.	Tedaniidae	Poecilosclerida	
19	*Acasta* cf. *flexuosa* 19	*Dysidea* sp.3	Dysideidae	Dictyoceratida	
19	*Acasta* cf. *flexuosa* 19	*Dysidea* MM2	Dysideidae	Dictyoceratida	
20	*Archiacasta hanainensis* 20	*Hyrtios erectus*	Thorectidae	Dictyoceratida	
20	*Archiacasta hanainensis* 20	*Hyrtios* KMB1	Thorectidae	Dictyoceratida	
20	*Archiacasta hanainensis* 20	*Hyrtios* SS2	Thorectidae	Dictyoceratida	
21	*Acasta* cf. *flexuosa* 21	*Lamellodsidea* KB1	Dysideidae	Dictyoceratida	
22	*Euacasta* 22	*Hyrtios* sp.	Thorectidae	Dictyoceratida	
23	*Neoacasta* cf. *planibasis* 23	*Cacospongia* P1	Thorectidae	Dictyoceratida	
23	*Neoacasta* cf. *planibasis* 23	*Luffariella* cf. SS10	Thorectidae	Dictyoceratida	

PSH	barnacle ID	Host ID	Host Family	Host Order	Remarks
23	*Neoacasta* cf. *planibasis* 23	*Luffariella* SS10	Thorectidae	Dictyoceratida	
23	*Neoacasta* cf. *planibasis* 23	*Luffariella* SS11	Thorectidae	Dictyoceratida	
24	*Neoacasta* cf. *coriobasis* 24	*Sarcotragus* DA1	Irciniidae	Dictyoceratida	
24	*Neoacasta* cf. *coriobasis* 24	*Sarcotragus* PB1	Irciniidae	Dictyoceratida	
24	*Neoacasta* cf. *coriobasis* 24	*Sarcotragus* PB2	Irciniidae	Dictyoceratida	
24	*Neoacasta* cf. *coriobasis* 24	*Sarcotragus* SS8	Irciniidae	Dictyoceratida	
25	*Neoacasta* 25	*Hippospongia* SS1	Spongiidae	Dictyoceratida	
26	*Acasta* 26	Unknown	Unknown	Unknown	
27	*Euacasta* 27	*Callyspongia* sp.	Callyspongiidae	Haplosclerida	
27	*Euacasta* 27	*Callyspongia* (*Toxochalina*) sp.	Callyspongiidae	Haplosclerida	
27	*Euacasta* 27	*Callyspongia* (*Toxochalina*) KMB1	Callyspongiidae	Haplosclerida	
27	*Euacasta* 27	*Callyspongia* (*Toxochalina*) MR1	Callyspongiidae	Haplosclerida	
27	*Euacasta* 27	*Ciocalypta* sp.	Halichondriidae	Suberitida	
27	*Euacasta* 27	*Haliclona* sp.	Chalinidae	Haplosclerida	
27	*Euacasta* 27	*Haliclona* amboinensis	Chalinidae	Haplosclerida	
27	*Euacasta* 27	*Haliclona* djeedara	Chalinidae	Haplosclerida	
27	*Euacasta* 27	*Petrosia* sp.	Petrosiidae	Haplosclerida	
27	*Euacasta* 27	*Petrosia* (*Strongylophora*) sp.	Petrosiidae	Haplosclerida	
27	*Euacasta* 27	*Tedania* (*Trachytedania*) sp.	Tedaniidae	Poecilosclerida	
28	*Euacasta* cf. *porata* 28	*Rhabdastrella globostellata*	Ancorinidae	Tetractinellida	
29	*Acasta* 29	*Siphonodictyon* SS9	Phloeodictyidae	Haplosclerida	
30	*Acasta* cf. *crucibasis* 30	*Siphonodictyon* SS9	Phloeodictyidae	Haplosclerida	
31	*Archiacasta tenuivalvata* 31	*Petrosia* SS5	Petrosiidae	Haplosclerida	
32	*Pyrgospongia stellula* 32	Clionaidae	Clionaidae	Clionaida	
32	*Pyrgospongia stellula* 32	*Spheciospongia*	Clionaidae	Clionaida	
32	*Pyrgospongia stellula* 32	*Spheciospongia* K1	Clionaidae	Clionaida	
32	*Pyrgospongia stellula* 32	*Spheciospongia vagabunda*?	Clionaidae	Clionaida	
33	*Euacasta* 33	*Acanthella* MR1	Dictyonellidae	Bubarida	

PSH	barnacle ID	Host ID	Host Family	Host Order	Remarks
34	*Membranobalanus* 34	*Petrosia* (*Strongylata*) cf. *strongylata*	Petrosiidae	Haplosclerida	
35	*Euacasta porata* 35	*Acanthella* MR1	Dictyonellidae	Bubarida	
35	*Euacasta porata* 35	*Acanthella pulcherrima*	Dictyonellidae	Bubarida	
35	*Euacasta porata* 35	*Diplastrella* ML1	Spirastrellidae	Clionaida	
35	*Euacasta porata* 35	*Halichondria*	Halichondriidae	Suberitida	
35	*Euacasta porata* 35	*Phycopsis* sp.	Axinellidae	Axinellida	
35	*Euacasta porata* 35	*Phycopsis* P1	Axinellidae	Axinellida	
36	*Euacasta* 36	*Echinodictyum mesenterium*	Raspailiidae	Axinellida	
37	*Acasta* 37	*Haliclona* KMB3	Chalinidae	Haplosclerida	
38	*Euacasta* 38	*Amphimedon*	Niphatidae	Haplosclerida	
38	*Euacasta* 38	*Amphimedon* cf. *paraviridis*	Niphatidae	Haplosclerida	
39	*Acasta* 39	*Chondropsis* sp.	Chondropsidae	Haplosclerida	
39	*Acasta* 39	*Chondropsis* sp.1	Chondropsidae	Haplosclerida	
39	*Acasta* 39	*Desmacidon*? sp.	Desmacididae	Poecilosclerida	
40	*Neoacasta* cf. *scuticosta* 40	*Placospongia* sp.	Placospongiidae	Clionaida	
40	*Neoacasta* cf. *scuticosta* 40	*Placospongia melobesioides*	Placospongiidae	Clionaida	
40	*Neoacasta* cf. *scuticosta* 40	*Tethya* cf. *robusta*	Tethyidae	Tethyida	
41	*Membranobalanus longirostrum* 41	Clionaidae	Clionaidae	Clionaida	
42	*Euacasta* 42	*Ciocalypta tyleri*	Halichondriidae	Suberitida	
43	*Euacasta acutaflava* 43	*Cymbastela* cf. *stipitata*	Axinellidae	Axinellida	
43	*Euacasta acutaflava* 43	*Cymbastela stipitata*	Axinellidae	Axinellida	
44	*Acasta* 44	*Stylissa flabelliformis*	Scopalinidae	Scopalinida	
45	*Euacasta* 45	Verongiida		Verongiida	
46	*Euacasta* 46	*Polymastia* sp.	Polymastiidae	Polymastiida	
47	*Euacasta* 47	Verongiida		Verongiida	
48	*Euacasta* 48	*Axinella* sp.	Axinellidae	Axinellida	
49	*Euacasta excoriatrix* 49	*Halichondria* BAR1	Halichondriidae	Suberitida	
49	*Euacasta excoriatrix* 49	*Halichondria* NW1	Halichondriidae	Suberitida	

PSH	barnacle ID	Host ID	Host Family	Host Order	Remarks
50	*Neoacasta* 50	*Spongia* (*Heterofibria*) SS1	Spongiidae	Dictyoceratida	
51	*Neoacasta* 51	*Spongia* (*Australospongia*) KMB1	Spongiidae	Dictyoceratida	
52	*Acasta* cf. *flexuosa* 52	*Dysidea* P1	Dysideidae	Dictyoceratida	
53	*Archiacasta* 53	*Sarcotragus* 2	Irciniidae	Dictyoceratida	
54	*Neoacasta* 54	*Sarcotragus* SS7	Irciniidae	Dictyoceratida	
55	*Neoacasta* cf. *coriobasis* 55	*Sarcotragus* SS14	Irciniidae	Dictyoceratida	
56	*Acasta* 56	*Clathria* (*Thalysias*)	Microcionidae	Poecilosclerida	
56	*Acasta* 56	*Monanchora* sp.	Crambeidae	Poecilosclerida	
57	*Membranobalanus* 57	*Cliona* sp.	Clionaidae	Clionaida	
57	*Membranobalanus* 57	*Cliona orientalis*	Clionaidae	Clionaida	
58	*Membranobalanus porphyrophilus* 58	*Spheciospongia purpurea*	Clionaidae	Clionaida	
59	*Euacasta* 59	*Dictyodendrilla* sp.	Dictyodendrillidae	Dendroceratida	
60	*Membranobalanus* 60	*Cliona* cf. *orientalis*	Clionaidae	Clionaida	
61	*Archiacasta membranacea* 61	*Pachastrella* sp.1	Pachastrellidae	Tetractinellida	
62	*Pyrgospongia stellula* 62	Clionaidae	Clionaidae	Clionaida	
63	*Armatobalanus palaoensis* 63	*Echinochalina*	Microcionidae	Poecilosclerida	
63	*Armatobalanus palaoensis* 63	*Monanchora*	Crambeidae	Poecilosclerida	
63	*Acasta* sp. 1 MCY-2020 63	*Mycale*	Mycalidae	Poecilosclerida	(Yu et al., 2020b)
64	*Acasta* 64	*Arenosclera*	Callyspongiidae	Haplosclerida	
64	*Acasta* 64	*Haliclona* 7	Chalinidae	Haplosclerida	
64	*Acasta* 64	*Haliclona* BAR39	Chalinidae	Haplosclerida	
64	*Acasta* 64	*Haliclona* NG4	Chalinidae	Haplosclerida	
64	*Acasta* sp. 3 MCY-2020 64	*Petrosia* (*Petrosia*)	Petrosiidae	Haplosclerida	(Yu et al., 2020b)
65	*Euacasta* cf. *sporillus* 65	*Halichondria*	Halichondriidae	Suberitida	
65	*Euacasta* cf. *sporillus* 65	*Halichondria* B1	Halichondriidae	Suberitida	
65	*Euacasta* cf. *sporillus* 65	*Halichondria*?	Halichondriidae	Suberitida	
65	*Euacasta* cf. *sporillus* 65	*Rhabdastrella* sp.	Ancorinidae	Tetractinellida	
65	*Euacasta* cf. *sporillus* 65	*Spheciospongia* sp.2	Clionaidae	Clionaida	

PSH	barnacle ID	Host ID	Host Family	Host Order	Remarks
66	*Acasta* cf. *flexuosa* 66	*Dysidea* MM1	Dysideidae	Dictyoceratida	
67	*Multatria filigranus* 67	*Monanchora* sp.	Crambeidae	Poecilosclerida	
68	*Pectinoacasta cancellorum* 68	*Agelas* KMB1	*Agelas*idae	*Agelas*ida	
69	*Acasta* cf. *aspera* 69	*Oceanapia* cf. 7	Phloeodictyidae	Haplosclerida	
70	*Acasta* cf. crucibasis 70	*Reniochalina stalagmitis*	Axinellidae	Axinellida	
71	*Membranobalanus* 71	*Spheciospongia* PB1	Clionaidae	Clionaida	
72	*Membranobalanus koreanus* 72	*Cliona* sp.	Clionaidae	Clionaida	
73	*Acasta* 73	*Haliclona* (*Reniera*)	Chalinidae	Haplosclerida	
74	*Acasta* 74	*Callyspongia* sp.	Callyspongiidae	Haplosclerida	
75	*Acasta* 75	*Pachastrella* sp.2	Pachastrellidae	Tetractinellida	
76	*Acasta sandwichi* 76	*Xestospongia testudinaria*	Petrosiidae	Haplosclerida	(Yu et al., 2017a)
77	*Acasta caveata* 77	Gelliodes KMB1	Niphatidae	Haplosclerida	
78	*Acasta huangi* 78	*Jaspis splendens*	Ancorinidae	Tetractinellida	
79	*Acasta* sp. 2 MCY-2020 79	*Haliclona* sp.	Chalinidae	Haplosclerida	
80	*Acasta fenestrata* 80	*Neopetrosia* chaliniformis	Petrosiidae	Haplosclerida	
80	*Acasta* sp. 4 MCY-2020 80	Unknown	Unknown	Unknown	(Yu et al., 2020b)
81	*Acasta* cf. *spongites* 81	*Clathria* sp.	Microcionidae	Poecilosclerida	(Yu et al., 2020b)
82	*Acasta* cf. *spongites* 82	*Dysidea* cf. *granulosa*	Dysideidae	Dictyoceratida	
82	*Acasta* cf. *spongites* 82	*Luffariella* SS11?	Thorectidae	Dictyoceratida	
83	*Neoacasta* cf. *laevigata* 83	*Phyllospongia* cf. *papyracea*	Thorectidae	Dictyoceratida	
83	*Neoacasta* cf. *laevigata* 83	*Phyllospongia foliascens*	Thorectidae	Dictyoceratida	
83	*Neoacasta* cf. *laevigata* 83	*Phyllospongia papyracea*	Thorectidae	Dictyoceratida	
84	*Neoacasta* 84	*Hyattella* SS2	Spongiidae	Dictyoceratida	
84	*Neoacasta* 84	*Spongia* (*Heterofibria*)	Spongiidae	Dictyoceratida	
85	*Neoacasta* 85	*Spongia* cf. PB1	Spongiidae	Dictyoceratida	
86	*Archiacasta* 86	*Dactylospongia elegans*	Thorectidae	Dictyoceratida	
86	*Archiacasta* 86	*Spongia* (*Heterofibria*) cf. NG1	Spongiidae	Dictyoceratida	
87	*Neoacasta fossata* 87	*Ircinia*	Irciniidae	Dictyoceratida	

PSH	**barnacle ID**	**Host ID**	**Host Family**	**Host Order**	**Remarks**
88	*Euacasta* cf. *aculeata* 88	*Cinachyrella* NG1	Tetillidae	Tetractinellida	
88	*Euacasta* cf. *aculeata* 88	*Cinachyrella tenuiviolacea*	Tetillidae	Tetractinellida	
88	*Euacasta* cf. *aculeata* 88	*Rhabdastrella*	Ancorinidae	Tetractinellida	
89	*Euacasta* 89	*Axinella* sp.	Axinellidae	Axinellida	
89	*Euacasta* 89	*Axinella* NG3	Axinellidae	Axinellida	
89	*Euacasta* 89	*Axos flabelliformis*	Hemiasterellidae	Tethyida	
89	*Euacasta* 89	*Caulospongia biflabellata*	Suberitidae	Suberitida	
89	*Euacasta* 89	*Ceratopsion montebelloensis*	Raspailiidae	Axinellida	
89	*Euacasta* 89	*Ciocalypta* PB3	Halichondriidae	Suberitida	
89	*Euacasta* 89	*Clathria* (*Thalysias*) *abietina*	Microcionidae	Poecilosclerida	
89	*Euacasta* 89	*Clathria* (*Thalysias*) *reinwardti*	Microcionidae	Poecilosclerida	
89	*Euacasta* 89	*Ectyoplaisia frondosa*	Raspailiidae	Axinellida	
89	*Euacasta* 89	*Ectyoplaisia tabula*	Raspailiidae	Axinellida	
89	*Euacasta* 89	*Halichondria*?	Halichondriidae	Suberitida	
89	*Euacasta* 89	*Hemiasterella* SS2	Hemiasterellidae	Tethyida	
89	*Euacasta* 89	*Higginsia*	Stellegeridae	Axinellida	
89	*Euacasta* 89	*Iotrochota*	Iotrochotidae	Poecilosclerida	
89	*Euacasta* 89	*Jaspis* cf. SS2	Ancorinidae	Tetractinellida	
89	*Euacasta* 89	*Petrosia* sp.	Petrosiidae	Haplosclerida	
89	*Euacasta* 89	*Reniochalina* sp.2	Axinellidae	Axinellida	
89	*Euacasta* 89	*Reniochalina stalagmitis*	Axinellidae	Axinellida	
89	*Euacasta* 89	*Stylissa flabelliformis*	Scopalinidae	Scopalinida	
89	*Euacasta* 89	*Svenzea* 1	Scopalinidae	Scopalinida	
89	*Euacasta* 89	*Thrinacophora*?	Raspailiidae	Axinellida	
89	*Euacasta* 89	*Trikentrion flabelliforme*	Raspailiidae	Axinellida	
89	*Euacasta* 89	*Xestospongia* cf. sp.3	Petrosiidae	Haplosclerida	
89	*Euacasta* 89	*Xestospongia* sp.3	Petrosiidae	Haplosclerida	
90	*Euacasta* 90	*Hemiasterella* CERF1	Hemiasterellidae	Tethyida	

PSH	barnacle ID	Host ID	Host Family	Host Order	Remarks
90	*Euacasta* 90	*Hemiasterella* cf. CERF1	Hemiasterellidae	Tethyida	
91	*Acasta* 91	*Clathria* (*Thalysias*) cf. *abietina*	Microcionidae	Poecilosclerida	
91	*Acasta* 91	*Clathria vulpina*	Microcionidae	Poecilosclerida	
92	*Acasta* cf. *conica* 92	*Clathria* (Thalysias) cf. *reinwardti*	Microcionidae	Poecilosclerida	
92	*Acasta* cf. *conica* 92	*Clathria* (Thalysias) *reinwardti*	Microcionidae	Poecilosclerida	
93	*Acasta* cf. *conica* 93	*Clathria* (Thalysias) cf. *reinwardti*	Microcionidae	Poecilosclerida	
93	*Acasta* cf. *conica* 93	*Clathria* (Thalysias) *reinwardti*	Microcionidae	Poecilosclerida	
94	*Acasta* 94	*Chondropsis*	Chondropsidae	Haplosclerida	
95	*Archiacasta* cf. *membranacea* 95	*Ciocalypta tyleri*	Halichondriidae	Suberitida	
95	*Archiacasta* cf. *membranacea* 95	*Topsentia halichondroides*	Halichondriidae	Suberitida	
96	*Pectinoacasta pectinipes* 96	*Trachytedania* L1	Tedaniidae	Poecilosclerida	
96	*Pectinoacasta pectinipes* 96	*Trachytedania* MM1	Tedaniidae	Poecilosclerida	
97	*Euacasta* 97	*Ianthella flabelliformis*	Ianthellidae	Verongiida	
98	*Euacasta* 98	*Ianthella basta*	Ianthellidae	Verongiida	
99	*Euacasta* 99	*Ianthella reticulata*	Ianthellidae	Verongiida	
100	*Euacasta* 100	Verongiida	Verongiida	Verongiida	
101	*Euacasta* 101	Verongiida	Verongiida	Verongiida	
102	*Armatobalanus quadrivittatus* 102	*Monanchora* sp.	Crambeidae	Poecilosclerida	
103	*Acasta* sp.2 103	*Polymastia* KMB1	Polymastiidae	Polymastiida	
104	*Neoacasta* 104	*Ircinia* KMB2	Irciniidae	Dictyoceratida	
105	*Neoacasta* glans 105	*Hyrtios* SS2	Thorectidae	Dictyoceratida	
106	*Acasta sulcata* 106	*Antho* (*Plocamia*)	Microcionidae	Poecilosclerida	
106	*Acasta sulcata* 106	*Callyspongia*	Callyspongiidae	Haplosclerida	(Yu et al., 2017b)
107	*Neoacasta liui*	*Spongia*	Spongiidae	Dictyoceratida	(Yu et al., 2020c)
108	*Neoacasta* cf. *coriobasis* 108	*Sarcotragus* KMB5	Irciniidae	Dictyoceratida	
108	*Neoacasta* cf. *coriobasis* 108	*Sarcotragus* SS11	Irciniidae	Dictyoceratida	
109	*Acasta* cf. *flexuosa* 109	*Candidaspongia flabellata*	Dysideidae	Dictyoceratida	
110	*Neoacasta* 110	*Phyllospongia* foliascens	Thorectidae	Dictyoceratida	

PSH	barnacle ID	Host ID	Host Family	Host Order	Remarks
111	*Neoacasta laevigata* 111	*Phyllospongia* foliascens	Thorectidae	Dictyoceratida	
112	*Neoacasta* 112	*Cacospongia* PB2	Thorectidae	Dictyoceratida	
112	*Neoacasta* 112	*Luffariella* PB1	Thorectidae	Dictyoceratida	
113	*Neoacasta* 113	*Hippospongia* P1	Spongiidae	Dictyoceratida	
114	*Neoacasta* 114	?*Cacospongia* DA1	Thorectidae	Dictyoceratida	
114	*Neoacasta* 114	*Hyrtios* SS4	Thorectidae	Dictyoceratida	
115	*Acasta spongites* 115	*Ircinia variabilis*	Irciniidae	Dictyoceratida	

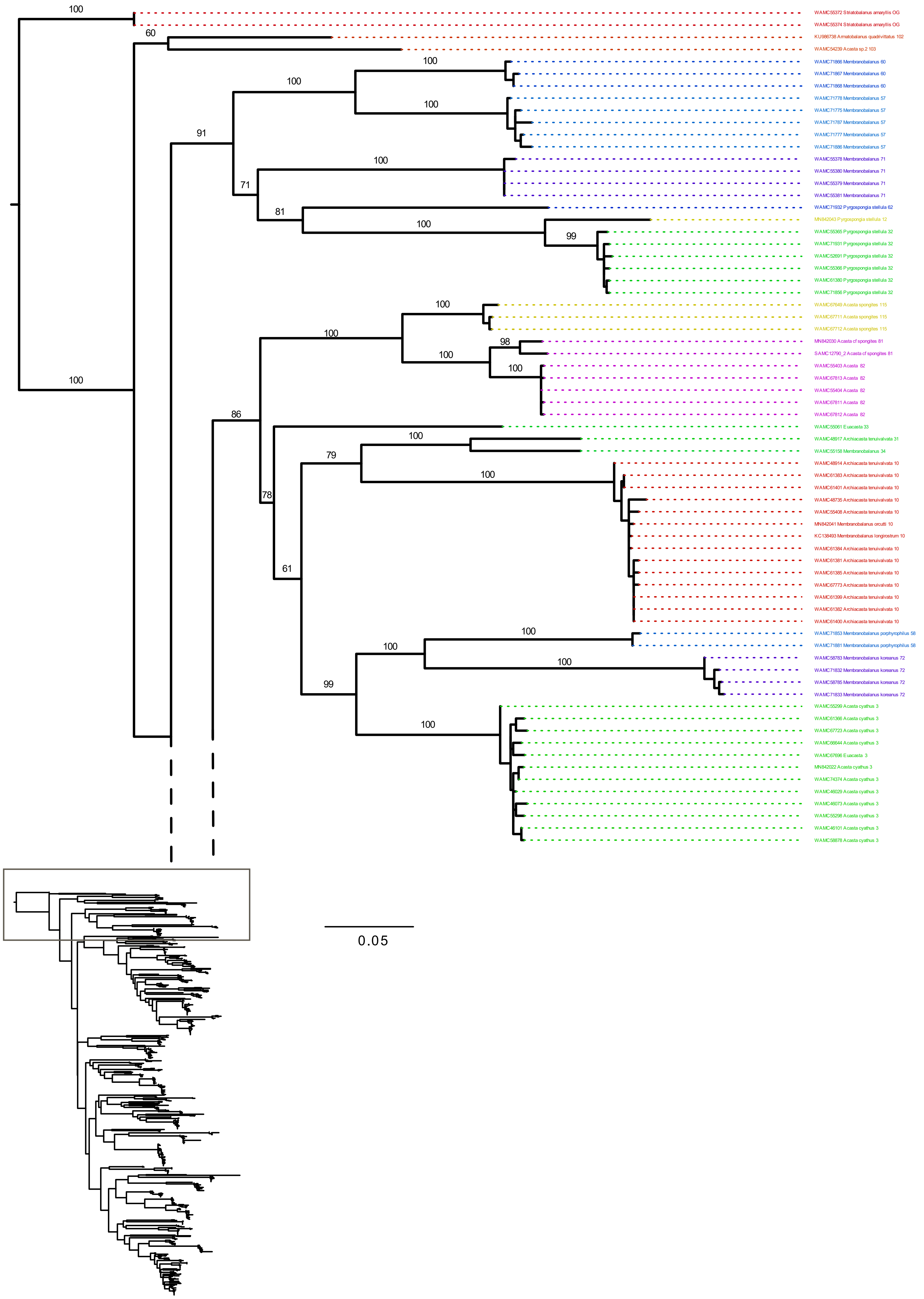

Figure S2.1. Maximum likelihood tree reconstructed from COI dataset showing the 115 sponge-inhabiting barnacle primary species hypotheses (PSH). Bootstrap support is given at the nodes, but removed for clarity within PSH clades, colours serve to highlight primary species hypotheses. Scale bar indicates substitutions per site.

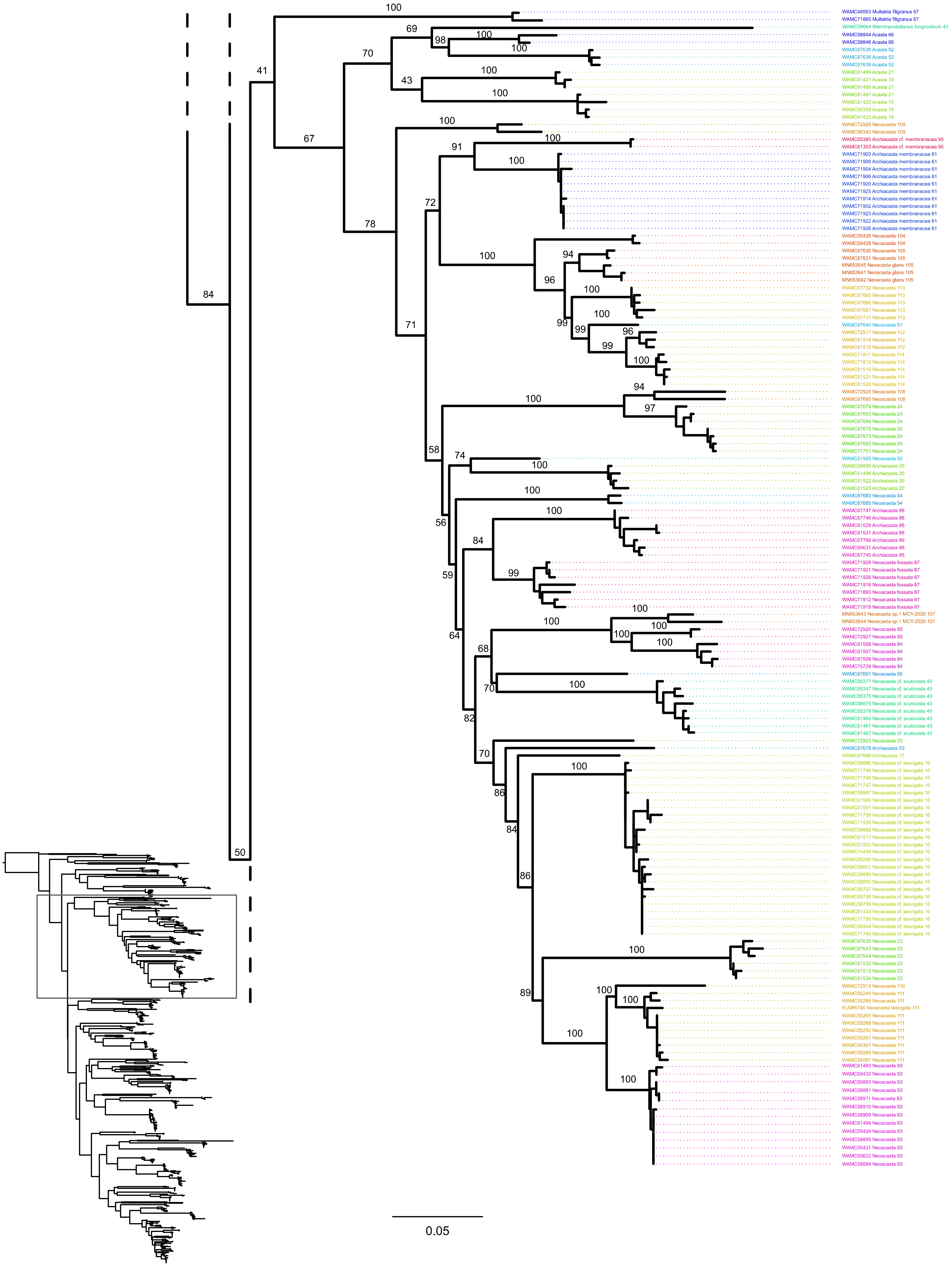

Figure S2.1 continued. Maximum likelihood tree reconstructed from COI dataset showing the 115 sponge-inhabiting barnacle primary species hypotheses (PSH). Bootstrap support is given at the nodes, but removed for clarity within PSH clades, colours serve to highlight primary species hypotheses. Scale bar indicates substitutions per site.

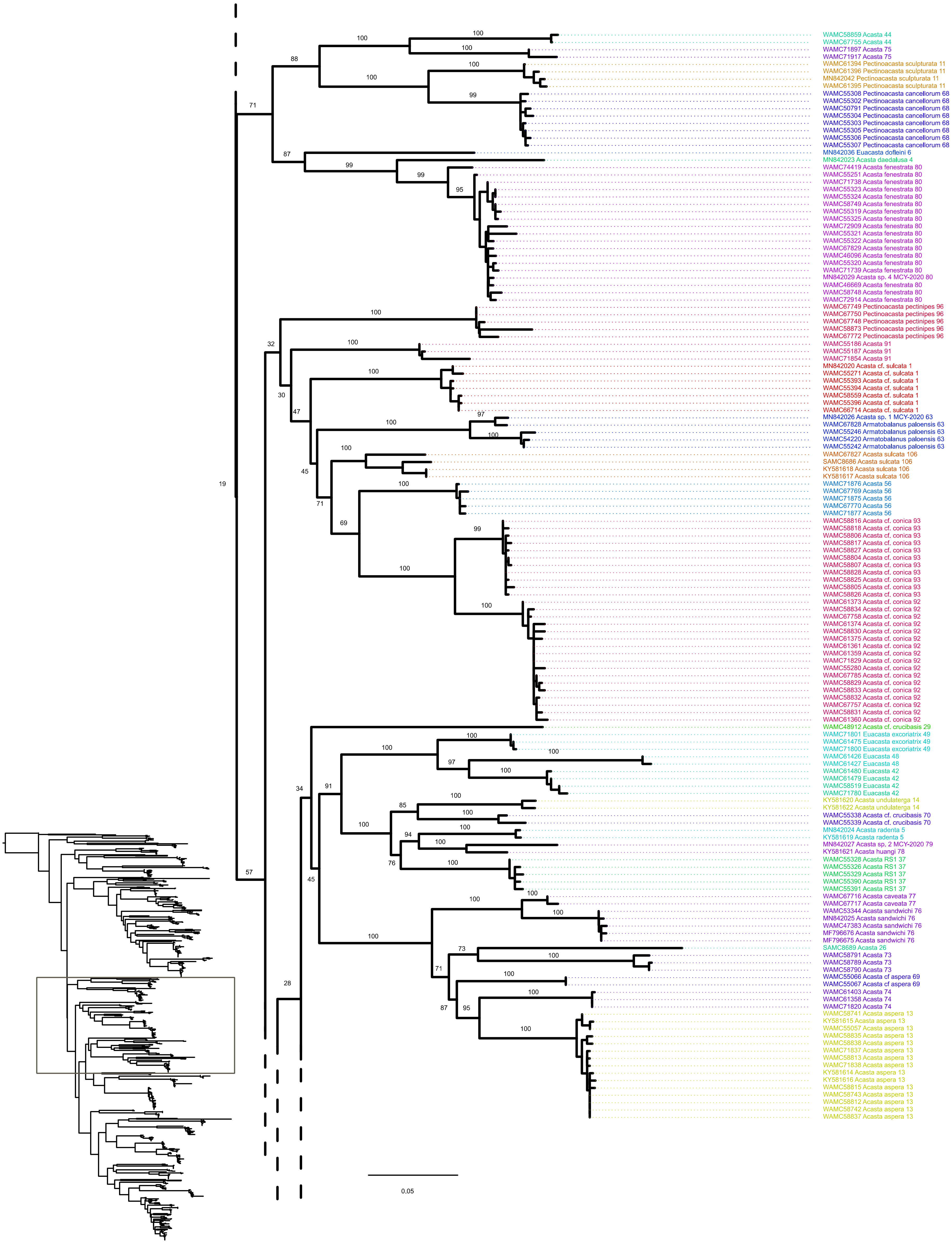

Figure S2.1 continued. Maximum likelihood tree reconstructed from COI dataset showing the 115 sponge-inhabiting barnacle primary species hypotheses (PSH). Bootstrap support is given at the nodes, but removed for clarity within PSH clades, colours serve to highlight primary species hypotheses. Scale bar indicates substitutions per site.

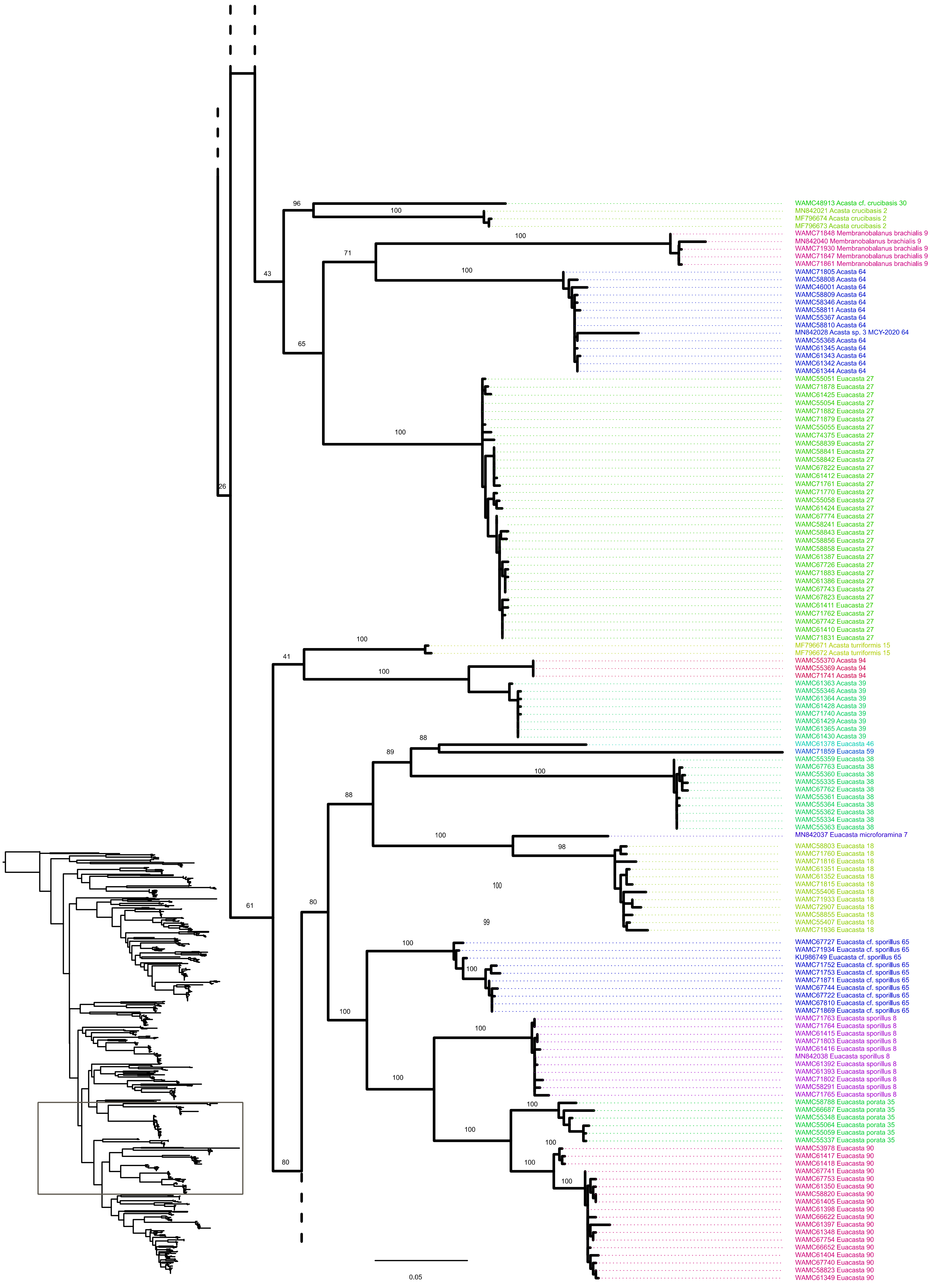

Figure S2.1 continued. Maximum likelihood tree reconstructed from COI dataset showing the 115 sponge-inhabiting barnacle primary species hypotheses (PSH). Bootstrap support is given at the nodes, but removed for clarity within PSH clades, colours serve to highlight primary species hypotheses. Scale bar indicates substitutions per site.

Figure S2.1 continued. Maximum likelihood tree reconstructed from COI dataset showing the 115 sponge-inhabiting barnacle primary species hypotheses (PSH). Bootstrap support is given at the nodes, but removed for clarity within PSH clades, colours serve to highlight primary species hypotheses. Scale bar indicates substitutions per site.

Chapter 3. Species descriptions

Synopsis

This chapter comprises two publications describing species identified through the techniques used in Chapter 2 and demonstrate the applicability of DNA barcoding as an important tool in discovering species. These publications represent some initial descriptions of sponge-inhabiting barnacles in Australia, an endeavour which will continue well after completion of this thesis.

The first publication describes a new species of *Membranobalanus* found inhabiting a southern Australian endemic sponge, *Spheciospongia membranacea*. This morphological study used traditional light microscopy, scanning electron microscopy and also provides the first example of using computed tomography (CT) in aiding in barnacle species descriptions. A key to identifying the known species of *Membranobalanus* is provided to aid future researchers.

The second publication reports on nine species including the description of three new species and the first Australian records of another three species previously known from southeast Asian waters. Four of the presented species are re-described to provide a modern integration of genetic, morphological and host data to link historical records with molecular based contemporary identifications. Part of this involved revisionary elements and taxonomic 'house-keeping' wherein the type series of *Pectinoacasta cancellorum and P. sculpturata* were re-examined and in the case of *P. cancellorum* a lectotype was selected to serve as the name-bearing type.

For both publications *COI* sequences of all species were compared with data available on GenBank. These newly generated sequences, including those from holotype specimens, are now publicly available on GenBank.

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RESEARCH ARTICLE

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Description of a new species of *Membranobalanus* (Crustacea, Cirripedia) from southern Australia

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http://zoobank.org/6149E423-3C28-47BB-89FC-927209B5D2DE

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Abstract

A new species of sponge-inhabiting barnacle, *Membranobalanus porphyrophilus* **sp. nov.**, is described herein. This species can be distinguished from all other congeners by a combination of characters, in particular by the shapes of the tergum and scutum and the armament of the cirri. COI sequence data from the type specimens have been lodged with GenBank and a morphological key to the species of *Membranobalanus* is provided to aid future research. The host of the new species is the southern Australian endemic demosponge *Spheciospongia purpurea*. The new species of barnacle is thought to be host species specific.

Keywords

Archaeobalanidae, bioeroder, commensal, Clionaidae, computed tomography, Demospongiae, specificity, *Spheciospongia purpurea*, symbiosis, temperate reef.

Introduction

Barnacles of the genus *Membranobalanus* Hoek, 1913 are obligate symbionts of sponges. While the identity of sponge hosts for most sponge-dwelling barnacles have been poorly documented, this is not the case for *Membranobalanus*. All species have been found embedded only in the genera *Cliona* Grant, 1826 and *Spheciospongia* Marshall, 1892 in the family Clionaidae D'Orbigny, 1851 (van Syoc 1988; van Syoc et al. 2015), with the exception of *M. longirostrum* (Hoek, 1913), which has been additionally reported from the genus *Suberites* Nardo, 1833 in the family Suberitidae Schmidt 1870 (Ilan et al. 1999; Wibowo et al. 2011; Sulistiono et al. 2014) and *M. orcuttiformis* (Kolosváry, 1941) where no host has been reported.

The Clionaidae (Demospongiae, Clionaida) is a group of sponges well known for bioeroding calcareous structures such as mollusc shells and scleractinian coral skeletons (Rutzler 1975). Sponges in the genus *Spheciospongia* excavate limestone substrates in early life history stages and can become massive sponges with age (Vicente et al. 1991). The barnacles are found embedded within the host, the tissues of which are in direct contact with the calcareous parietes of the barnacles, seemingly undeterred by the potential bioeroding effects of the sponge.

This study describes a new species *Membranobalanus* collected as part of a broader study on sponge-inhabiting barnacles in Australian waters. The host species, *Spheciospongia purpurea* (Lamarck, 1815), is endemic to southern Australia and easily recognised due to its vibrant purple colouration, which it retains even in ethanol or a dry state. The dense royal purple pigment reported in this species and other species of *Cliona* and *Spheciospongia* is a porphyrin, specifically spongioporphyrin (Bergquist 1978).

Methods

Prior to dissection, the designated holotype was scanned via µCT using a Zeiss Versa XRM-520 X-ray microscope at the Centre for Microscopy, Characterisation and Analysis at the University of Western Australia. Processing of the resulting data followed the methods described in Semple et al. (2019) using the software packages Drishti 2.6.4 (Limaye 2012), Meshlab 2016 (Cignoni et al. 2008), and Adobe Acrobat Pro X.

For direct morphological examination of barnacle shell plates and arthropodal characters, the body and associated soft tissues were removed from the shell. The remnants of the barnacle tissue and host sponge on the surfaces of the parietes, scutum and tergum were removed using forceps. The shell was then immersed in 2% bleach for ~2 h to completely digest the organic tissue and subsequently rinsed in purified water. Any remaining debris or contaminants were then removed by cleaning in an ultrasonic cleaner for less than 20 s for shell plates and 5 s for arthropodal parts. The specimens were examined under a Leica M205 C (Leica, Germany) stereomicroscope and digital photographs produced with a Leica DMC4500. For scanning electron microscopy, specimens were first dehydrated in an ethanol series (70%, 80%, 90%, 100%, 5 minutes each) then transferred to hexamethyldisilazane for 10 min. Excess liquid was then removed with an eye-dropper and specimens were left to dry in a fume hood for 30 min. The dissected specimens were mounted on stubs, sputter coated with gold, and observed using a Hitachi TM3030 tabletop SEM. All images were processed using Adobe Photoshop CS3.

Adductor or depressor muscle tissues were subsampled from specimens, and genomic DNA was extracted using either a Bioline Isolate II or Qiagen DNeasy extraction kit following the manufacturers' instructions. Partial fragments of the cytochrome c oxidase I gene were amplified using the primers dgLCO1490 5'-GGTCAACAAATCATAAAGAYATYGG-3' and dgHCO2198 5'-GGTCAACAAATCATAAAGAYATYGG-3' (Meyer et al. 2003) in a 25 µL reaction volume consisting of 1 unit MyTaq DNA polymerase, 1× MyTaq PCR buffer, 0.5 µL of each primer, and 2 µL template. The following polymerase chain reaction conditions were used: 2 min at 95 °C for initial denaturing, then 35 cycles of 30 s at 95 °C, 30 s at 46 °C, 45 s at 72 °C, and a final extension for 7 min at 72 °C. The resulting amplicons were sequenced by the Australian Genome Research Facility, Perth, using the same primers. The sequences were assembled and trimmed using Geneious Prime and submitted to GenBank (Table 1; https://www.ncbi.nlm.nih.gov/genbank/).

Specimens of both barnacles and sponges are housed at the Western Australian Museum, Perth (WAM) and South Australian Museum, Adelaide (SAMA).

Systematics

Suborder Balanomorpha Pilsbry, 1916
Superfamily Balanoidea Leach, 1817
Family Archaeobalanidae Newman & Ross, 1976

Genus *Membranobalanus* Hoek, 1913

Type species. *Balanus declivis* Darwin, 1854: 275, pl. 7 fig. 4a–d; by subsequent designation (Pilsbry 1916: 229).

Species composition. *M. brachialis* (Rosell, 1972); *M. costatus* Zullo & Standing, 1983; *M. cuneiformis* (Hiro, 1936); *M. declivis* (Darwin, 1854); *M. koreanus* Kim & Kim, 1983; *M. longirostrum* (Hoek, 1913); *M. nebrias* (Zullo & Beach, 1973); *M. orcutti* (Pilsbry, 1907); *M. porphyrophilus* sp. nov.; *M. robinae* Van Syoc, 1988.

Nomen dubium. *M. orcuttiformis* (Kolosváry, 1941).

Diagnosis. Parietes solid, unornamented, weakly articulated, basis membranous. Rostrum scoop or boat-shaped, often elongate relative to other parietes. Tergum with spur furrow open. Cirrus IV with erect spines, with or without recurved teeth on anterior ramus.

Remarks. With the addition of the below described species, there are now 10 species included within *Membranobalanus.* Utinomi (1968) synonymised the taxa *Balanus* (*Membranobalanus*) *longirostrum* var. *krusadaiensis* Daniel, 1955, *B.* (*M.*) *basicupula* Suhaimi, 1966, and *B.* (*M.*) *roonwali* Prem-Kumar & Daniel, 1968 under *M. longiro-*

Table 1. Accession details for COI sequences of *Membranobalanus porphyrophilus* sp. nov. deposited with GenBank.

Specimen catalogue	GenBank #
WAM C66803	MK900684
WAM C71853	MK789771
WAM C71881	MK789772

strum, proposing that the differences observed are within the bounds of intraspecific variability. Recently, van Syoc et al. (2015) transferred *Acasta acuta* (Kolbasov, 1993) out of *Membranobalanus* based primarily on the presence of calcareous spines on the parietal wall, a character no other *Membranobalanus* possess and in reference to a cladistic analysis in an unpublished thesis. The fact that *A. acuta* is found in sponges of the family Petrosiidae (order Haplosclerida), not the Clionaidae as reported for the remaining members of the genus, separates this species ecologically from *Membranobalanus*, was used as further justification. The general appearance, membranous basis and elongated rostrum of *A. acuta* are typical features of *Membranobalanus*, however. While we treat this reassignment with caution, we have no evidence with which to dispute it.

Kolosváry (1941) described *Balanus* (*M.*) *orcuttiformis* based on the parietes of a single empty specimen. The locality details of the specimen are vague, only given as "India Orient.", but presumably meaning eastern India. No detail regarding a host was given. The description is very brief, giving very few clues to the identification of this species, and the only illustration of the specimen, in lateral view, could belong to a number of genera, but not *Membranobalanus* as currently defined. Most notable is the absence of any elongation of the rostrum and the largely horizontal basal rim of the parietal wall gives the appearance that it was attached to, rather than embedded within, a substrate. Additionally, the exceptionally broad alae and absent radii are reminiscent of the Pachylasmatoidea, which possess solid parietes and often have a membranous base (see Jones 2000). *Membranobalanus orcuttiformis* has not been recorded since its description and unfortunately the specimens are missing from the Museo di Storia Naturale dell'Università di Firenze, Italy and thus cannot be reexamined (Innocenti 2006). For these reasons, this species is considered herein a *nomen dubium* and has been excluded from the key below.

The remaining *Membranobalanus* species can be separated into two morphological lineages, approximating an American centred group and an Indo-West Pacific group. The former have recurved teeth, similar to those present in some members of the Acastinae, as well as erect spines on cirrus IV, smooth growth lines on the scutum and the articular ridge and groove of the scutum is prominent, extending well beyond the articular margin, with a correspondingly wide articular groove on the tergum. The latter group bears only the erect spines on cirrus IV, finely striated growth lines, and has relatively weak articular structures on the opercular plates. From a biogeographic perspective one species disrupts this pattern: *Membranobalanus koreanus* from the waters around the Korean Peninsula. As described and figured by Kim and Kim (1983), *M. koreanus* has recurved teeth and a large articular ridge on the scutum. The records of *M. orcutti* by Barnard (1924) and Rosell (1973, 1975) from South Africa and the Sulu Archipelago, respectively, were considered suspect by Zullo and Beach (1973) and Van Syoc and Winther (1999). The Sulu Archipelago specimens lack the recurved teeth on cirrus IV of the specimens described from Catalina Island by Zullo and Beach (1973), and while Barnard's description specifically mentions recurved teeth on cirrus IV, most of his description is deferred back to either Pilsbry's (1907, 1916) descriptions of *M. orcutti* or Hoek's (1913) description of *M. longirostrum.* Of particular note in Barnard's description is that the scutum has an external, setose membrane, a character seen in some species of the Acastinae, but not *Membranobalanus*. Both reports should be considered *species inquirenda*, but potentially represent previously undescribed species.

Membranobalanus porphyrophilus Hosie & Jones sp. nov.

http://zoobank.org/170E814F-E3ED-4120-8622-EC4230353C65

Figures 1–6

Material examined. Holotype. AUSTRALIA • WAM C66803, 1 hermaphrodite; 9 mm rostro-carinal diameter; Western Australia SE of Rottnest Island, Wallace Island, The Count; 32°0.89'S, 115°33.53'E; 12 m; coll. A.M. Hosie; 23 Feb 2017; host: WAM Z86929, *Spheciospongia purpurea*.

Paratypes. AUSTRALIA • WAM C71852, 1 hermaphrodite; 8 mm rostro-carinal diameter; empty shell; same as data as for holotype. • WAM C71853, 1 hermaphrodite; same as data as for holotype. • WAM C71881, 1 hermaphrodite; same as data as for holotype. • SAMA C12706, 1 hermaphrodite; South Australia, Kangaroo Island, off Second Gully between Western River Cove and Snug Cove; 32 m; coll. J. Thiselton; 19 Nov 2002; host: SAMA S2910, *S. purpurea*. • SAMA C12707, 1 hermaphrodite; same data as for previous. • SAMA C12708, 1 hermaphrodite; 14 mm rostro-carinal diameter; same data as for previous.

Diagnosis. Shell wall robust, cylindrical, growth ridges weak; orifice toothed, large; rostrum basal margin broadly rounded, extending below basal plane of remaining parietes. Tergum narrow, beaked, spur narrow, separated from basiscutal angle by half its own width; scutum with faint, external longitudinal striations; basitergal angle broadly rounded. Cirri III and IV with row of strong, erect spines on anterodistal margin of anterior ramus; cirrus IV pedicel without erect spines; cirri IV and V with row of stout spines on posterior margin of anterior ramus basal segment.

Description. All shell plates, prosoma, and internal organs stained purple *in vivo*, otherwise white. Shell walls (Figs 1, 2) parallel, except bowed rostrum; parietes externally with horizontal growth lines raised, ridge-like, giving shell a roughened appearance; radii prominent, summits oblique, sutural edges roughened, alae wide, summits oblique. Internally parietes smooth, sheath occupying approximately half of shell height, with horizontal growth lines, basal margin adpressed. Carina approximately as wide as lateral plate, carinolateral narrowest plate, approximately one-third width of lateral plate. Rostrum elongate, extending below basal margin of other parietes, almost twice length and twice width of lateral plate, basal margin broadly rounded below basal margin of latera. Basal margins of carina and carinolatera more or less perpendicular to shell vertical axis, latera basal margins curving basally to form contiguous rim connecting latera with rostrum. Basis membranous, follows contour of basal rim, not depending below parietes.

Scutum (Fig. 3A–D, I, J) triangular, height 1.3–1.8 times width, growth lines prominent with faint longitudinal striations; basal and tergal margins separated by broadly rounded basitergal angle. Internal surface, slightly ridged apically near tergal

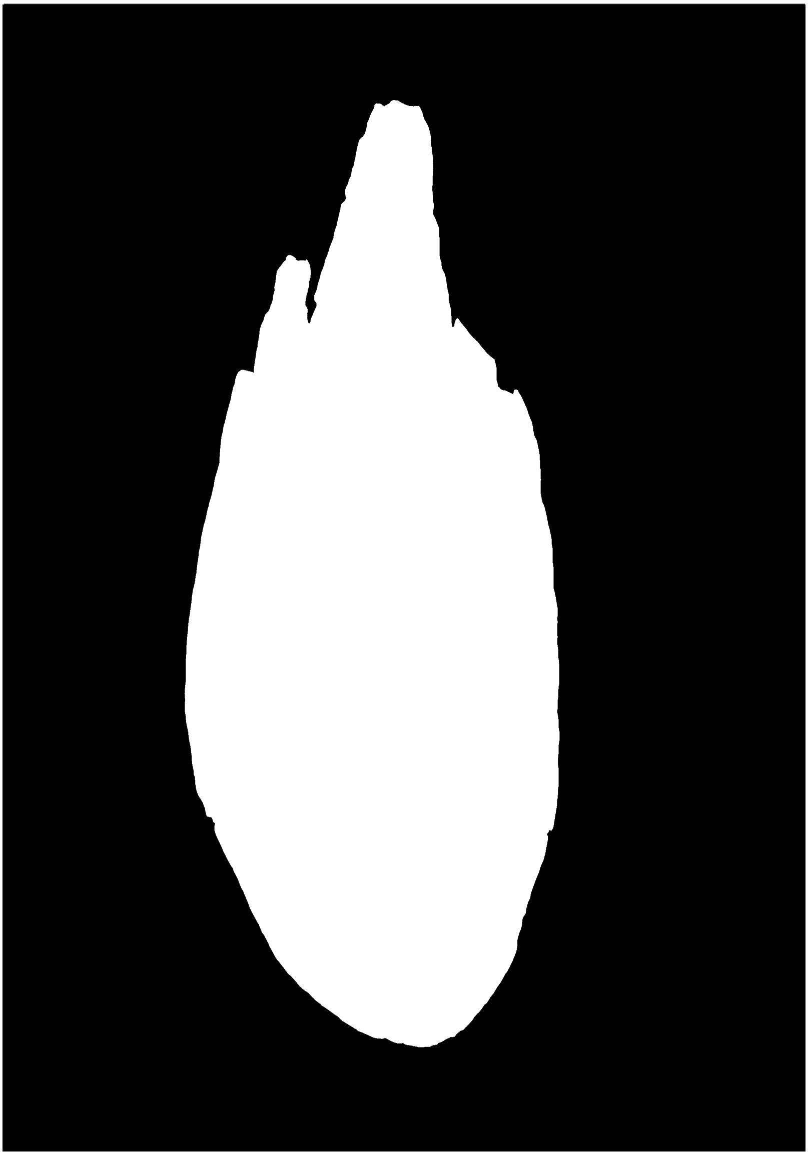

Figure 1. Interactive 3D, µCT derived volume reconstruction of *Membranobalanus porphyrophilus* sp. nov. holotype (WAM C66803). Only the well-calcified plates are illustrated as scanning limitations prevented the softer prosoma from being differentiated. Note: To enable the interactive function of this figure, open the PDF in Adobe Reader program or web plug-in.

margin, otherwise smooth; adductor muscle pit distinct; lateral depressor muscle pit distinct, without depressor muscle crests, extending one-third distance to beginning of articular ridge bounded by low, rounded adductor muscle ridge. Articular groove deep, narrow; articular ridge barely projecting beyond articular margin, basal margin curved.

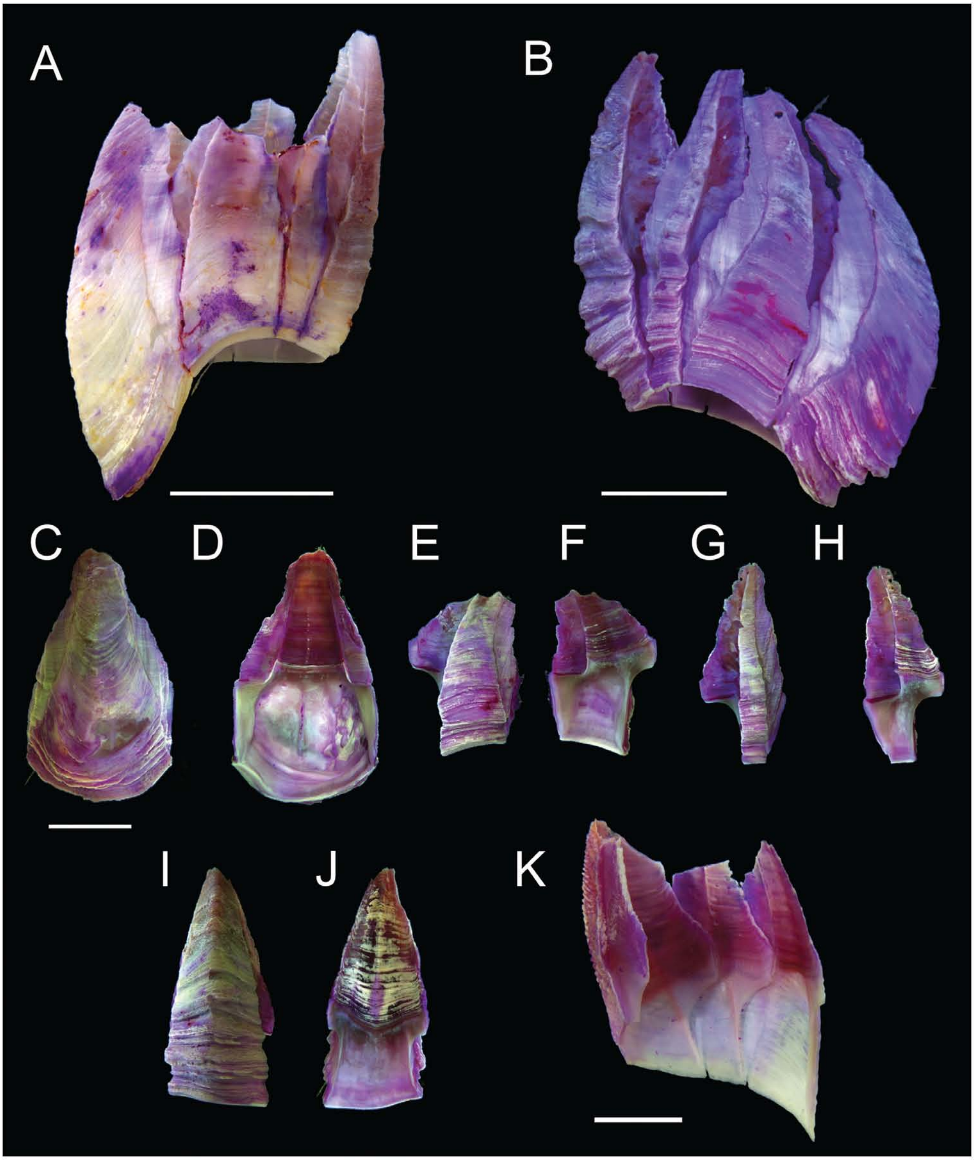

Figure 2. *Membranobalanus porphyrophilus* sp. nov. parietes **A** holotype (WAM C66803) **B–J** paratype (SAMA C12708) **K** paratype (SAMA C12706). **A** Whole shell lateral view **B** whole shell lateral view **C, D** rostrum, external and internal view **E, F** left lateral plate, external, and internal view **G, H** left carinolateral, external and internal view **I, J** carina external and internal view **K** internal view of articulated right carina, carinolateral and lateral plates. Scale bars: 5 mm (**A–J**); 2 mm (**K**).

Tergum (Fig. 3E–H, K, L) narrow, height more than twice width, articular and carinal margins arcuate with beaked apex; external growth lines conspicuous, but less raised than those of scutum; spur furrow indicated by shift in growth lines and slight depression; basiscutal angle sloping into spur; spur narrow, separated from basiscutal

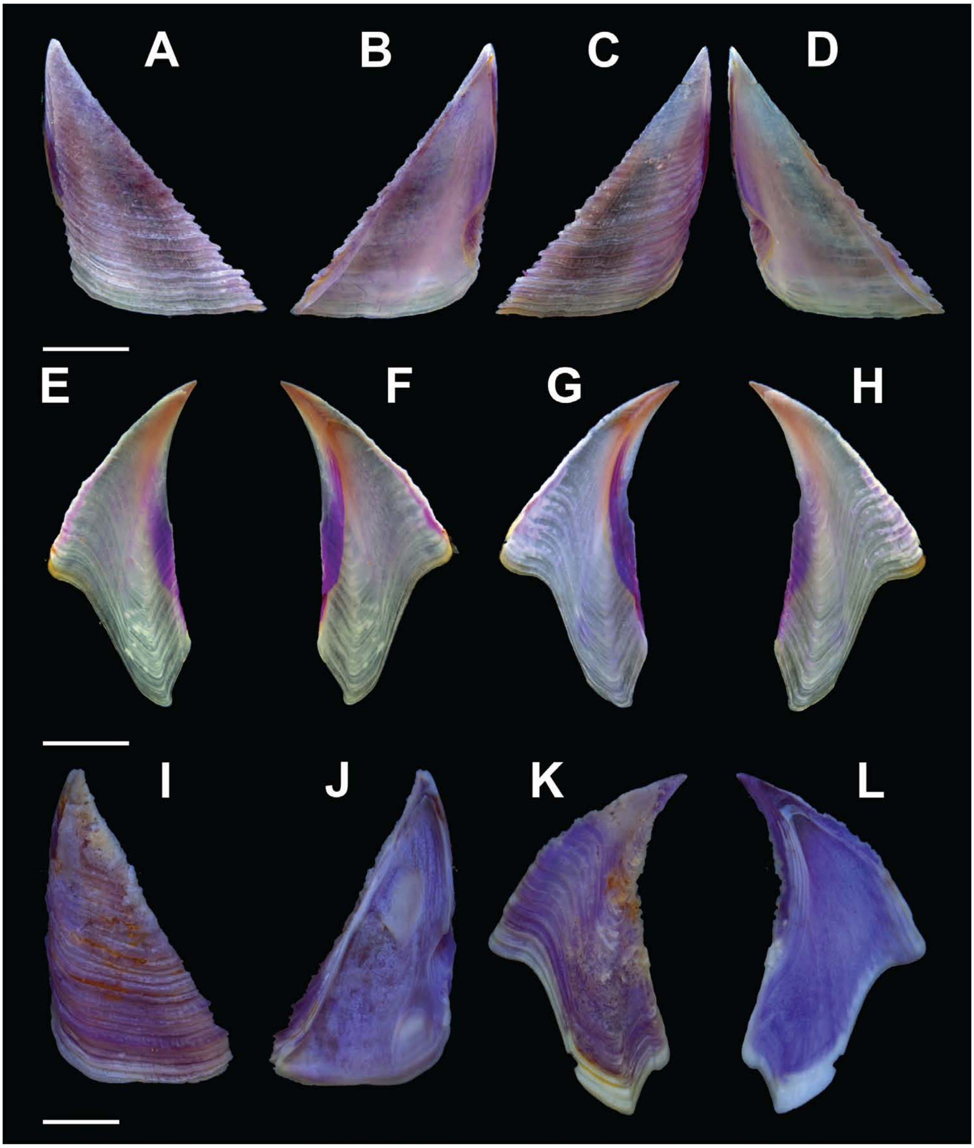

Figure 3. *Membranobalanus porphyrophilus* sp. nov. opercular plates **A–H** holotype (WAM C66803) **I–L** paratype (SAMA C12708). **A** Left scutum, external view **B** left scutum, internal view **C** right scutum, external view **D** right scutum, internal view **E** left tergum, external view **F** left tergum, internal view **G** right tergum, external view **H** right tergum, internal view **I** left scutum, external view **J** left scutum, internal view **K** left tergum, external view **L** left tergum, internal view. Scale bars: 2 mm.

angle by half its width, basally truncate. Internally smooth, depressor muscle crests weak (may be absent in small specimens), articular groove wide, open, shallow; articular ridge low, becoming confluent with scutal margin basally.

Labrum (Fig. 4A–F) bilobed, with deep medial notch bounded by rounded crests, each with two or three marginal teeth and numerous fine setae.

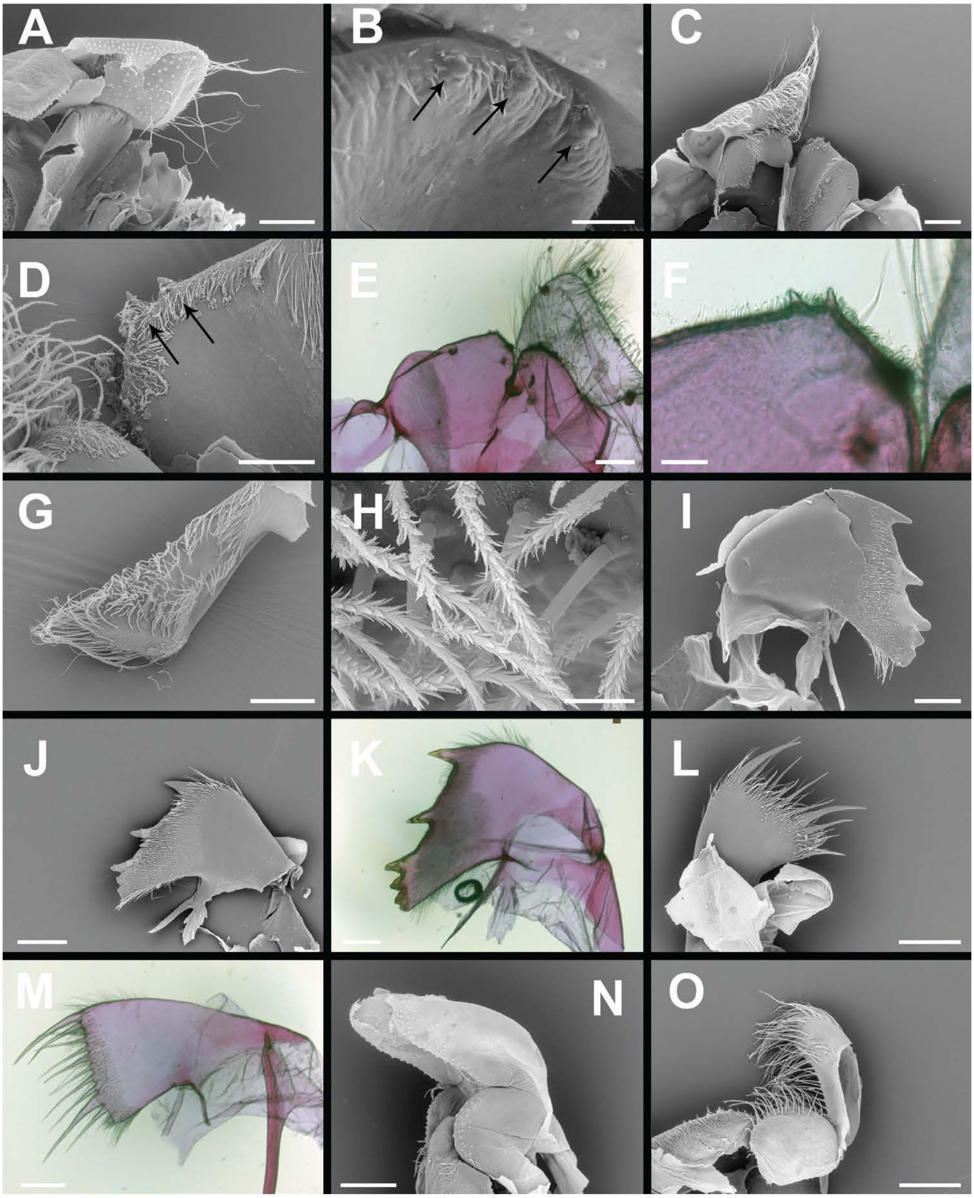

Figure 4. *Membranobalanus porphyrophilus* sp. nov. mouthparts **A, B, G, H, I, L, N** holotype (WAM C66803) **C, D, J, O** paratype (SAMA C12708) **E, F, K, M** paratype (SAMA C12706). **A, C** Labrum and right mandiblular palp (left removed, damaged) **B, D** close up of A and D, arrows indicate teeth on labrum **E** left mandibular palp **F** detail of serrulate setae on mandibular palp ventral face **G–I** mandibles **J** maxillule **K, L** maxilla. Note: G, H, L damaged, setae lost during sonication in A & K. Scale bars: 200 µm (**A, C, E, G, I–O**); 40 µm (**B, F**); 100 µm (**D**); 50 µm (**H**).

Mandibular palp (Fig. 4A, C, E, G, H) rhomboid, apex obliquely truncate, anterior margin concave, posterior margin straight; setae (Fig. 4F) heavily serrulate, becoming longer and denser distally.

Mandible (Fig. 4I–K) with four distinct teeth, 2nd and 3rd tooth bifid, 4th tooth much smaller than preceding three, 5th tooth obsolescent, confluent with molariform inferior angle; short setae covering inner and outer faces, longer fine setae on inferior and superior margins.

Maxillule (Fig. 4l, M) with 10 robust setae on cutting margin, first, second, and ninth longer and more robust than remaining setae, inferior angle with several short robust setae. Cutting margin straight, with very slight notch below second seta. Dense, short setae regularly spaced on inner and outer faces, longer fine setae on inferior and superior margin

Maxilla (Fig. 4N, O) bilobed, basal lobe ovate, serrulate setae arranged on anterior margin; distal lobe elongate, serrulate setae on anterior margin becoming more dense at apex, longer than those on basal lobe.

Cirrus I (Fig. 5A) with unequal rami, anterior ramus twice length of posterior ramus, both rami bearing serrulate and simple setae. Posterior ramus segments with protuberant anterior margins, more densely setose than anterior ramus, arranged in tufts on anterior margins.

Cirrus II (Fig. 5B) shorter than other cirri, rami subequal; anterior margins of both rami slightly protuberant with serrulate and simple setae.

Cirrus III (Fig 5C, D) pedicel with plumose setae on anterior and posterior margins of both segments; rami equal; anterior ramus with erect spines and ctenoid scales on anterodistal portion of medial segments, tuft of long serrulate setae on rounded anterior margin up to approximately three times as long as segment, tuft of serrulate setae as long as segment at posterodistal angle.

Cirrus IV (Fig. 5E–L) pedicel without erect teeth on anterodistal margins, pedicel with numerous small denticles on posterior and anterior margins of mesial face, tuft of short setae at posterodistal angle, small ctenoid scale-like denticles at anterodistal margin. Rami subequal in length; basal-most segment with up to 13 stout spines along posterior margin (holotype with six), basal segments with one or two stout spines at posterodistal angle. Anterior ramus intermediate segments with row of erect spines on anterodistal portion of all but most distal segments, much reduced in posterior ramus, without recurved teeth on anterior faces, posterodistal angles with tuft of setae.

Cirrus V (Fig. 6A–C) characters intermediate between cirri IV and VI; pedicel with numerous small denticles on posterior and anterior margins of mesial face, tuft of short setae at posterodistal angle, small ctenoid scale-like denticles on anterodistal margin. Rami equal, segments becoming elongate distally from half as long as wide to three times longer than wide, both rami with four pairs of serrulate setae on anterior margin, distal most pair longest, approximately 3 times length of segment; tuft of simple setae at anterodistal angle, setae up to half length of segment; erect teeth on anterior margins of intermediate segments less pronounced than those on cirrus IV; stout spines on posterior margins of rami similar to cirrus IV.

Cirrus VI (Fig. 6D–G) rami equal, pedicel with numerous small denticles on posteromesial face, tuft of simple setae at posterodistal angle; intermediate segments of both rami becoming elongate distally from 1.5 times wider than long to three times

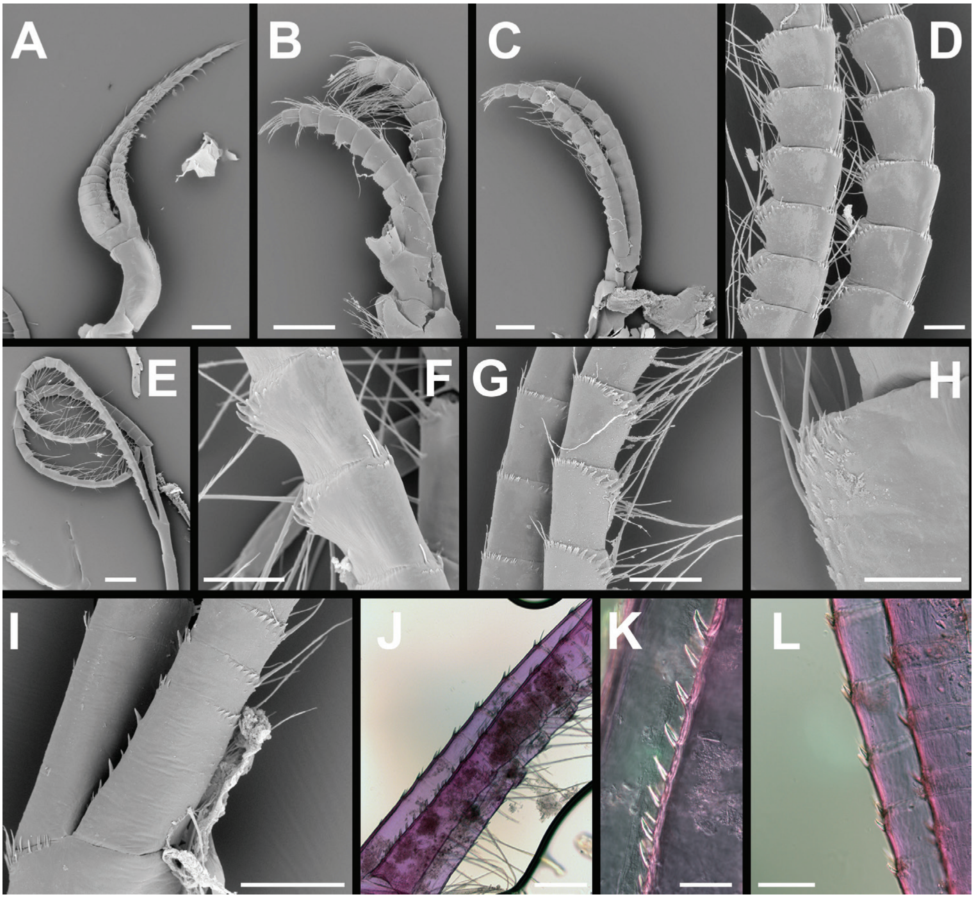

Figure 5. *Membranobalanus porphyrophilus* sp. nov. cirri **A–F** holotype (WAM C66803) **G–I** paratype (SAMA C12706) **J–L** paratype (SAMA C12708). **A–C** Right cirrus I–III lateral view **D** right cirrus III intermediate segments **E** right cirrus IV lateral view **F** same, anterior ramus intermediate segments **G** left cirrus IV anterior ramus intermediate segments **H** right cirrus IV anterodistal angle of distal segment of pedical showing ctenoid scales **I, J** left cirrus IV basal segments of rami showing posterior spines **K** close up of spines on posterior margin of J **L** close up of spines and posterodistal spines basal segments of J. Note: B, C, E damaged. Scale bars: 400 μm (**A–C, E**); 100 μm (**D, F, L**); 150 μm (**G, I**); 50 μm (**H, K**); 200 μm (**J**).

longer than wide, both rami with four pairs of serrulate setae on anterior margin, distal most pair longest, approximately three times the length of segment, basal pair 0.3 times length of segment; tuft of simple setae at anterodistal angle, setae up to 0.5 length of segment; anterior margins of all segments without erect teeth, posterior margins without stout spines.

Cirral segment counts as follows (anterior ramus, posterior ramus):

	Cirrus	I	II	III	IV	V	VI
WAM C66803	L	21, 9	9, 11	17, 13	27, 30	34, 32	33, 33
	R	20, 9	11, 9	17, 14	30, 30	32, 34	36, 34

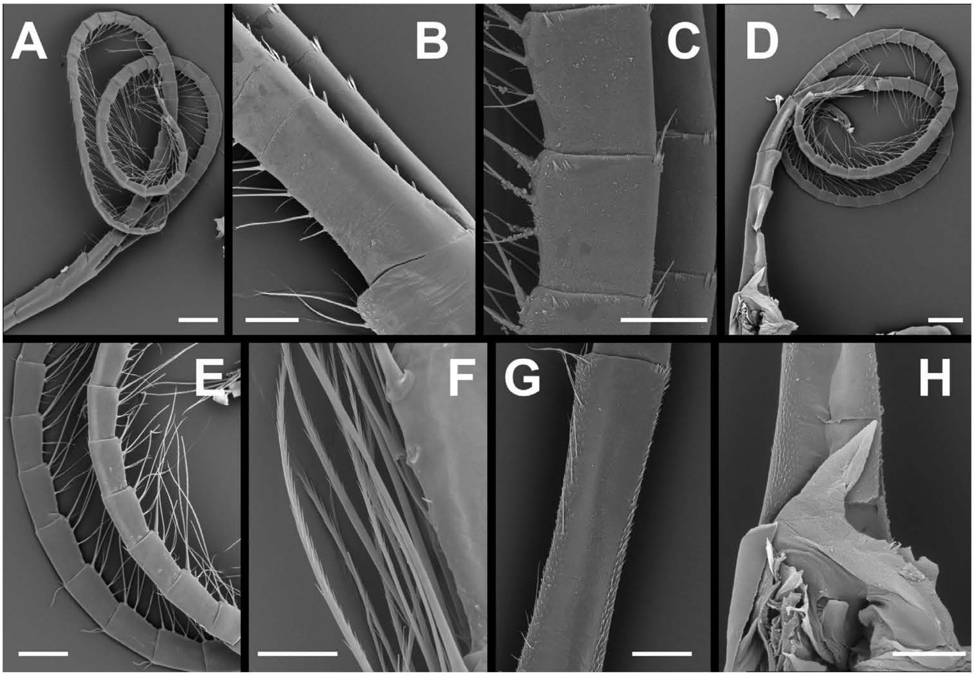

Figure 6. *Membranobalanus porphyrophilus* sp. nov. cirri **A, B, D, E, H** holotype (WAM C66803) **C, F, G** paratype (SAMA C12706). **A** Right cirrus V lateral view **B** basal segments of cirrus V rami **C** intermediate segments of cirrus V anterior ramus **D** right cirrus VI mesial view (damaged) **E** same, intermediate segments **F** example of long serrulate setae on cirrus VI **G** basal segment of pedicel of right cirrus VI, mesial view showing denticles on anterior and posterior margin **H** basidorsal point of penis. Scale bars: 400 µm (**A, D**); 100 µm (**B, C**); 50 µm (**F**); 150 µm (**G, H**); 80 µm (**E**).

Penis longer than CVI, annulated, sparsely setose along length; basidorsal point (Fig. 6H) prominent, triangular, height twice width.

Distribution. Southern Australia, from Perth to Adelaide.

Etymology. From Greek *porphyra*, purple and *philos*, indicating a love of; gender masculine. In reference to the vibrant purple colour of the only known host.

Remarks. *Membranobalanus porphyrophilus* sp. nov. is most readily distinguished from its congeners by the narrow, beaked tergum. The absence of recurved teeth on cirrus IV, the finely striated scutal growth lines, and the weak articular structure of the opercular plates further separates the newly described species from the predominantly American group of species, viz. *M. costatus*, *M. declivis*, *M. koreanus*, *M. nebrias*, *M. orcutti*, and *M. robinae*. The remaining species in the genus, *M. brachialis*, *M. cuneiformis*, and *M. longirostrum* all bear prominent, erect spines on the pedicel of cirrus IV and lack the stout spines on the posterior margins of the rami of cirri IV–VI. This is only the second member of the genus reported from Australian waters. The other, *M. cuneiformis*, is known from near Darwin and was reported by Hiro (1936) as commensal with an unidentified species of *Cliona* that was bioeroding the shell of *Pinctada maxima* (Jameson, 1901). Externally, *M. cuneiformis* can be separated from *M. porphyrophilus* by the conical shape of the shell, resulting in a small orifice and absent radii.

Discussion

Only a single sequence, identified as *M. longirostrum* (GenBank accession #KC138493; Chen et al. 2013), represents the genus *Membranobalanus* on GenBank, and the sequences generated herein are less than 85% similar, indicating a rather distant relationship with *M. porphyrophilus* sp. nov.

The degree of elongation and curvature of the rostrum is variable in *M. porphyrophilus* sp. nov. and does not appear to be directly related to increasing size, as the rostrum of both the larger and smaller specimens can be relatively short. The development of the rostrum will be in large part an adaptation to prevent being overgrown by the host, and it is likely that the aspects of the rostral form will be determined by the placement of the barnacle relative to the direction of growth of the host.

While *Spheciospongia* are bioeroders generally only in early life history stages, the bioeroding capacity does appear to have impacted on the barnacle shells. The older parts of the shell plates are often pitted and scarred, indicative of the potential bioeroding effects of the sponge. The shell plates, exoskeleton, and tissues are brightly stained by the purple pigments of the host sponge (persistent even in ethanol), and are the most obvious impact of the sponge on the barnacle.

Spheciospongia purpurea has had a complex taxonomic history and at one stage many species were listed in synonymy and thus the species was considered to be widely distributed (see Vosmaer 1911: 6 for list of synonyms). Topsent (1918) brought many of these species back out of synonymy and *S. purpurea* is now considered to be endemic to southern Australia (Atlas of Living Australia 2019). In Hoek's (1913) report on the cirripedes collected during the *Siboga* Expedition he listed *S. purpurea* as the host sponge in his description of *M. longirostrum* collected from the seas around Indonesia, far outside the known range of *S. purpurea*. Hoek's record is, thus, considered to be a misidentification, most likely based on the identifications in Vosmaer's (1911) account of the sponges from the same expedition. It is unclear if the records of *S. purpurea* as the host by Rosell (1972) from the Philippines and by Utinomi (1968) from Japan are based on their material or simply repeated from Hoek's report, but here they are considered to be errors for the same reason.

No other barnacle species were found inhabiting any of the 15 *S. purpurea* specimens examined during the course of this study. Over 200 morphospecies of sponge have been found to host barnacles in Australian waters (Hosie and Fromont unpublished data), including five other species of *Spheciospongia*, and *Membranobalanus porphyrophilus* sp. nov. has been found inhabiting only *S. purpurea*, making it likely to be restricted to this species and therefore also an Australian endemic.

Host specificity of *Membranobalanus* was first discussed by van Syoc (1988), and the newly described species supports the hypothesis that they are restricted to inhabiting species of the Clionaidae. The exception to this is *M. longirostrum*, which has also been reported inhabiting species of the Suberitidae in the Red Sea (Ilan et al. 1999) and Indonesia (Wibowo et al. 2011; Sulistiono et al. 2014). The potential for the misidentification of host species by Ilan et al. (1999) was raised by van Syoc (2015), as the genus *Suberites* is morphologically similar to *Spheciospongia.* This similarity has led to species of both genera being confounded; as an example, *Suberites wilsoni* Carter, 1885 is considered a subjective synonym of *S. purpurea*. The existing records of *Membranobalanus* embedded in *Suberites*, as well as any future collections, need to be examined by sponge specialists to determine if they have been correctly assigned.

Key to the genus *Membranobalanus*

1	Cirrus IV anterior ramus bearing recurved teeth and erect spines	**2**
–	Cirrus IV anterior ramus bearing only erect spines	7
2	Rostrum much longer than other parietes	**3**
–	Rostrum approximately as long as other parietes	**5**
3	Radii absent	***M. orcutti***
–	Radii present	**4**
4	Scutum with radius-like ledge on occludent margin	***M. koreanus***
–	Scutum occludent margin normal, lacking ledge	***M. declivis***
5	Parietes costate	***M. costatus***
–	Parietes not costate	**6**
6	Basal margin of all parietes rounded; tergal articular ridge low, articular groove open	***M. robinae***
–	Basal margin of laterals more or less straight; tergal articular ridge overhanging articular groove	***M. nebrias***
7	Radii broad, conspicuous; tergal spur narrow, longer than wide, cirrus IV pedicel without erect spines on anterodistal margins	***M. porphyrophilus* sp. nov.**
–	Radii absent or very narrow, tergal spur wider than long, cirrus IV pedicel with erect spines on anterodistal margins	**8**
8	Rostrum with median furrow, elongated basal portion tapering, very narrow	**10**
–	Rostrum without median furrow, basal portion wedge-shaped	***M. cuneiformis***
9	Basal membrane with spine-like processes	***M. brachialis***
–	Basal membrane without spine-like processes	***M. longirostrum***

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New Species and New Records of Sponge-Inhabiting Barnacles (Cirripedia, Balanidae, Acastinae) from Australia

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Abstract: The subfamily Acastinae contains a diverse group of barnacles that are obligate symbionts of sponges and alcyonacean and antipatharian corals. Integrating morphological and genetic (*COI*) data to compare against known species, this paper reports on nine species of sponge-inhabiting barnacles of the subfamily Acastinae, including three undescribed species (*Acasta caveata* sp. nov., *Euacasta acutaflava* sp. nov., and *E. excoriatrix* sp. nov.) and three species previously not recorded in Australian waters (*A. sandwichi*, *Pectinoacasta cancellorum*, and *P. sculpturata*). The new species are distinguished from similar species by a suite of morphological characters as well as genetic distances. A lectotype for *Pectinoacasta cancellorum* is designated. Sponge hosts were identified for all specimens where possible and are represented by 19 species from eight families and five orders.

Keywords: biodiversity; commensalism; symbiosis; barcodes; Porifera; Crustacea; host specificity

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1. Introduction

Barnacles can be found as obligate commensals with a variety of taxa, but those in symbiosis with sponges are proving to be particularly diverse [1–4]. The majority of sponge symbionts are classified under the subfamily Acastinae [5], with approximately 90 described species, and this number is expected to at least double [1,4]. Historically, this group had been arranged within informal groups based on characters of the fourth cirrus by Broch [6] and opercular plates by Hiro [7] under the genus *Acasta sensu* Leach, 1817 [8]. Neither author took this further, largely due to the close affinity with *Conopea* Say, 1812 [9], and *Membranobalanus* Hoek, 1913 [10], whose members are obligate commensals with cnidarians and sponges, respectively, but also *Armatobalanus* [10], which contained a mixture of free-living and commensal species. This caution has proven to be warranted, as a number of species have been transferred between these genera by subsequent workers [11]. Further to this, phylogenetic studies have also shown that the subfamily and family level arrangement is also unsupported within the Balanoidea [12,13]; as a result, the family Archaeobalanidae was recently synonymised with the Balanidae [14]. Kolbasov [5], in his revision of *Acasta*, was the first to evaluate host usage in the *Acasta* and how that was reflected in his newly proposed phylogeny and generic arrangement, which revealed some loose trends, but was hampered by a distinct lack of previously published host data.

Since then, more studies on sponge-inhabiting barnacles have been placing emphasis on host identification [1–3,15,16] to build a better understanding of host usage. Not only have the evolutionary relationships of the hosts begun to be looked at, but also the morphology of the host has been examined to test larval barnacle biology [17]. Integrating modern techniques such as genetic sequencing and computed tomography [18,19] has also provided greater precision when evaluating inter- and intra-specific variation by shedding light on character evolution.

The waters surrounding the Australian coast are inhabited by a highly diverse sponge fauna [20–22], leading to an expectation of a correspondingly diverse community of sponge-inhabiting barnacles. This paper reports on a collection of sponge-inhabiting barnacles from across Australian territorial waters as part of a broader study on the biodiversity of commensal barnacles.

2. Materials and Methods

2.1. Sampling and Morphological Examination

Specimens of both the barnacles and the sponges examined in this study are deposited in the following institutions: Western Australian Museum, Perth (WAM), Queensland Museum, Brisbane (QM), University of Copenhagen Zoological Museum, Denmark (ZMUC), and Seto Marine Biological Laboratory, Japan (SMBL). For direct morphological examination of barnacle shell plates and arthropodal characters, the body and associated soft tissues were removed from the shell. The remnants of the barnacle tissue and host sponge on the surfaces of the parietes, scutum and tergum, were removed using a brush and forceps. The shell was then immersed in 2% bleach for <2 h to completely digest the organic tissue and was subsequently rinsed in water. Any remaining debris or contaminants were then removed by cleaning in an ultrasonic cleaner for <5 s. The specimens were examined under a Leica M205 C (Leica, Germany) stereomicroscope and digital photographs produced with a Leica DMC4500. All images and figures were processed using GIMP 2.10 (www.gimp.org accessed on 20 June 2021) or Inkscape 0.92 (www.inkscape.org accessed on 20 June 2021). Barnacle size is measured in millimetres along the rostro-carinal (RC) axis at the basal rim. Setal terminology follows that of Chan et al. [23].

Sponge identifications were partly facilitated by examining gross morphology, surface characteristics, and microscopic skeletal characteristics of specimens. Subsamples of sponge tissue were sectioned at right angles to the surface of the sponge and processed for microscopic examination using a Shandon Elliott tissue processor. This included ethanol dehydration, histolene to clear the tissue, and subsequent paraffin impregnation. Thick sections (~90 μm) were cut with a Leitz slide microtome from wax blocks. Sections were de-waxed in histolene and mounted using Shandon EZ-Mountant. Skeletal slides were examined with an Olympus BX50.

2.2. Molecular Analysis

Adductor or depressor muscle tissues of barnacles were subsampled from specimens, and genomic DNA was extracted using either a Bioline Isolate II or Qiagen DNeasy extraction kit following the manufacturer's instructions. Partial fragments of the cytochrome c oxidase I (*COI*) gene were amplified using the primers dgLCO1490 5′-GTCAACAAATCATAAAGAYATYGG-3′ and dgHCO2198 5′- TAAACTTCAGGGTGACCAAARAAYCA-3′ [24] in a 25 μL reaction volume and consisting of 2 μL DNA extract, 1 unit MyTaq DNA polymerase, MyTaq PCR buffer, and 0.1 μM of each primer. The following polymerase chain reaction conditions were used: 2 min at 95 °C for initial denaturing, then 35 cycles of 30 s at 95 °C, 30 s at 46 °C, 45 s at 72 °C, and a final extension for 7 min at 72 °C. The resulting amplicons were sequenced at the Australian Genome Research Facility, Perth, using the same primers via Sanger (cycle) sequencing.

The sequences were assembled and trimmed using Geneious Prime and submitted to GenBank (Table 1, https://www.ncbi.nlm.nih.gov/genbank/ accessed on 20 June 2021). Quality control of sequences involved trimming low-quality bases, inspecting for stop codons, verifying the reading frame, checking for matches on BLAST, and re-examining original specimens.

Representative *COI* sequences identified as belonging to the genera studied herein were downloaded from GenBank and BoLD (www.boldsystems.org) (Table 1). *Membranobalanus porphyrophilus* Hosie and Jones, 2019 [18], was selected to serve as an outgroup in the phylogenetic analyses. The combined dataset was aligned in Geneious Prime 2020.2.5 (https://www.geneious.com) and checked manually. The Assemble Species by Automatic

Partitioning (ASAP; [25]) software was used to compare the genetic data with the morphological identifications by delimiting putative species under three substitution models: Jukes-Cantor (JC69) [26], Kimura 2-parameter model (K2P) [27], and uncorrected p-distance. Pairwise genetic distances were calculated using the software MEGA v10 [28]. Phylogenetic reconstructions using a maximum likelihood analysis were conducted using the IQ-TREE webserver [29]. Model selection was automatically assessed by the webserver, with the *COI* data partitioned by codon, and branch support was calculated by conducting 1000 ultra-fast bootstraps [30]. Bayesian inference analyses were conducted in MrBayes 3.2.6 [31] utilising the CIPRES webserver [32] with four heated chains, a General Time Reversible model with proportion of invariable sites and rate heterogeneity across sites (GTR+I+G), an MCMC of 11 million generations, and a burn-in of 10%.

Table 1. Specimen details of sequences used in the molecular analysis. Records in bold indicate specimens newly sequenced for this study.

Species	Accession	Host Species	GenBank
Acasta aspera	SGI20-1	*Iotroata* sp.	KY581615 [3]
Acasta aspera	SGI20-2	*Iotroata* sp.	KY581616 [3]
Acasta aspera	SGI2-1	*Iotroata* sp.	KY581614 [3]
Acasta aspera	WAM C55057	*Crella* (*Yvesia*) *spinulata*	KY581613 [3]
Acasta aspera	WAM C58741	*Crella* (*Yvesia*) *spinulata*	KY581610 [3]
Acasta aspera	WAM C58742	*Crella* (*Yvesia*) *spinulata*	KY581611 [3]
Acasta aspera	WAM C58743	*Crella* (*Yvesia*) *spinulata*	KY581612 [3]
Acasta aspera	**WAM C58812**	***Lissodendoryx* (*Acanthodoryx*) KMB1**	**MZ086820**
Acasta aspera	**WAM C58813**	***Lissodendoryx* (*Acanthodoryx*) KMB1**	**MZ086821**
Acasta aspera	**WAM C58815**	***Lissodendoryx* (*Acanthodoryx*) KMB1**	**MZ086822**
Acasta aspera	**WAM C58835**	***Hamigera* PB1**	**MZ086823**
Acasta aspera	**WAM C58837**	***Hamigera***	**MZ086824**
Acasta aspera	**WAM C58838**	***Hamigera***	**MZ086825**
Acasta aspera	**WAM C71837**	***Lissodendoryx* (*Acanthodoryx*) KMB1**	**MZ086844**
Acasta aspera	**WAM C71838**	***Lissodendoryx* (*Acanthodoryx*) KMB1**	**MZ086845**
***Acasta caveata* sp. nov.**	**WAM C67716**	***Gelliodes* KMB1**	**MZ086833**
***Acasta caveata* sp. nov.**	**WAM C67717**	***Gelliodes* KMB1**	**MZ086834**
Acasta crucibasis	MF796674	Unknown	MF796674
Acasta crucibasis	S32-1	*Xestospongia vansoesti*	MN842021 [17]
Acasta cyathus	SGI265-1	*Xestospongia testudinaria*	MN842022 [17]
Acasta daedalusa	SGI28-2	*Petrosia* (*Petrosia*) sp.	MN842023 [17]
Acasta fenestrata	**WAM C46669**	***Neopetrosia chaliniformis***	**MZ086796**
Acasta fenestrata	**WAM C55251**	***Neopetrosia chaliniformis***	**MZ086800**
Acasta fenestrata	**WAM C55319**	***Neopetrosia chaliniformis***	**MZ086808**
Acasta fenestrata	**WAM C55320**	***Neopetrosia chaliniformis***	**MZ086809**
Acasta fenestrata	**WAM C55321**	***Neopetrosia chaliniformis***	**MZ086810**
Acasta fenestrata	**WAM C55322**	***Neopetrosia chaliniformis***	**MZ086811**
Acasta fenestrata	**WAM C55323**	***Neopetrosia chaliniformis***	**MZ086812**
Acasta fenestrata	**WAM C55324**	***Neopetrosia chaliniformis***	**MZ086813**
Acasta fenestrata	**WAM C55325**	***Neopetrosia chaliniformis***	**MZ086814**

Table 1. *Cont.*

Species	Accession	Host Species	GenBank
Acasta fenestrata	**WAM C58748**	***Neopetrosia chaliniformis***	**MZ086818**
Acasta fenestrata	**WAM C58749**	***Neopetrosia chaliniformis***	**MZ086819**
Acasta fenestrata	**WAM C67829**	***Neopetrosia chaliniformis***	**MZ086839**
Acasta fenestrata	**WAM C71738**	***Neopetrosia chaliniformis***	**MZ086840**
Acasta fenestrata	**WAM C71739**	***Neopetrosia chaliniformis***	**MZ086841**
Acasta fenestrata	**WAM C72909**	***Neopetrosia chaliniformis***	**MZ086846**
Acasta fenestrata	**WAM C72914**	***Neopetrosia chaliniformis***	**MZ086847**
Acasta fenestrata	**WAM C74419**	***Neopetrosia chaliniformis***	**MZ086848**
Acasta huangi	SNE47-4	*Jaspis splendens*	KY581621 [3]
Acasta radenta	SLQ32-1	*Jaspis splendens*	MN842024 [17]
Acasta radenta	SNE47-1	*Jaspis splendens*	KY581619 [3]
Acasta sandwichi	SGI208-1	*Xestospongia testudinaria*	MN842025 [17]
Acasta sandwichi	SN77-1	Unknown	MF796675
Acasta sandwichi	SN77-2	Unknown	MF796676
Acasta sandwichi	**WAM C47383**	***Xestospongia testudinaria***	**MZ086797**
Acasta sandwichi	**WAM C53344**	***Xestospongia testudinaria***	**MZ086799**
Acasta sp. 1 MCY-2020	SJP55-N1	*Mycale* sp.	MN842026 [17]
Acasta sp. 2 MCY-2020	SLQ20-2	*Haliclona* sp.	MN842027 [17]
Acasta sp. 3 MCY-2020	SN81-3	*Petrosia* (*Petrosia*) sp.	MN842028 [17]
Acasta sp. 4 MCY-2020	SDS4-2	Unknown	MN842029 [17]
Acasta spongites	STI18-1	*Clathria* sp.	MN842030 [17]
Acasta sulcata	SN48-1	*Callyspongia* sp.	KY581617 [3]
Acasta sulcata	SN48-3	*Callyspongia* sp.	KY581618 [3]
Acasta turriformis	SGI178-1	Unknown	MF796671
Acasta turriformis	SGI178-2	Unknown	MF796672
Acasta undulaterga	SNE47-3	*Jaspis* splendens	KY581620 [3]
Acasta undulaterga	SNE47-5	*Jaspis* splendens	KY581622 [3]
Acasta vipensis	CAS:IZ:187687A	*Menella* sp.	KF587277 [33]
Acasta vipensis	CAS:IZ:187764A	*Menella* sp.	KF587282 [33]
***Euacasta acutaflava* sp. nov.**	**WAM C58744**	***Cymbastela stipitata***	**MZ086815**
***Euacasta acutaflava* sp. nov.**	**WAM C58745**	***Cymbastela stipitata***	**MZ086816**
***Euacasta acutaflava* sp. nov.**	**WAM C58746**	***Cymbastela stipitata***	**MZ086817**
***Euacasta acutaflava* sp. nov.**	**WAM C61434**	***Cymbastela* cf. *stipitata***	**MZ086830**
***Euacasta acutaflava* sp. nov.**	**WAM C61435**	***Cymbastela* cf. *stipitata***	**MZ086831**
***Euacasta excoriatrix* sp. nov.**	**WAM C61475**	***Halichondria* NW1**	**MZ086832**
***Euacasta excoriatrix* sp. nov.**	**WAM C71800**	***Halichondria* BAR1**	**MZ086842**
***Euacasta excoriatrix* sp. nov.**	**WAM C71801**	***Halichondria* BAR1**	**MZ086843**
Euacasta dofleini	SGI168-2	*Haliclona* sp.	MN842036 [17]
Euacasta microforamina	SJJ2-1	*Haliclona* sp.	MN842037 [17]
Euacasta sporillus	RMNH:CRUS:C.10235	*Axinyssa* sp.	KU986749

Table 1. *Cont.*

Species	Accession	Host Species	GenBank
Euacasta sporillus	S14-1	*Aaptos suberitoides*	MN842038 [17]
Membranobalanus porphyrophilus	WAM C71853	*Spheciospongia purpurea*	MK789771 [18]
Membranobalanus porphyrophilus	WAM C71881	*Spheciospongia purpurea*	MK789772 [18]
Pecitnoacasta sculpturata	**WAM C61394**	***Amphinomia sulphurea***	**MZ086827**
Pecitnoacasta sculpturata	**WAM C61395**	***Amphinomia sulphurea***	**MZ086828**
Pecitnoacasta sculpturata	**WAM C61396**	***Amphinomia sulphurea***	**MZ086829**
Pectinoacasta cancellorum	**WAM C50791**	***Agelas* KMB1**	**MZ086798**
Pectinoacasta cancellorum	**WAM C55302**	***Agelas* KMB1**	**MZ086801**
Pectinoacasta cancellorum	**WAM C55303**	***Agelas* KMB1**	**MZ086802**
Pectinoacasta cancellorum	**WAM C55304**	***Agelas* KMB1**	**MZ086803**
Pectinoacasta cancellorum	**WAM C55305**	***Agelas* KMB1**	**MZ086804**
Pectinoacasta cancellorum	**WAM C55306**	***Agelas* KMB1**	**MZ086805**
Pectinoacasta cancellorum	**WAM C55307**	***Agelas* KMB1**	**MZ086806**
Pectinoacasta cancellorum	**WAM C55308**	***Agelas* KMB1**	**MZ086807**
Pectinoacasta pectinipes	**WAM C58873**	***Tedania* (*Trachytedania*) L1**	**MZ086826**
Pectinoacasta pectinipes	**WAM C67748**	***Tedania* (*Trachytedania*) MM1**	**MZ086835**
Pectinoacasta pectinipes	**WAM C67749**	***Tedania* (*Trachytedania*) MM1**	**MZ086836**
Pectinoacasta pectinipes	**WAM C67750**	***Tedania* (*Trachytedania*) MM1**	**MZ086837**
Pectinoacasta pectinipes	**WAM C67772**	***Tedania* (*Trachytedania*) MM1**	**MZ086838**
Pectinoacasta sculpturata	SGI131-1	*Agelas nemoechinata*	MN842042 [17]

3. Results

3.1. Systematics

Balanomorpha Pilsbry, 1916 [34]
Balanidae Leach, 1817 [8]
Acastinae Kolbasov, 1993 [5]

3.1.1. *Acasta* Leach, 1817 [8]

Acasta aspera Yu et al., 2017 [3]

Acasta aspera Yu et al., 2017: 155, Figures 1–10 [3]

Material examined: WAM C58326, WAM C58835–8, all from NE of Ah Chong Island, Montebello Islands, WA, 20°29′57″ S 115°35′23″ E, 14.5 m, NCB Muirons and Montebellos April 2015 Expedition, stn. 6/MM15, coll. A.M. Hosie & A. Hara, host: WAM Z84165 *Hamigera* PB1. WAM C58332, WAM C58812–15, WAM C71837–8, all from NE of Ah Chong Island, Montebello Islands, WA, 20°29′57″ S 115°35′23″ E, 14.5 m, NCB Muirons and Montebellos Expedition, stn. 6/MM15, 16 Apr 2015, coll. A.M. Hosie & A. Hara, host: WAM Z84171 *Lissodendoryx* (*Acanthodoryx*) KMB1.

Diagnosis: Shell pinkish or yellow-brown, orifice edge toothed. Basis cup-shaped with crenate edge. Radii with creased edges. Externally, parietes rugged with several irregularly spaced calcareous projections; internally, sheath extending over half of parietes with vesicular structure, inner surface below sheath with longitudinal ribs. Scutum with feeble growth ridges and longitudinal striations, articular furrow shallow. Tergum beaked, apex tinged with red, spur truncated, width less than 0.5 of basal margin. Curved teeth on anterior ramus of cirrus IV feeble. Cirrus V protopod with vertical row of denticles on posterior edge.

Distribution: Australia: Perth—Montebello Islands, WA. Taiwan [3]. 0–16 m.

Hosts: *Lissodendoryx* (*Acanthodoryx*) KMB1 (Coelosphaeridae), and *Hamigera* PB1 (Hymedesmiidae). Previous records: *Crella* (*Yvesia*) *spinulata* (Hentschel, 1911) [35] (Crellidae), and *Iotroata* sp. [3] (Iotrochotidae).

Remarks: This species was originally identified inhabiting *Iotroata* sp. and *Crella* (*Yvesia*) *spinulata* from the central western coast of Australia and Taiwan, respectively. Here, we report two additional host species from the families Coelosphaeridae and Hymedesmiidae, demonstrating that *A. aspera* is a relative generalist, capable of colonising sponge species from several families within the order Poecilosclerida.

Acasta caveata sp. nov. (Figures 1–4)

http://zoobank.org/urn:lsid:zoobank.org:act:822DA9C9-F414-4E2E-9C44-E065990C08E3

Material examined: *Holotype*: WAM C67716, 5.5 mm RC, 3 slides, S of Sponge Garden, NW side of Exmouth Gulf, WA, 21°49′15″ S 114°12′34″ E, 22 m, NCB Exmouth/Muiron Expedition, stn. 14/EM16, 6 Jun 2016, coll. A.M. Hosie & A. Hara, Host: WAM Z97140 *Gelliodes* KMB1.

Paratype: WAM C67717, 5.2 mm RC, same data as holotype.

Other material: WAM C66772, specimens still with host, same data as holotype.

Diagnosis: Shell fenestrate; very large, subrectangular windows present between each parietal junction, occupying over half of parietal height, as wide as or wider than adjacent parietes at basal rim. Parietes with blunt, calcareous projections, spaced irregularly in longitudinal rows. Basis saucer-shaped, rim undulating, crenate where it interlocks with parietes, otherwise smooth. Cirrus IV protopod with single horizontal tooth, anterior and posterior rami with hooked teeth arranged in triangular shape. Cirrus V anterior ramus with hooked teeth. Penis basidorsal point prominent.

Description: *Shell* (Figure 1A–M) erect, slightly elongate vertically, plates semitransparent, white or tinged red or burgundy near apices. Externally, parietes with fine, horizontal growth lines and short, irregularly spaced spines; apices of parietes curved toward orifice. Radii and alae summits oblique, not reaching basal margin of corresponding parietes, leaving elongate, subrectangular membranous windows between parietes. With ontogeny, windows secondarily filled with calcareous shell, maintaining lower margin approximately level with basal margin of sheath. Internally, sheath adpressed with vesicular structure, faint horizontal growth lines, lower margin separated from inner lamina except on carina; inner lamina with weak longitudinal ribs extending to basal rim, lateral margins inflected or thickened.

Basis (Figure 1H,M) saucer-shaped, making up approximately a quarter of total shell height, with six wide and shallow longitudinal furrows corresponding to the bases of parietes; rim undulating, crenate where interlocking with parietes, inter-parietal rim concave, smooth.

Scutum (Figure 1N–P) semitransparent, triangular, approximately as high as wide, growth lines prominent with fine crenulations and fringed with short, inconspicuous setae; basitergal angle broadly rounded; occludent margin toothed. Internally smooth, adductor muscle pit weakly defined, lateral depressor muscle pit well defined; articular ridge low, parallel with tergal margin, with shallow articular furrow, extending approximately 0.75 length of tergal margin.

Tergum (Figure 1Q,R) semitransparent, apex acute, tinged with red; external growth lines fringed with short inconspicuous setae; articular margin concave in apical half, carinal margin evenly arcuate, basal margin slightly sinuous on carinal side of spur; scutal side straight, but obtuse to, articular margin; spur length approximately twice width, occupying approximately half of basal margin, positioned approximately half own width from scutal margin; spur and furrow margins coincident, defined by abrupt change in growth lines and corresponding groove on articular side and gentle change on carinal side; distal margin convex, obliquely truncate. Internally smooth, crests for depressor muscles faint or absent.

Labrum (Figure 2A,B) bilobed, lobes separated by deep, medial, v-shaped notch, each rounded lobe with two or three marginal teeth and numerous fine setae.

Mandibular palp (Figure 2A,C) rhomboid, apex obliquely truncate, anterior margin slightly concave, almost straight, posterior margin straight; setae heavily serrulate, becoming longer and denser distally; distal angle with long, simple setae.

Mandible (Figure 2D–F) with five teeth, second to third teeth bifid, fourth and fifth teeth serrate of moloriform, inferior angle with denticles. Dense, short setae regularly spaced on inner and outer faces, longer, fine setae on inferior and superior margin.

Maxillule (Figure 2G,H) cutting margin straight, with 11 cuspidate setae, upper and lower pairs longer than remaining setae, medial setae serrulate on inferior margin. Dense, short setae regularly spaced on inner and outer faces, longer, fine setae on inferior and superior margin.

Maxilla (Figure 2I) bilobed, lobes ovate, distal lobe elongate, curved towards mouth, serrulate setae arranged on anterior margins, becoming more dense at apex, longer on distal lobe than those on basal lobe.

Cirral segment counts are given in Table 2.

Table 2. Number of segments on each left (L) and right (R) cirrus (CI–CVI; anterior, posterior ramus) of species described herein, * denotes damaged cirrus.

Specimen		CI	C II	C III	C IV	C V	C VI
Acasta caveata sp. nov.							
WAM C67716	L	17, 8	11, 8	15, 13	23, 26	32, 34	34, 33
	R	17, 9	11, 10	15, 12	24, 30	33, 38	34, 36
Acasta fenestrata							
WAM C58749	L	16, 6	9, 8	12, 10	26, 27	17*, 26	32, 33
	R	16, 6	8, 7	11, 9	27, 26	23, 23	34, 31
Euacasta acutaflava sp. nov.							
WAM C58744	L	20, 6	10, 7	14, 12	17, 22	29, 28	28*, 31
	R	20, 6	*,*	11, 11	17*, 21	27, 28	29, 29
WAM C74601	L	17, 6	9, 7	12, 11	18, 24	28, 29	11*, 26*
	R	17, 6	11, 6	12, 12	15*, 22	29, 31	31, 22*
WAM C76451	L	17, 5	8, 6	10, 9	19, 18*	29, 30	33, 34
	R	18, 5	8, 6	10, 9	19, 26	31, 32	33, 12*
Euacasta excoriatrix sp. nov.							
WAM C71800	L	30, 7	13, 9	17, 14	27, 29	32,29*	33, 34
	R	30, 7	12, 8	16, 13	22, 30	25*,31	37, 26*
WAM C61475	L	29, 7	12, 8	16, 14	20, 21*	26*,28*	17*, 23*
	R	28, 6	13, 9	14, 15	14*, 22*	30,22*	20*, 22*
Pectinoacasta cancellorum							
WAM C55305	L	20, 6	10, 8	13, 11	21*, 16*	15*, 17*	35, 33
	R	20, 6	10, 7	13, 11	22, 21	28, 29	36, 32
Pectinoacasta pectinipes							
WAM C58871	L	15, 7	9, 8	11, 11	17, 19	21*, 23	22, 23
	R	12, 7*	9, 7	9, 9	3*, 18	23, 22	23, 23
Pectinoacasta sculpturata							
WAM C61395	L	22, 6	9, 7	12, 5*	14*, 23	24, 2*	24, 24
	R	*,*	9, 7	11, 10	22, 17*	24, 25	26, 24

Cirrus I (Figure 3A) protopod with pappose setae basally on posterior margin. Rami unequal, anterior ramus approximately 2.3 times longer than posterior ramus, setation lasiopod, segments with densely arranged serrulate and simple setae on mesial face.

Cirrus II (Figure 3B) protopod anterior margin lined with long, plumose setae, posterior margin with pappose setae basally, plumose setae distally. Rami unequal, anterior ramus approximately 1.25 times longer than posterior ramus, setation lasiopod, segments with densely arranged serrulate and simple setae on mesial face.

Cirrus III (Figure 3C–E) protopod anterior margin lined with long, plumose setae, posterior margin with pappose setae basally and plumose setae distally. Rami unequal, anterior ramus approximately 1.25 times longer than posterior ramus, setation lasiopod, segments with serrulate and simple setae on mesial face, less densely arranged than cirrus I and II. Anterior ramus with row of sharp, erect spines on anterodistal portion of all segments, except terminal segment, most prominent on medial segments. Posterior ramus similar but spines smaller.

Cirrus IV (Figure 4A–E) protopod elongate, length 1.8 times width, with simple setae on anterior and posterior margins, tuft of simple setae at posterodistal angles of both segments; basis with single tooth at anterodistal angel. Rami subequal, setation ctenopod, segments with 3 pairs of serrulate setae on anterior margin. Anterior ramus with up to 5 hooked teeth arranged in a rough triangular formation on anterior margin of first 15 segments, anterodistal angle with group of erect spines. Posterior ramus with 1 or 2 hooked teeth on segments 10–21, anterodistal angle with group of erect spines.

Cirrus V (Figure 4F–H) protopod elongate, length 1.38 times width, with simple setae on anterior and posterior margins, anterodistal angle unarmed, tuft of simple cuspidate setae at posterodistal angles of both segments. Rami subequal, setation ctenopod, anterior ramus with 3 and posterior ramus with 4 pairs of serrulate setae on anterior margin, posterior ramus with four and both rami of cirrus VI with 4 pairs of serrulate setae; posterodistal angles with tuft of simple setae. Anterior ramus with 1 or 2 hooked teeth on segments 13–21.

Cirrus VI (Figure 4I) protopod elongate, length 1.4 times width simple setae on anterior and posterior margins, lacking denticles or erect spines on anterodistal angles, tuft of simple cuspidate setae at posterodistal angles of both segments. Rami subequal, setation ctenopod, with 4 pairs of serrulate setae; posterodistal angles with tuft of simple setae; anterior margins without teeth or erect spines.

Penis (Figure 4I,J) longer than cirrus VI, annulated, sparsely setose; basidorsal point triangular, prominent, apex rounded.

Hosts: *Gelliodes* KMB1 (Niphatidae).

Distribution: Western Australia: Exmouth Gulf. 23 m.

Etymology: The specific epithet is derived from the Latin noun *cavea* (cage, hollow, cavity), in reference to the large membrane-covered windows that give the shell a cage-like appearance.

Remarks: This species, with its very conspicuous membranous windows, is externally similar to a number of species of *Acasta*. The most similar are *A. sandwichi* Yu et al. 2017 [2] and *A. pertusa* Kolbasov 1990 [36], which exhibit close morphological similarities in the form of the windows and opercular plates. The external shell and opercular plates are nearly identical, but with some potential differences in the relative widths of the windows and adjacent parietes. The windows of *A. caveata* sp. nov. occupy more than half the shell height (excluding basis) and are level with, or just above, the lower margin of the sheath, thus larger than in *Acasta sandwichi* and *A. pertusa* where the margin is distinctly lower than the sheath. In *A. caveata,* the free, lower margins of the parietes are parallel with the basis, giving the windows a more rectangular shape, whereas in *A. pertusa* and *A. sandwichi,* they are curved, giving them a more arched look. The key arthropodal character to distinguish these species is the armature of cirri IV and V. For *A. caveata*, both the anterior and posterior rami of cirrus IV and the anterior ramus of cirrus V bear strong hooked teeth, whereas only a single, straight "denticle" is found on each segment of the anterior ramus of cirrus IV in *A. sandwichi*, while such armature is completely absent in *A. pertusa*.

Of the other species with conspicuous windows (*A. armata* Gravier, 1921 [37], *A. crucibasis* Yu et al., 2017 [2], *A. fenestrata* Darwin, 1854 [38], *A. foraminifera* Broch, 1931 [6], and *A. tzetlini* Kolbasov, 1992 [39]), only *A. tzetlini* bears teeth, but only on cirrus IV anterior ramus, and it has much smaller windows with the parietes articulated with the basis over most of its circumference. In addition to lacking teeth on cirrus IV, *A. armata* and *A. fenestrata* lack longitudinal ribs on the inner lamina of the parietes; *A. armata* also has very distinct opercular plates, and the windows of *A. fenestrata* are significantly smaller. The carinolatus of *A. foraminifera* and *A. crucibasis* do not reach the basis at all but are instead suspended between the latus and the carina.

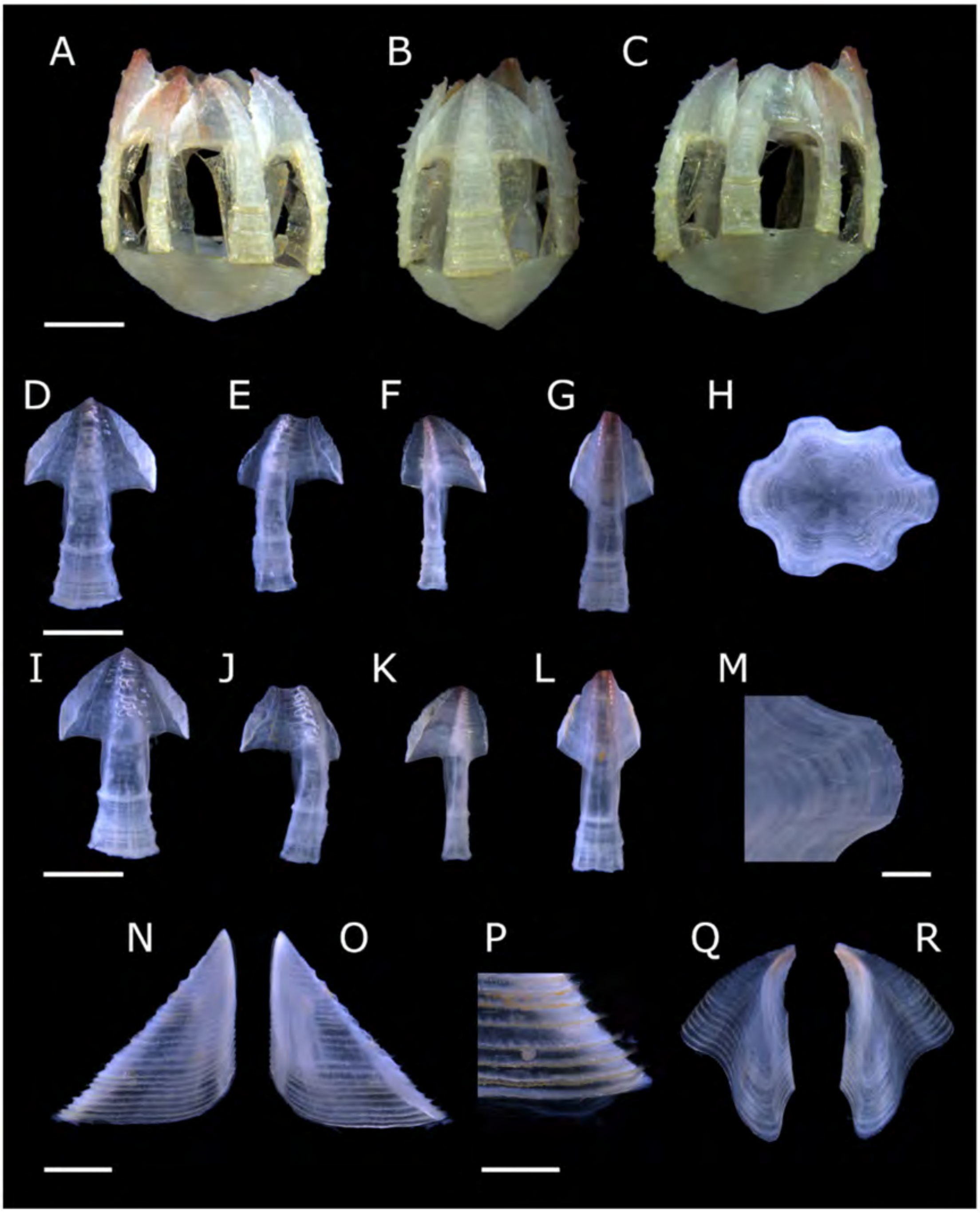

Figure 1. *Acasta caveata* sp. nov. shell plates (all WAM C 67716, holotype). (**A**–**C**) right, rostral, and left external views, respectively, of whole specimen; (**D**–**H**) external views of rostrum, right lateral, right carinolateral, carina, and basis; (**I**–**L**) internal views of rostrum, right lateral, right carinolateral, and carina; (**M**) close up of carinal portion of basis rim; (**N**–**O**) external and internal view of right scutum; (**P**) close up of growth lines on scutum showing setae; (**Q**–**R**) internal and external views of right tergum. Scale bars: A–L = 2 mm; M, P = 0.5 mm; N–O, Q–R = 1 mm.

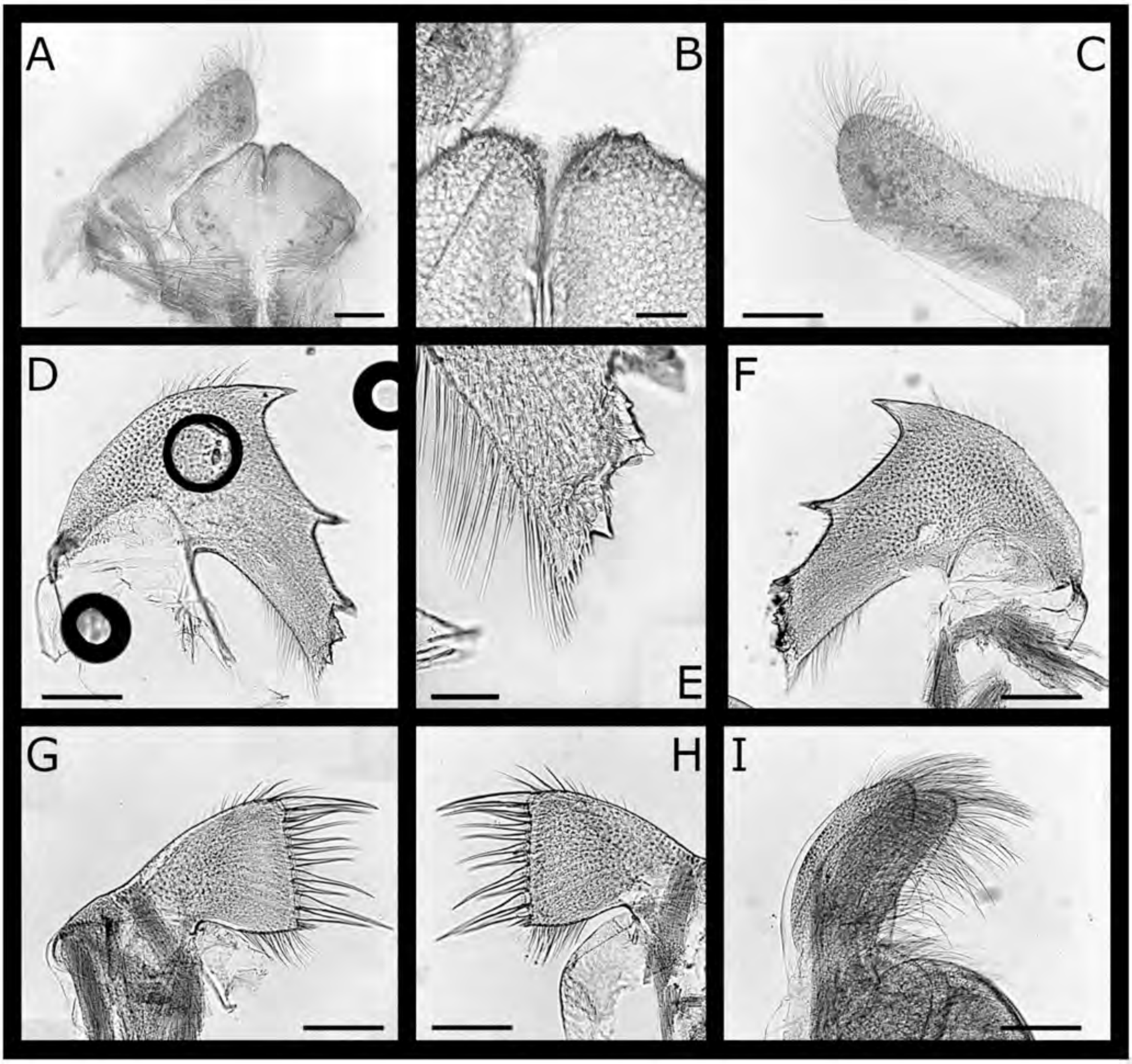

Figure 2. *Acasta caveata* sp. nov. mouthparts (all WAM C67716, holotype). (**A**) labrum and right mandibular palp; (**B**) crest of labrum; (**C**) left mandibular palp; (**D**) left mandible; (**E**) close up of inferior angle of mandible showing fourth and fifth serrated teeth; (**F**) right mandible; (**G**) left maxillule; (**H**) right maxillule; (**I**) left and right maxilla, lateral view. Scale bars: A, C–D, F–I = 200 µm; B, E = 50 µm.

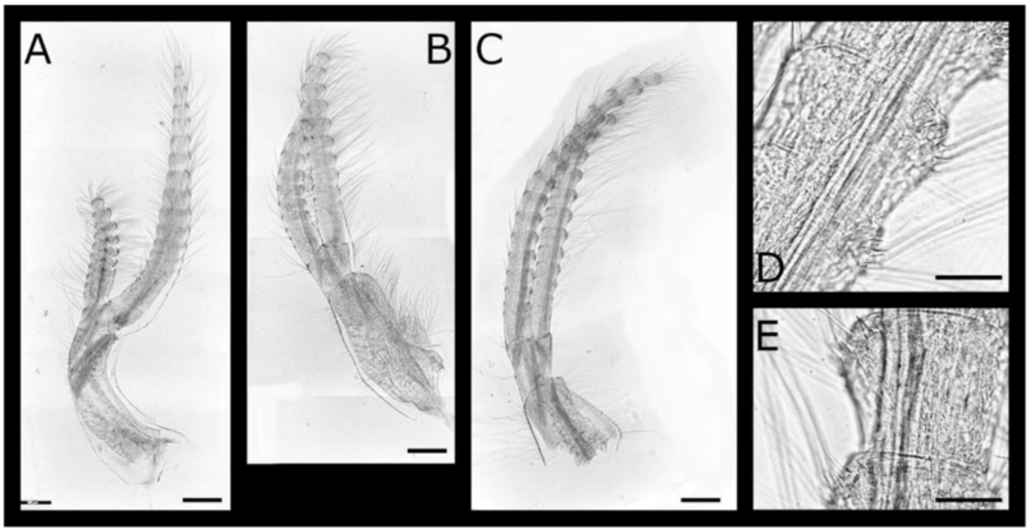

Figure 3. *Acasta caveata* sp. nov. cirri I–III (all WAM C67716, holotype). (**A**) left cirrus I; (**B**) left cirrus II; (**C**) left cirrus III; (**D**) anterior margin of medial segments of left cirrus III anterior ramus; (**E**) anterior margin of medial segments of right cirrus III anterior ramus. Scale bars: A–C = 200 µm, D–E = 50 µm.

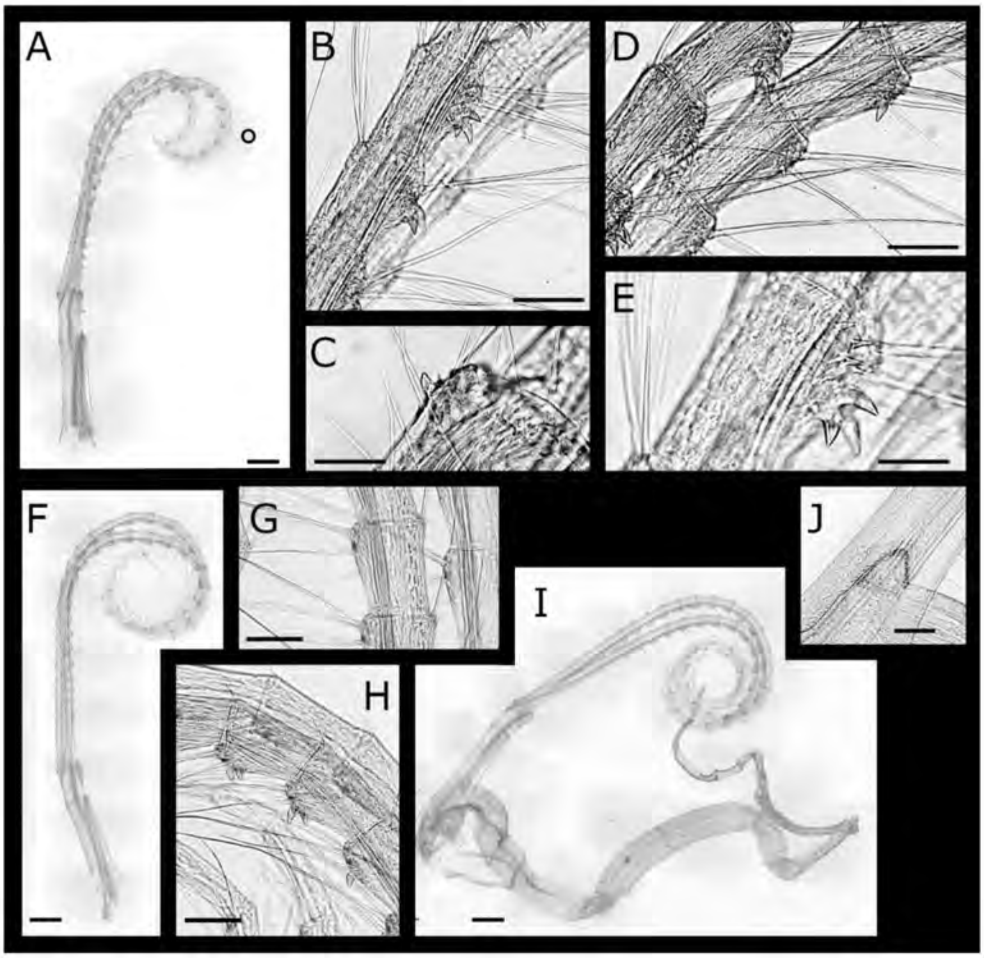

Figure 4. *Acasta caveata* sp. nov. cirri IV–VI (all WAM C67716, holotype). (**A**) left cirrus IV; (**B**) hooked teeth on medial segments of left cirrus IV anterior ramus; (**C**) close up of tooth on basis of right cirrus IV protopod; (**D**) medial segments of cirrus IV; (**E**) detail of erect spines on medial segments of cirrus IV anterior ramus; (**F**) cirrus V; (**G**) setae on medial segments of cirrus V; (**H**) hooked teeth on medial segments of cirrus V anterior ramus; (**I**) cirrus VI and penis; (**J**) basidorsal point of penis. Scale bars: A, F, I = 300 µm; B, D = 100 µm; C, E = 50 µm; J = 200 µm.

Acasta fenestrata Darwin, 1854 [38] (Figures 5–8)

Acasta fenestrata Darwin, 1854: p. 316, Tab. 9, Figure 7 [38]. Weltner 1897: p. 259 [40]. 1922, p. 104 [41]. Nilsson-Cantell 1938: p. 57 [42]. Hiro, 1939: p. 243 [43].Newman & Ross 1976: p. 53 [44]. Ren 1984 [45]. Rosell 1989: p. 33, Pl. 9b [46]. Liu & Ren 2007: p. 417, Figure 187 [47]. Wibowo et al. 2011: p. 227, Figures 10–13 [48]. Sulistiono et al. 2014: p. 182, Figure 4 [49]. Jones & Hosie 2016: p. 275 [50].

Acasta sp.4 Yu et al., 2020 [17]

? *Acasta fenestrata*: Utinomi 1958: p. 57, Figures 6–7 [51]. Rosell 1972: p. 194, Pl. XXI, XXII 1–3, XXIII 3, 4 [52]. Foster & Buckeridge 1994: p. 374, Figure 15A–I [53].

Material examined: WAM C20856, between Powerful and Survey Islands, Buccaneer Archipelago, WA, 16°05′ S 123°27′ E, intertidal, WAM Kimberley Islands & Reefs Survey, stn. 41, 26 Aug 1991, coll. D.S. Jones, host: *Neopetrosia chaliniformis*. WAM C43897, Montgomery Reef, Camden Sound, WA, 15°53.815′ S 124°19.531′ E, intertidal, Woodside Kimberley Survey, stn. 14/K09-A, 19 Oct 2009, coll. A.M. Hosie, host: *Neopetrosia chaliniformis*. WAM C45274, Montgomery Reef, Camden Sound, WA, 15°52.588′ S 124°19.793′ E, intertidal, Woodside Kimberley Survey, stn. 18/K09-T2, 20 Oct 2009, coll. A.M. Hosie, host: *Neopetrosia chaliniformis*. WAM C45275, WAM C55291, 4.9 mm RC, Montgomery Reef, Camden Sound, WA, 16°00.865′ S 124°10.389′ E, intertidal, Woodside Kimberley Survey, stn. 24/K09-T1, 23 Oct 2009, coll. A.M. Hosie; host: WAM Z29255 *Neopetrosia chaliniformis*. WAM C45278, Montgomery Reef, Camden Sound, WA, 15°51.323′ S 124°18.875′ E, intertidal, Woodside Kimberley Survey, stn. 17/K09-A, 20 Oct 2009, coll. A.M. Hosie, host: *Neopetrosia chaliniformis*. WAM C45280, Montgomery Reef, Camden Sound, WA, 15°55′08.6″ S 124°17′43.9″ E, intertidal, Woodside Kimberley Survey, stn. 16/K09, 19 Oct 2009, coll. A.M. Hosie; host: *Neopetrosia chaliniformis.* WAM C46096, Pt Cloates, Ningaloo Reef, WA, 22°46.35′ S 113°39.996′ E, 30 m, CReefs Ningaloo, stn. NR10-085, 31 May 2010, coll. L.L. Betteridge, host: *Neopetrosia chaliniformis*. WAM C46640, WAM C55273–4, all from Long Reef, Admiralty Gulf, WA, 13°48.593′ S 125°49.448′ E, intertidal, Woodside Kimberley Survey, stn. 52/K10-T1, 22 Oct 2010, coll. A.M. Hosie, host: WAM Z29256 *Neopetrosia chaliniformis*. WAM C46669, 5.7 mm RC, Long Reef, WA, 13°49.925′ S 125°48.712′ E, 12 m, Woodside Kimberley Biodiversity Survey 2010, stn. 54/K10-Q1, 23 Oct 2010, coll. A.M. Hosie, Host: WAM Z29257 *Neopetrosia chaliniformis*. WAM C48490, WAM C55409, WAM C58748,WAM C58749, 3 slides, all from E of Numanbu Island, Champagny Islands, Bonaparte Archipelago, 15°19.844′ S 124°13.015′ E, intertidal, Woodside Kimberley Survey, stn. 63/K11-T1, 14 Oct 2011, coll. A.M. Hosie, host: WAM Z54173 *Neopetrosia chaliniformis*. WAM C48495 from E of Numanbu Island, Champagny Islands, Bonaparte Archipelago, 15°19.844′ S 124°13.015′ E, intertidal, Woodside Kimberley Survey, stn. 63/K11-T2, 14 Oct 2011, coll. A.M. Hosie, host: WAM Z54220 *Neopetrosia chaliniformis*. WAM C54382, SE corner of Hibernia Reef, WA, 11°58′33.8″ S 123°23′22.8″ E, 13 m, Woodside Kimberley Survey 2013, stn. 145/K13, 5 Oct 2013, coll. A.M. Hosie, Host: WAM Z69888 *Neopetrosia chaliniformis.* WAM C55251–4, all from Ashmore Reef, 12°16.638′ S 123°08.166′ E, intertidal, Woodside Kimberley Survey, stn. 129/K13-T1, 28 Sept 2013, coll. A.M. Hosie, host: WAM Z29257 *Neopetrosia chaliniformis*. WAM C56252, WAM C55319–22, all from Mermaid Reef, Rowley Shoals, WA, 17°04.344′ S 119°37.626′ E, 12–14 m, Woodside Kimberley Survey, stn. 150/K14-T1, 2 Oct 2014, coll. A.M. Hosie; host: WAM Z84014 *Neopetrosia chaliniformis*. WAM C56867, WAM C55323–5 all from Clerke Reef, Rowley Shoals, WA, 17°18.858′ S 119°22.5′ E, 6–8 m, Woodside Kimberley Survey, stn. 171/K14-T2, 10 Oct 2014, coll. A.M. Hosie; host: WAM Z83364 *Neopetrosia chaliniformis*. WAM C66924, WAM C74354, WAM C74419–20, QM W29554 all from Ian Pt, Hook Island, Whitsunday Islands, QLD, 20°06′ 15.84″ S 148°54′ 8.99″ E, 2 m, Bush Blitz Coral Sea Expedition, Stn. BBCS16/2, 14 Jun 2016, coll. A.M. Hosie, Host *Neopetrosia chaliniformis*. WAM C67829, 3 slides, WAM C71738–9, WAM C71884, all from West Lewis Island, Dampier Archipelago, WA, 20°35′25″ S 116°36′20″ E, 9.7 m, NCB Dampier Archipelago Expedition, 23/D17, 29 Mar 2017, coll. A.M. Hosie & A. Hara, host: WAM Z86889 *Neopetrosia chaliniformis*. WAM C72909–10, WAM

C72914 all from Norwegian Bay, Ningaloo Reef, WA, 8–10 m, 22°39′45.2″ S 113°38′22.6″ E, 4 Jan 2017, coll. Abdul Wahab, M.A., host: *Neopetrosia chaliniformis*.

Diagnosis: Shell typically globuloconic, parietes with irregularly spaced spines, radii and alae oblique, membranous windows present between each shell plate, windows may reach half height of shell plates, maximum width approximately same as carinolatus at basal margin. Tergal spur truncate, basal margin concave with disto-articular angle projecting. Cirri III and IV anterior rami with row of sharp erect spines on anterodistal portion segments. Both rami of cirri IV–VI with specialised multicuspidate setae at posterodistal angles of basal-most segments.

Description: *Shell* (Figure 5A–G) plates white or tinged red or burgundy, typically globuloconic, but may elongate to match growth of host. Externally, parietes with fine, horizontal growth lines and short, irregularly spaced spines; apices of parietes curved toward orifice. Radii and alae oblique, not reaching basal margin of corresponding parietes, leaving elongate membranous windows between parietes. With ontogeny, windows secondarily filled with calcareous shell to maintain apical margin with internal basal margin of sheath. Internally, smooth below sheath, without longitudinal ribs, lateral margins not inflected or thickened. Sheath adpressed.

Basis (Figure 5G) cup-shaped, depth varying from nearly flat to making up more than twice total shell height (Figure 5A); rim smooth.

Scutum (Figure 5H–I) triangular, apex coloured dark red or purple, slightly higher than wide, growth lines prominent with fine crenulations and fringed with short, inconspicuous setae; basitergal angle broadly rounded; occludent margin strongly toothed. Internally smooth with slight depressions for adductor and lateral depressor muscles; articular ridge prominent, with deep furrow, extending halfway along tergal margin.

Tergum (Figure 5J,K) apex acute, tinged dark red or purple, growth lines fringed with short, inconspicuous setae; articular margin concave in apical half, carinal margin slightly convex almost straight, basal margin straight; spur length 0.5 times width, occupying approximately half of basal margin, positioned less than half own width from scutal margin; spur and furrow margins coincident, defined by abrupt change in growth lines and corresponding groove on articular side and gentle change on carinal side; spur truncate distal margin slightly concave with, disto-articular angle projecting (Figure 5J–K). Internally smooth, crests for depressor muscles faint.

Labrum (Figure 6A,B) bilobed, lobes separated by deep medial v-shaped notch, each rounded lobe with two or three marginal teeth and numerous fine setae.

Mandibular palp (Figure 6A) rhomboid, apex obliquely truncate, anterior margin concave, posterior margin straight; setae heavily serrulate, becoming longer and denser distally; distal angle broadly rounded with long, simple setae.

Mandible (Figure 6C,D) with five teeth, second to fourth teeth bifid, inferior angle with denticles. Dense, short setae regularly spaced on inner and outer faces, longer fine setae on inferior and superior margin.

Maxillule (Figure 6E–G) cutting margin straight, with 9–11 cuspidate setae, upper and lower pairs longer than remaining setae, 3 medial setae serrulate on inferior margin. Dense, short setae regularly spaced on inner and outer faces, longer fine setae on inferior and superior margin.

Maxilla (Figure 6H) bilobed, lobes ovate, serrulate setae arranged on anterior margins, becoming more dense at apex, longer on distal lobe than those on basal lobe.

Cirral segment counts are given in Table 2.

Cirrus I (Figure 7A–B) protopod with pappose setae basally on protopod posterior margin. Rami unequal, anterior ramus twice length of posterior ramus, segments with densely arranged serrulate and simple setae on mesial face.

Cirrus II (Figure 7C) protopod anterior margin lined with long plumose setae, posterior margin with pappose setae basally, plumose setae distally. Rami unequal, anterior ramus 1.25 times longer that posterior ramus, segments with densely arranged serrulate and simple setae on mesial face.

Cirrus III (Figure 7D,E) protopod anterior margin lined with long plumose setae, posterior margin with pappose setae basally and plumose setae distally. Rami subequal, anterior ramus 1.15 length of posterior, segments with serrulate and simple setae on mesial face, less densely arranged than cirrus I and II. Anterior ramus with row of sharp, erect spines on anterodistal portion of all segments, except terminal segment, most prominent on medial segments.

Cirrus IV (Figure 8A–D) protopod elongate, length 1.83–1.95 times width, with simple setae on anterior and posterior margins, lacking denticles or erect spines on anterodistal angles, tuft of simple, cuspidate setae at posterodistal angles of both segments. Rami subequal, setation ctenopod, segments with 3 pairs of serrulate setae on anterior margin; posterodistal angles of basal-most segments with specialised, multicuspidate setae with pair of denticles situated midway along setae. Anterior ramus with row of sharp, erect spines on anterodistal portion of all segments except terminal segment, most prominent on medial segments.

Cirrus V (Figure 8E–G) and *VI* similar, protopod elongate length 1.32–1.38 and 1.21–1.31 times width, respectively, with simple setae on anterior and posterior margins, lacking denticles or erect spines on anterodistal angles, tuft of simple cuspidate setae at posterodistal angles of both segments. Rami subequal, setation ctenopod, cirrus V anterior ramus with 3 pairs of serrulate setae margin, posterior ramus and both rami of cirrus VI with 4 pairs of serrulate setae; posterodistal angles of basal-most segments with specialised multicuspidate setae with 1 pair of denticles situated midway along setae.

Penis longer than cirrus VI, annulated, sparsely setose, basidorsal point may be low and rounded or triangular and pointed.

Distribution: Australia: northern Western Australia and Queensland. Japan, Thailand, Indonesia [50]. Intertidal–195 m.

Hosts: *Neopetrosia chaliniformis* (Thiele, 1899) [54] (Petrosiidae). Previous records: *Discodermia japonica* Döderlein, 1884 [40,55] (Theonellidae); *N. similis* (Ridley & Dendy, 1886) [42,56]; "*Geodia*-like hard tetraxon sponge" and "soft siliceous sponge" [51]; *Haliclona* sp. [5] (Chalinidae); and *N. chaliniformis* (as *N. exigua*) and *Neopetrosia sp.* [48,49].

Remarks: In the literature, descriptions attributed to this species show significant variations that lead us to conclude that more than one species has been confounded under the name *A. fenestrata.* Darwin [38] only described the shell and opercular plates, stating that the body was poorly preserved, but that as far as he could tell, the cirri and mouthparts were similar to *Neoacasta glans* (Lamarck, 1818) [57]. The first description of the mouthparts and cirri to be attributed to *A. fenestrata* was provided by Utinomi [51], who stated that cirrus IV had hooked teeth on the anterior ramus, a feature not found in *N. glans*. Another departure from Darwin's description is that the tergum, as figured, is much narrower in Utinomi's specimens with the spur rounded, rather than truncated, and situated confluent with the basiscutal angle. Rosell [52] noted several differences between his accounts and those by Darwin and Utinomi, but maintained the identification based on the similarity with Utinomi's description of the mouthparts and cirri. Key differences that Rosell highlighted were the presence of pliable, chitinous spines seated on calcareous "elevations" on the parietes, as opposed to the simple, short, blunt, calcareous spines described in other accounts, internal basal ribs on the parietes, and a crenated rim on the basis. The specimen figured by Foster and Buckeridge [53] has a generally globose appearance, with relatively broader radii, smaller windows, and hooked teeth on cirrus IV. Their records also extended the known depth range from 65 to 195 m.

These records contrast with the present specimens and the descriptions and illustrations given by Ren [45], Liu and Ren [47], Sulistiono et al. [49], and Wibowo et al. [48], where the examined specimens only have erect spines on the anterior margins of cirrus IV. Our material also presents a novel character not mentioned by previous authors: the multicuspidate setae on the posterodistal angles of cirri IV–VI (Figure 8D,G). A re-examination of type specimens, and possibly type host, along with additional specimens from across the reported geographic and host range would provide clarity to this species concept.

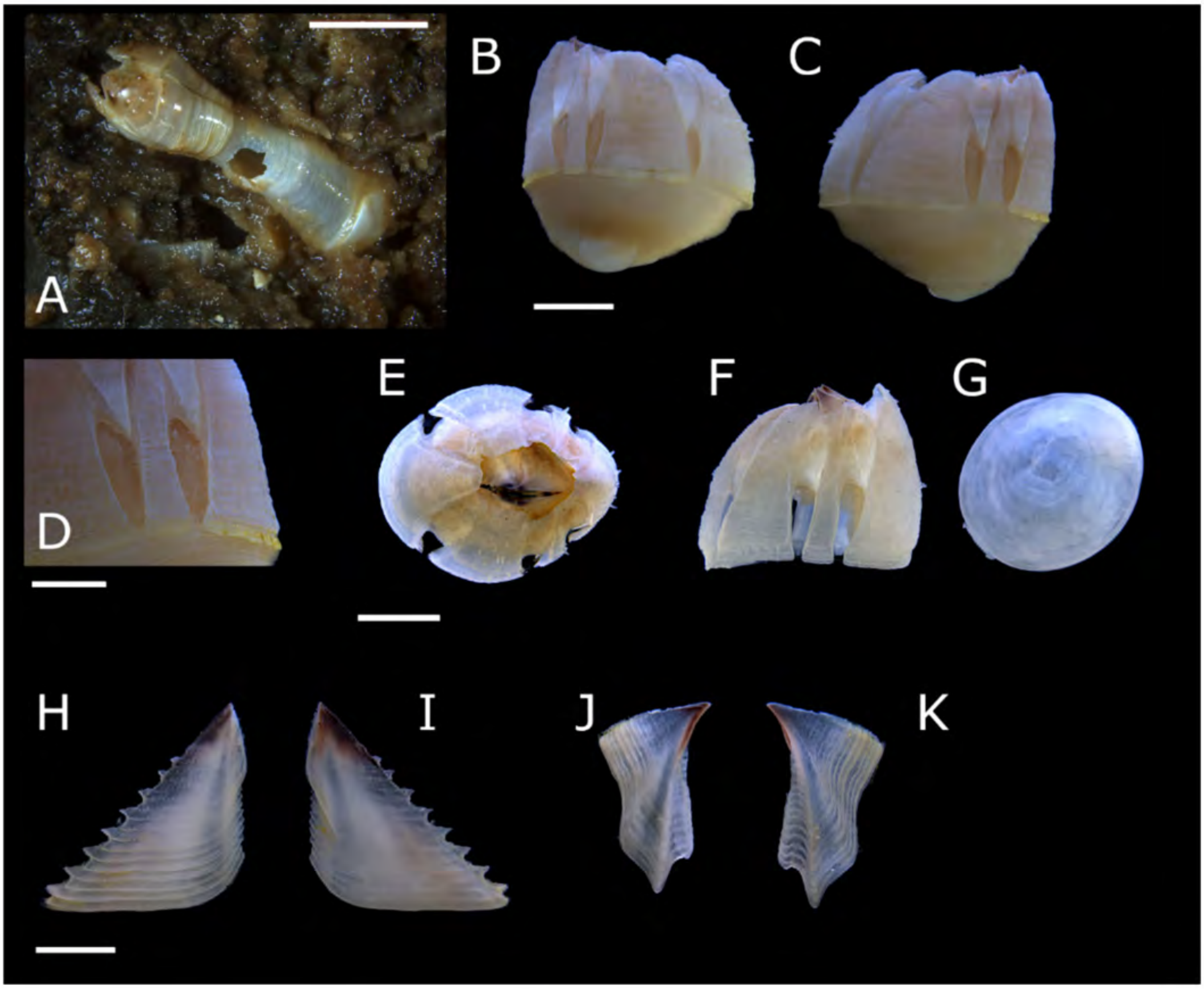

Figure 5. *Acasta fenestrata* Darwin, 1854 shell plates (A, WAM C66924; B–D WAM C46669; E–J, WAM C55291). (**A**) whole, enormously elongate specimen still embedded in host; (**B**,**C**) left and right lateral views of whole specimen; (**D**) close up of fenestrae on right side; (**E**,**F**) ventral and lateral view of specimen (basis removed); (**G**) internal view of basis; (**H**,**I**) external and internal view of right scutum; (**J**,**K**) internal and external view of right tergum. Scale bars: A = 5 mm; B, C, E–G = 2 mm; H–K = 1 mm.

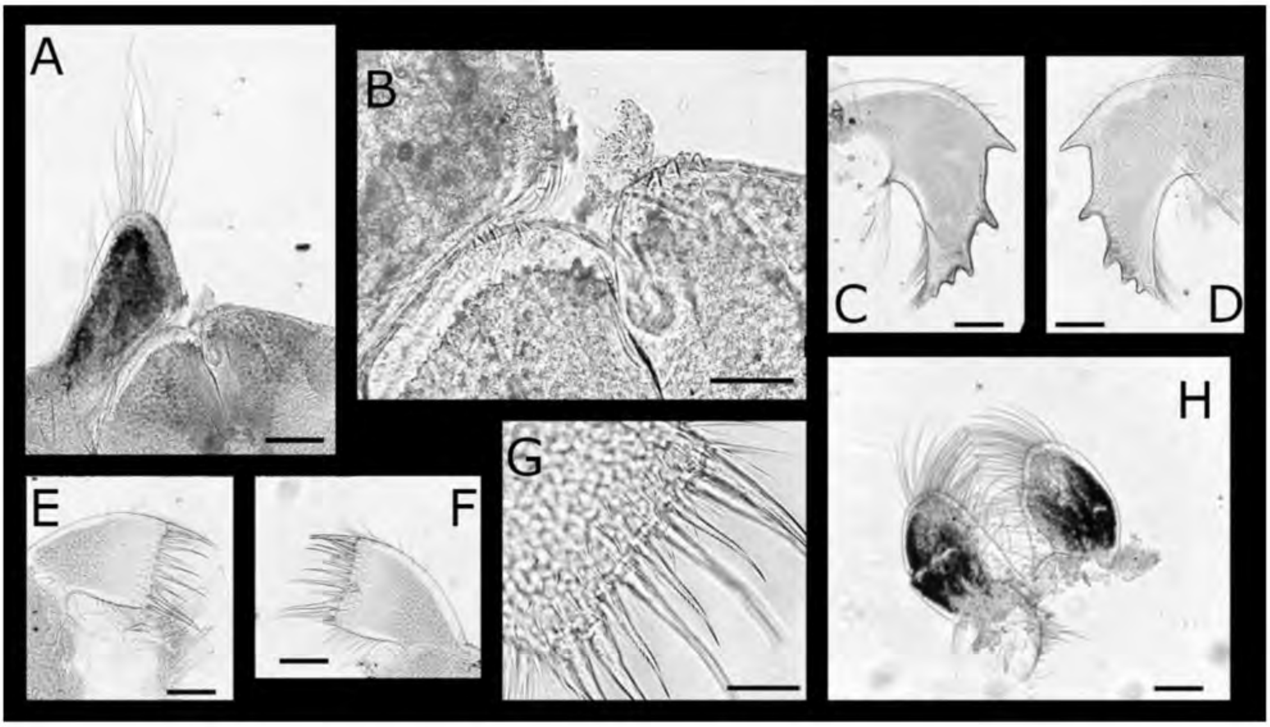

Figure 6. A*casta fenestrata* Darwin, 1854 mouth parts (all WAM C58749 except G, WAM C67829). (**A**) labrum and right mandibular palp; (**B**) close up of labrum crest; (**C**,**D**) left and right mandible; (**E**,**F**) left and right maxillule; (**G**) close up of setae on left maxillule; (**H**) left and right maxillae. Scale bars: A–B = 100 µm; C–F, H = 200 µm; G = 50 µm.

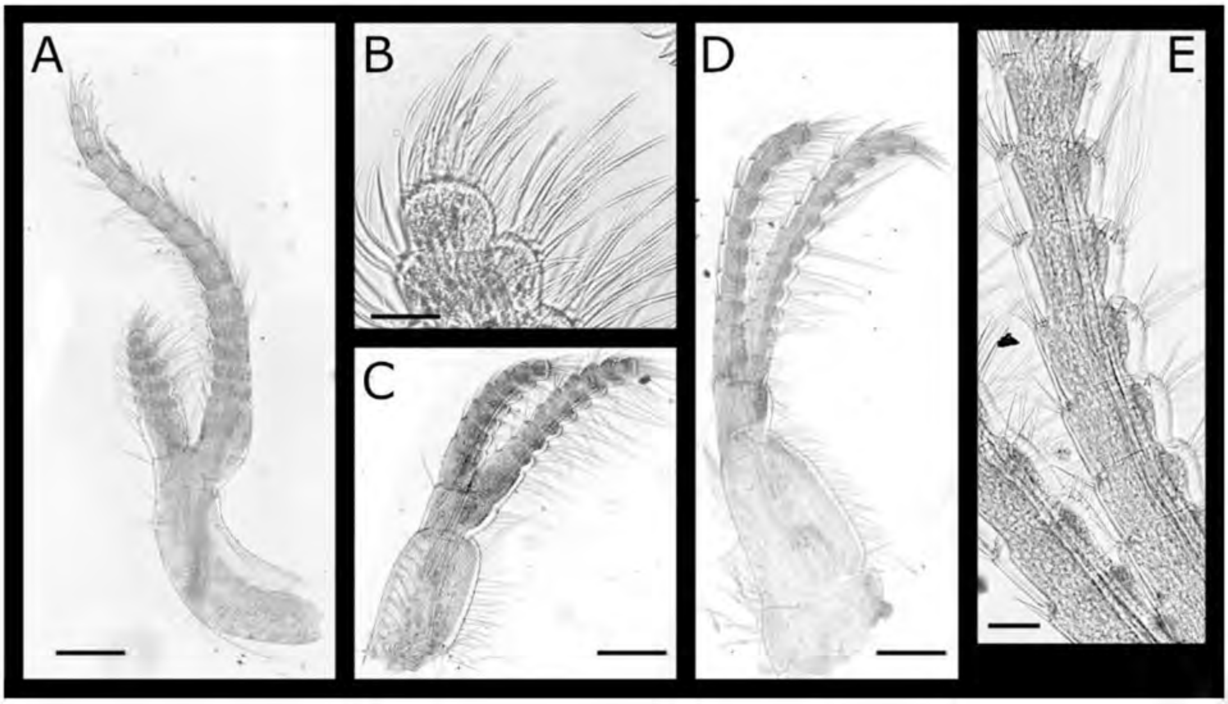

Figure 7. *Acasta fenestrata* Darwin, 1854 cirri I–III (all WAM C58749). (**A**) left cirrus I; (**B**) serrulate setae on left cirrus I distal segments of posterior ramus; (**C**) left cirrus II; (**D**), left cirrus III; (**E**) erect spines on left cirrus III anterior ramus. Scale bars: A, B–C = 200 µm; D, E = 50 µm.

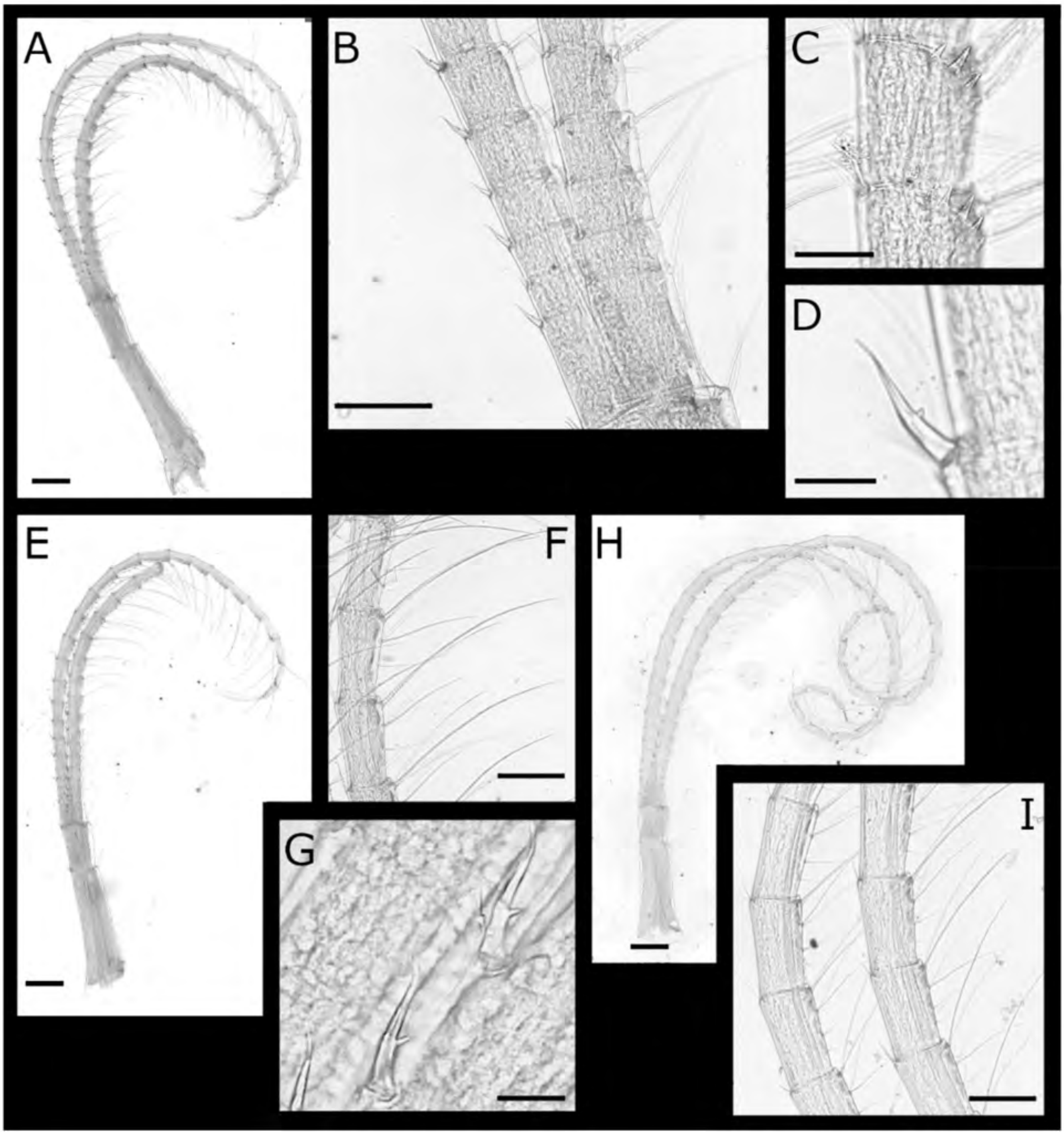

Figure 8. *Acasta fenestrata* Darwin, 1854 cirri IV–VI (all WAM C58749). (**A**) left cirrus IV; (**B**) basal segments of left cirrus IV; (**C**) erect spines on medial segments of cirrus IV anterior ramus; (**D**) multicuspidate seta on posterodistal angle of cirrus IV posterior ramus; (**E**) left cirrus V; (**F**) setation on medial segments of cirrus V anterior ramus; (**G**) multicuspidate setae on basal segments of cirrus V anterior ramus; (**H**) left cirrus VI; (**I**) setation on intermediate segments of cirrus VI posterior and anterior rami. Scale Bars: A, E, H = 200 µm; B =100 µm; C, F, I = 50 µm; D, G 20 µm.

Acasta sandwichi Yu, Chan, Achituv & Kolbasov, 2017 [2]

Acasta sandwichi Yu et al., 2017: p. 606, Figures 22–28 [2].

Material examined: WAM C47383, Long Reef, WA, 13°49.121′ S 125°46.7796′ E, 12 m, Woodside Kimberley Biodiversity Survey 2010, stn. 53/K10, 23 Oct 2010, coll. A.M. Hosie, host: WAM Z29261 *Xestospongia testudinaria.* WAM C53344, S of Lesueur Island, WA, 28.3–29.5 m, 13°49′52″ S 127°15′52″ E to 13°49′56″ S 127°15′49″ E, CSIRO King George River Expedition 2013, stn. S04, 6 Jun 2013, coll. A.M. Hosie, C.S. Whisson & A. Hara, host: *Xestospongia testudinaria.*

Diagnosis: Shell fenestrate, windows present between each parietal junction, very large, occupying over half of shell height, as wide as or wider than adjacent parietes at basal rim. Parietes with blunt, calcareous projections, spaced irregularly in longitudinal rows. Basis shallow saucer-shaped, rim undulating, crenate where it interlocks with parietes, otherwise smooth. Cirrus IV anterior ramus with single denticle on anterior margin of segments.

Distribution: Western Australia: Kimberley. Taiwan [2]. 18–30 m.

Hosts: *Xestospongia testudinaria* (Lamarck, 1815) [58] (Petrosiidae).

Remarks: This species was only recently described from Taiwanese waters [2], and thus the specimens examined herein represent the first records from Australian waters.

This species has a morphologically and genetically close relationship to *A.* caveata sp. nov., and the morphological characters separating the two are dealt with under the treatment for that species. Distinguishing *A. sandwichi* from other *Acasta* with large windows was detailed by Yu et al. [2], and of these, the only *A. fenestrata* currently known is from Australia. This species can be distinguished by the relatively smaller windows, the lack of longitudinal ribs on the internal surface of the parietes, and the broader and more truncate tergal spur; the cirrus IV anterior ramus has erect spines on the anterodistal angles of segments and the stout multicuspidate setae are present on the posterodistal angles of cirri IV–VI. Further to this, there is no indication that either species inhabit the same hosts.

3.1.2. *Euacasta* Kolbasov, 1993 [5]

Euacasta acutaflava sp. nov. (Figures 9–12)

http://zoobank.org/urn:lsid:zoobank.org:act:4A7D853C-F70E-46E4-A01B-A8249C53CBE8

Material examined: *Holotype*: WAM C58744, 4.6 mm RC, 3 slides, Montgomery Reef, Camden Sound, WA, 15°53.895′ S 124°10.901′ E, intertidal, Woodside Kimberley Biodiversity Survey 2009, stn. 20/K09-T2, 21 Oct 2009, coll. A.M. Hosie; host: WAM Z29216 *Cymbastela stipitata.*

Paratypes: WAM C58745–7, WAM C76401, 3 slides, same data as for holotype. WAM C61434, WAM C61435, 5.6 mm RC, E of Trimouille Island, Montebello Islands, WA, 20°22′18″ S 115°33′50″ E, 11 m, NCB Montebello/Muiron Islands Expedition, 1/MM15, 14 Apr 2015, coll. A.M. Hosie & A. Hara, Host: WAM Z84101 *Cymbastela stipitata*. WAM C 76451, 3.0 mm RC, 3 slides, Montgomery Reef, Camden Sound, WA, 15°54′ S 124°08′ E, intertidal, 15 Jul 1990, coll. L.M. Marsh, host: WAM Z59175 *Cymbastela stipitata.*

Other material: WAM C43667, 4.0 mm RC, more specimens still with host, same data as for holotype. WAM C54629, WAM C55289, both from Montgomery Reef, Camden Sound, WA, 15°54′ S 124°08′ E, intertidal, 15 Jul 1990, coll. L.M. Marsh, host: WAM Z59175 *Cymbastela stipitata*. WAM C54631, Enderby Island, Dampier Archipelago, WA, 20°35.15′ S 116°35.63′ E, 17 m, Woodside Dampier Expedition, stn. DA3/99/55, 2 Sep 1999, coll. J. Fromont, host: WAM Z5468 *Cymbastela vespertina*. WAM C71476, Camden Sound, WA, 15°25′42.72″ S 124°16′23.39″ E, 16.9–17.2 m, WAMSI Survey 1B Camden Sound, stn. SOL160/WA025, 21 May 2015, coll. O.A. Gomez & J.A. Ritchie, Host: WAM Z87011 *Cymbastela* cf. *stipitata*.

Diagnosis: Shell squat, cuboid; parietes thick, strongly articulated, growth lines pronounced, inflected upwards at lateral margins, inner lamina with broad, prominent longitudinal ribs. Basis flat, square in outline with angular corners, diagonal grooves running from each corner. Opercular plates with yellow-orange, chitinous cuticle in apical section, particularly prominent on tergum; scutum with growth lines scalloped by longitudinal ridges. Cirrus IV with 2–4 hooked teeth on basis of protopod; anterior ramus with up to 3 teeth on basal segments.

Description: The *shell* (Figure 9A–Q) is white and squat with maximum diameter greater than shell height and square in outline. The parietes are thick and strongly articulated; externally having variably pronounced and irregularly spaced longitudinal ribs, with horizontal growth lines inflected upward on raised lateral margins; the parietes are slightly curved toward the orifice, the latter only slightly smaller than the diameter of the shell. The opercular plates are exposed, with the apices extending beyond the apices of the parietes. The radii and alae reach the basal margin of the corresponding parietes, and the summits are oblique and broad with horizontal striations. Rostrum, laterals, and carina are approximately equal in width; carinolateral is exceptionally narrow, the parietal area is represented by a beaded strip, and radii and alae are similar to other plates. Internally, the sheath has conspicuous horizontal growth lines, and the lower margin is separated from the inner lamina; below the sheath, broad, longitudinal, parietal ribs are very prominent.

The *basis* (Figure 9H,I) is flat and quadrangular with distinct angular corners; the concentric growth lines are conspicuous; the basal rim is strongly crenate, interlocking with internal ribs on the parietes.

The *scutum* (Figure 9R,S) is triangular, with height 1.35 times its width, and growth lines scalloped by longitudinal ridges; the ridges are increasing in number basally; the basitergal angle is rounded, and the tergal section is narrow; the occludent margin is strongly toothed. Internally smooth, the apex has a yellow chitinous cuticle, and adductor and lateral depressor muscle pits are present; the articular groove is deep, bounded by a distinct articular ridge, the latter extending halfway along the tergal margin.

The *tergum* (Figure 9T,U) apex is acute and beaked, with calcification giving way to a yellow–orange chitinous point, and the apex projecting beyond scutum when articulated; growth lines are prominent, fringed with short, inconspicuous setae; the yellow chitinous cuticle extends onto the carinal half; and the articular margin is concave in the apical half. The carinal margin is evenly concave; the basal margin is straight; the spur is truncate, the length is 0.5 times the width, occupying approximately half the basal margin, positioned less than half its own width from the scutal margin; the spur and furrow margins are coincident, the spur furrow is defined by an abrupt change in growth lines and a corresponding groove on the articular side, and a gentle change on the carinal side; internally smooth, the chitinous cuticle covers the upper half, and the crests for depressor muscles are faint. The articular furrow is broad, the articular ridge is low and rounded, occupying 0.25 of the scutal margin.

The *labrum* (Figure 10A,B) is bilobed, divided by a deep, medial, v-shaped notch, and each rounded lobe has two or three marginal teeth and numerous fine setae.

The *mandibular palp* (Figure 10A,C) is rhomboid, distal, and obliquely truncate, the anterior margin is concave, and the posterior margin is straight; the setae are heavily serrulate, becoming longer and denser distally; the distal angle has long, simple setae.

The *mandible* (Figure 10D–G) cutting margin has four distinct teeth, the second to fourth teeth are bifid, and the fifth tooth is congruent with molariform or spinose inferior angle; the superior and inferior margins have a row of long, fine, simple setae, with dense short setae covering the inner and outer faces.

The *maxillule* (Figure 10H) cutting margin is straight with 9–10 cuspidate setae, the upper and lower pairs are larger and more robust than the remaining setae, and the inferior angle has a tuft of shorter cuspidate setae. Dense, short setae are regularly spaced on the inner and outer faces, with longer fine setae on the inferior and superior margin.

The *maxilla* (Figure 10I) is bilobed, the lobes are ovate, and serrulate setae are arranged on the anterior margins, becoming denser at the apex and longer on the distal lobe than those on the basal lobe.

Cirral segment counts are given in Table 2.

The *cirrus I* (Figure 11A) protopod has pappose setae basally on the posterior margin. The rami are unequal, with anterior ramus 3.9 times the length of the posterior ramus and lasiopod setation, and segments have densely arranged serrulate and simple setae on the mesial face.

The *cirrus II* (Figure 11B,C) protopod anterior margin is lined with long plumose setae, posterior margin with pappose setae basally and plumose setae distally. The rami are unequal, the anterior ramus is 1.25 times longer than the posterior ramus, and segments have densely arranged serrulate and simple setae on the mesial faces.

The *cirrus III* (Figure 11D–F) protopod anterior margin is lined with long plumose setae, the posterior margin with pappose setae basally and plumose setae distally. The rami are subequal with anterior ramus 1.1 times the length of the posterior ramus, and segments have serrulate and simple setae on the mesial face, less densely arranged than cirrus I and II. The anterior ramus has a row of ctenoid scales on the anterodistal portion of all segments, most prominent on medial segments.

The *cirrus IV* (Figure 12A–F) protopod has simple setae on the anterior and posterior margins, and a tuft of simple, short setae at the posterodistal angles of both segments; the basis is elongate, with length 3.1–3.4 times the width, and the distal quarter of the anterior margin has a row of 2–4 hooked teeth increasing in size distally. The rami are subequal with ctenopod setation. The anterior ramus has 1–3 hooked teeth on the first nine segments, basal segments have one pair of serrulate setae at the anterodistal angle, and intermediate segments have two pairs. The posterior ramus with three pairs of setae on intermediate segments.

The *cirrus V* (Figure 12G–I) and *VI* (Figure 12J,K) protopods both have simple setae on the anterior and posterior margins and a tuft of simple, short setae at the posterodistal angles of both segments; the basis is less elongate than cirrus IV, with length 1.7–2 and 1.5–1.7 times width, respectively, without hooked teeth; the rami are subequal with intermediate segments having three or four pairs of setae. The anterior rami lack hooked teeth or erect spines.

The *penis* (Figure 12L) is longer than cirrus VI, annulated, and sparsely setose. The basidorsal point is low and rounded.

Distribution: Western Australia: Onslow to northern Kimberley, 0–15 m.

Hosts: *Cymbastela stipitata* (Bergquist and Tizard, 1967) [59], *C.* cf *stipitata,* and *C. vespertina* (Hooper and Bergquist, 1992) [60] (Axinellidae).

Etymology: The species epithet is derived from the Latin *acuta* (point, sharp) and *flava* (yellow) in reference to the yellow–orange chitinous tips of the terga.

Remarks: This species presents interesting variability in the details of the parietes. The longitudinal ribbing may be very faint, as it is in the holotype, to very pronounced (compare Figure 9A–E with Figure 9F,G). In some specimens, the basal margins are markedly convex, making the basal perimeter scalloped. The junctions between the rostrum, carina, and latera in these specimens cause the basal plate to form acute angles that are drawn up from the basal plane. This in turn causes grooves to run diagonally across the basis. In small specimens (~2 mm diameter), the horizontal growth lines appear denticulate and fringed with chitinous setae. The growth lines are especially pronounced at the lateral margin, where they inflect upwards and seem almost spine-like.

These projecting growth lines, however, are not comparable with the sharp, acicular, and fragile parietal spines present on the majority of the *Euacasta*: *E. abnormis* (Kolbasov, 1991) [61], *E. aculeata* (Nilsson-Cantell 1921) [62], *E. ctenodentia* (Rosell, 1972) [52], *E. dofleini* (Krüger, 1911) [63], *E. microforaminia* (Rosell, 1970) [64], *E. porata* (Nilsson-Cantell, 1921) [62], and *E. tabachniki* (Kolbasov, 1990) [65]. In *E. zuiho* (Hiro, 1936) [66] and *E. excoriatrix* sp. nov., the parietes have blunt calcareous projections, but are otherwise smooth, lacking any trace of longitudinal ridges. In *E. sporillus* (Darwin, 1854) [38], the parietes are perforated in a regular, grid-like arrangement. The only species with smooth parietes is *E. antipathidis* (Broch, 1916) [67], described based solely on dead, empty shells embedded in the skeleton of a moribund alcyonacean [11]. Despite the lack of opercular plates or cirri, it can be separated easily by the overall globose shape of the shell as compared to the box-like shape of *E. acutaflava* sp. nov.

The chitinous apex to the opercular plates is also a character unique to the *E. acutaflava* sp. nov. among the *Euacasta*. Further distinguishing features include the hooked teeth of cirrus IV protopod, which are restricted to the distal-most portion, whereas E. *excoriatrix* sp. nov., *E. ctenodentia*, *E. dofleini*, *E. porata,* and *E. zuiho* all have numerous teeth lining at least half of the basis (but see Yu et al. [68]). Both *E. abnormis* and *E. tabachniki* completely lack hooked teeth on cirrus IV, while *E. sporillus,* as figured by Kolbasov [5] and Yu [68], has three well-spaced teeth.

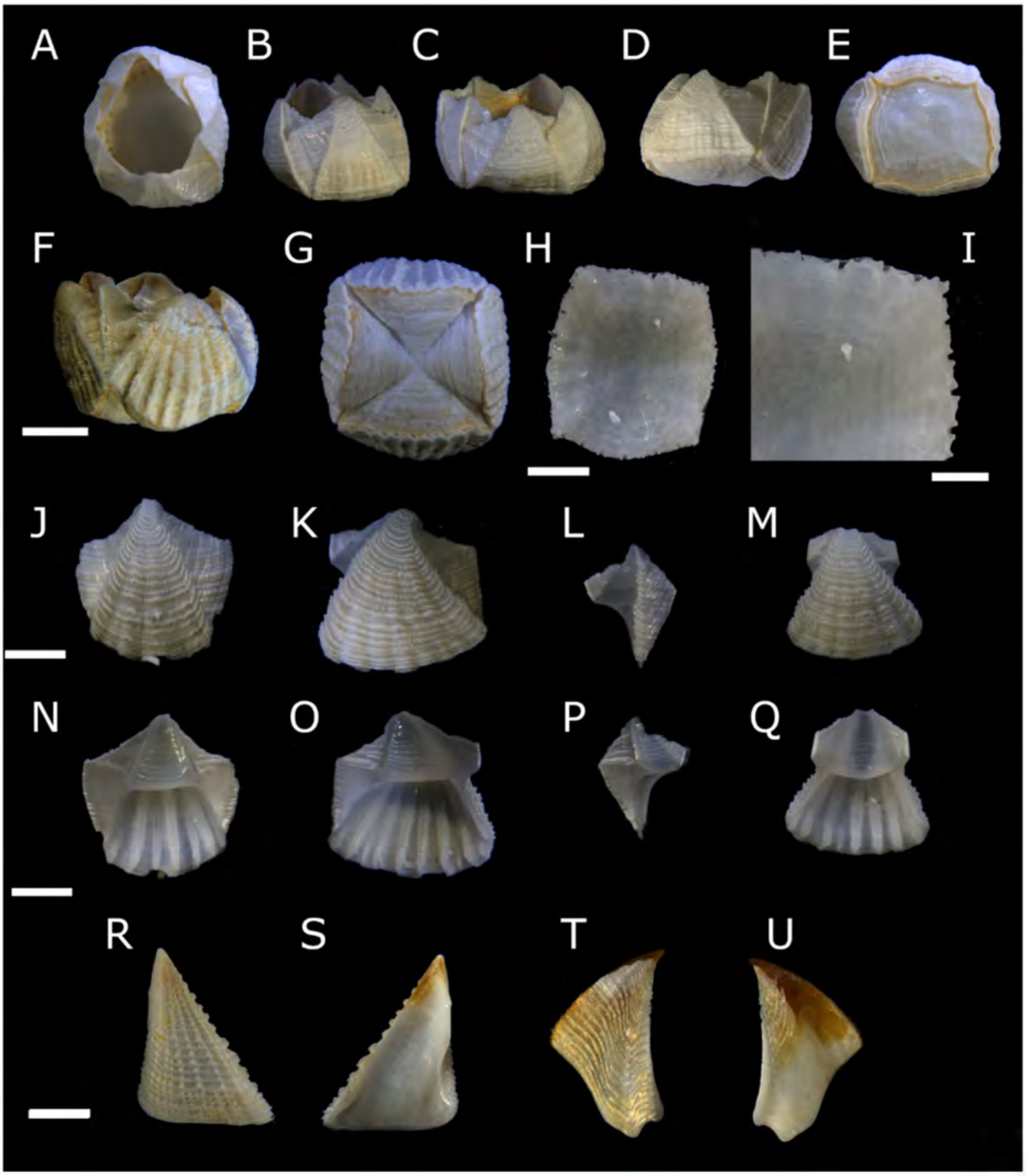

Figure 9. *Euacasta acutaflava* sp. nov. (**A**–**E**) top, rostral, left, right and basal views, respectively, of holotype (WAM C58744), opercular plates removed; (**F**,**G**) left lateral and basal views, respectively, of paratype (WAM C61435), opercular plates removed; (**H**) internal view of basis; (**I**) enlarged portion of basis rim showing crenate margin; (**J**–**M**) external and (**N**–**Q**) internal views of rostrum, right lateral, right carinolateral and carina, respectively of paratype (WAM C76451); (**R**,**S**) external and internal view of scutum; (**T**,**U**) external and internal view of tergum of holotype (WAM C58744). Scale bars: A–G = 2 mm; H, J–U = 1 mm; I = 0.5 mm.

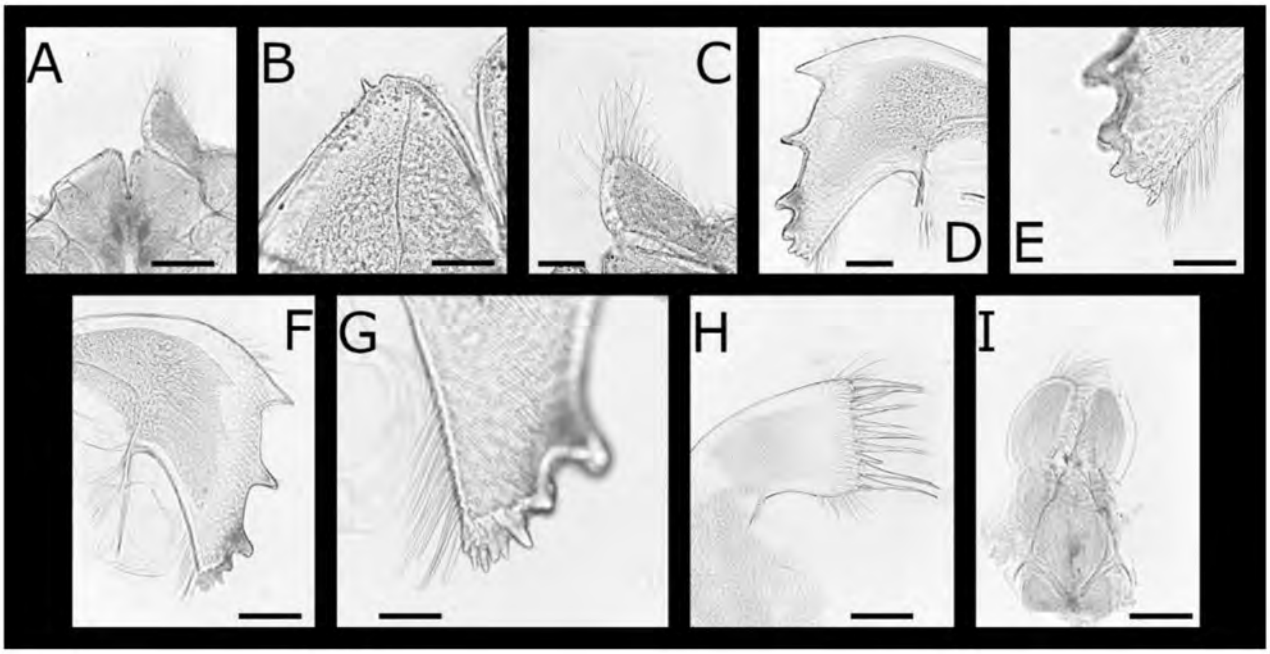

Figure 10. *Euacasta acutaflava* sp. nov. mouthparts of holotype (WAM C58744) (**A**) labrum and right mandible palp; (**B**) close up of crest of labrum; (**C**) right mandible palp; (**D**) right mandible; (**E**) close up of inferior angle of right mandible; (**F**) left mandible; (**G**) close up of inferior angle of left mandible; (**H**) left maxillule; (**I**) left and right maxillae. Scale bars: A, I = 200 µm; B, E, G = 50 µm; C–D, F, H = 100 µm.

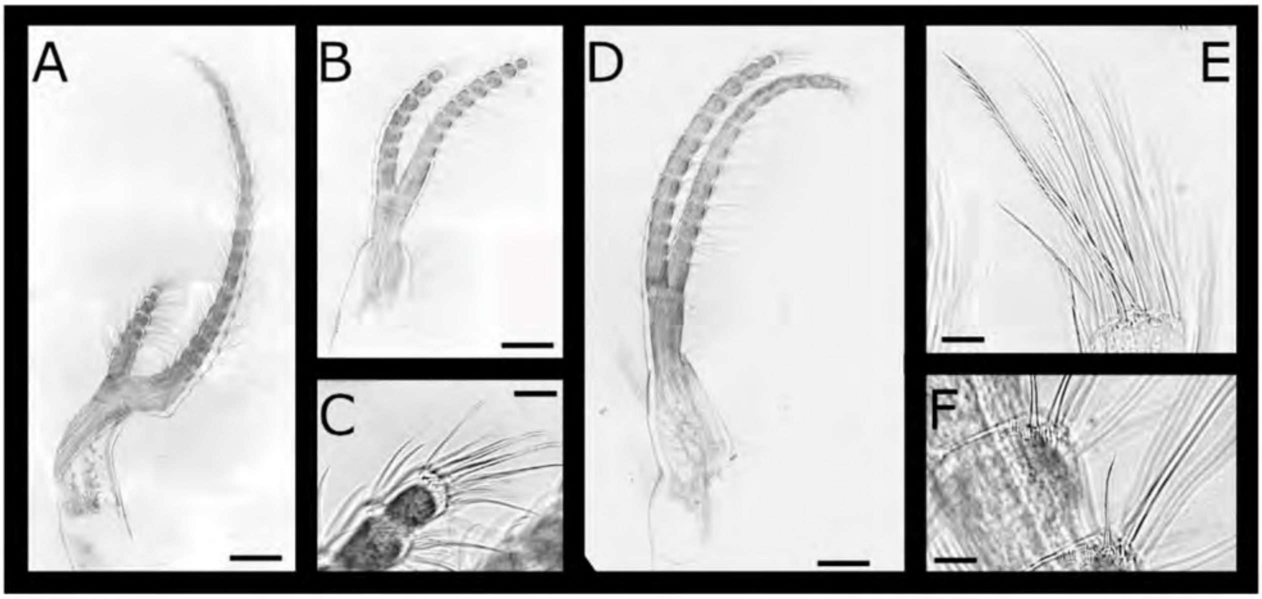

Figure 11. *Euacasta acutaflava* sp. nov. cirri I–III of holotype (WAM C58744) (**A**) left cirrus I; (**B**) left cirrus II; (**C**) terminal segment of left cirrus II posterior ramus; (**D**) left cirrus III; (**E**) serrulate setae on terminal segment of right cirrus III posterior ramus; (**F**) medial segments of left cirrus III anterior ramus, arrows indicate ctenoid scales. Scale bars: A–B, D = 200 µm; C, E–F = 50 µm.

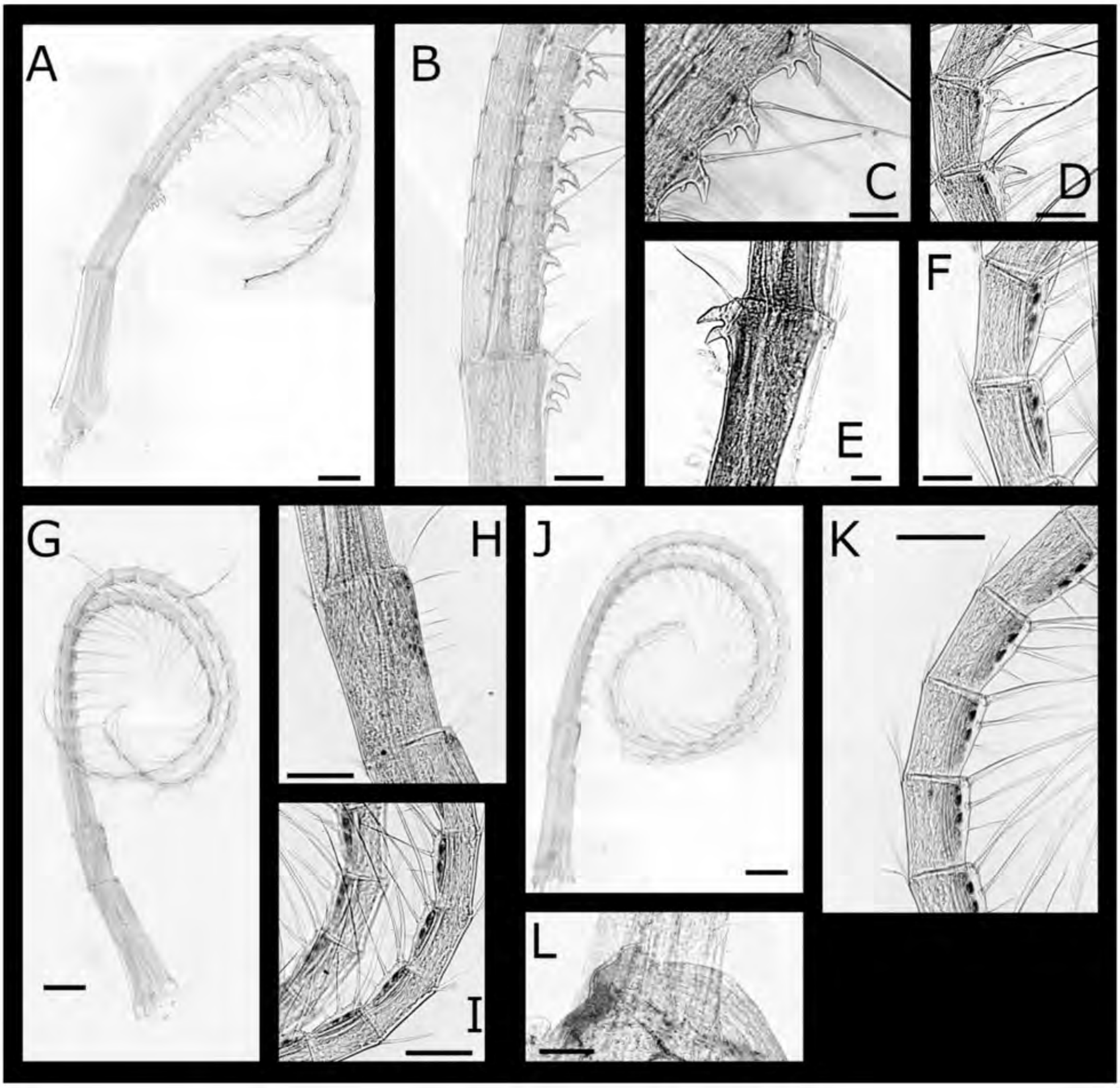

Figure 12. *Euacasta acutaflava* sp. nov. cirri IV–VI of holotype (WAM C58744) (**A**) left cirrus IV; (**B**) basal segments of rami and basis of left cirrus IV protopod; (**C**,**D**) medial segments of left cirrus IV anterior ramus; (**E**) teeth on basis of right cirrus IV protopod; (**F**), medial segments of left cirrus IV posterior ramus; (**G**) left cirrus V; (**H**) basis of left cirrus V protopod; (**I**) medial segments of right cirrus V; (**J**) left cirrus VI; (**K**) medial segments of left cirrus VI; (**L**) basidorsal point of penis. Scale bars: A, G, J =200 µm; B, H–I, K–L 100 µm; C–E = 50 µm.

Euacasta excoriatrix sp. nov. (Figures 13–16)

http://zoobank.org/urn:lsid:zoobank.org:act:6147D22A-07A7-4F11-9C8F-BD2CC968E9C4

Material examined: *Holotype*: WAM C71800, 5.0 mm RC, 3 slides, Flying Foam Passage, Dampier Archipelago, WA, 20°28′3″ S 116°49′40″ E, 9 m, NCB Dampier Archipelago Expedition, stn. 4/D17, 23 Mar 2017, coll. A.M. Hosie & A. Hara, host: WAM Z86895 *Halichondria* BAR1

Paratypes: WAM C61475, 3 slides, S of Champagny Island, Buccaneer Archipelago, WA, 15°19′56.71″ S 124°14′09.49″ E, intertidal, Woodside Kimberley Survey, stn. 62/K11-T3, 15 Oct 2011, coll. O.A. Gomez, Host: WAM Z54014 *Halichondria* NW1; WAM C71801, same data as for holotype.

Other material: WAM C58573, same data as for holotype.

Diagnosis: Shell white, parietes studded with irregularly spaced, short calcareous spines. Basis concave, quadrangular, drawn up into angular corners at junctions of parietes, diagonal grooves crossing at the centre. Scutum elongate, prominent growth ridges crossed with longitudinal ridges, giving a beaded appearance. Tergum narrow, falcate apex beaked, spur broad, occupying over half of basal margin. Mandibular palp with distal corner produced into long narrow projection. Cirrus I posterior ramus ~5 times length of anterior ramus. Cirrus III anterior ramus with small, erect spines on anterodistal angle. Cirrus IV protopod with row of hooked teeth on 0.75 of anterior margin and group of erect spines on anterodistal angle of basis; anterior ramus with 2-3 hooked teeth on anterior margin and group of erect spines on anterodistal angle. Cirrus V with or without hooked teeth on protopod, anterior ramus with single tooth on medial segments.

Description: *Shell* (Figure 13A–O) white, slightly globose, parietes divergent, only slightly curved toward orifice, diameter of orifice equal to or greater than basis. Parietes externally with irregularly spaced, short, blunt calcareous projections, horizontal growth lines faint, basal margins convex. Radii and alae reaching basal margin of corresponding parietes, summits oblique, broad with fine horizontal and oblique striations. Rostrum and carina broadest plates, approximately equal in width; carinolateral exceptionally narrow, parietal area represented by thin strip, radii and alae similar to those on other plates. Internally, sheath occupying one third of inner lamina, with conspicuously raised, horizontal, growth ridges, lower margin separated from inner lamina, below sheath, narrow, longitudinal, parietal ribs extending to basal margin.

Basis (Figure 13J,O) shallow, subrectangular in outline, with rounded corners and convex sides; corners drawn up into junctions between parietes; conspicuous grooves running diagonally from each corner in “x”-shape; concentric growth lines conspicuous; basal rim finely crenate, interlocking with internal ribs on parietes.

Scutum (Figure 13P,Q) triangular, height 1.5 times width, concave on apicobasal axis, growth lines scalloped by longitudinal ridges; basitergal angle rounded, tergal section narrow; occludent margin strongly toothed. Internally smooth, adductor and lateral depressor muscle pits faint, not well defined; articular groove narrow, bounded by distinct articular ridge, latter extending halfway along tergal margin, not projecting beyond tergal margin.

Tergum (Figure 13R,S) narrow, apex tinged with red, acute, strongly beaked, projecting beyond scutum when articulated; growth lines fine, well-spaced, fringed with short, inconspicuous setae; carinal margin evenly concave; basal margin straight; spur distally truncate, broad, length 0.3 times width, occupying approximately 0.6 of basal margin, positioned approximately 0.15 own width from scutal margin; spur and furrow margins coincident, spur furrow defined by abrupt change in growth lines on both sides; internally smooth, crests for depressor muscles absent; articular furrow narrow, articular ridge low, rounded occupying approximately 0.3 scutal margin.

Labrum (Figure 14A,B) bilobed, divided by deep, medial, v-shaped notch, each rounded lobe with 3 marginal teeth and numerous fine setae.

Mandibular palp (Figure 14A,C) rhomboid, distal angle produced ventrally into long, narrow projection, anterior margin concave, posterior margin straight; setae heavily serrulate, becoming longer and denser distally; distal angle with long, simple setae.

Mandible (Figure 14D,E) cutting margin with five distinct teeth, second and third teeth bifid, fourth tooth becoming molariform, fifth tooth congruent with molariform or spinose inferior angle; superior and inferior margins with row of long, fine simple setae; dense, short setae covering inner and outer faces.

Maxillule (Figure 14F,G) cutting margin straight with 10–12 cuspidate setae, upper and lower pairs larger and more robust than remaining setae; inferior angle with tuft of shorter cuspidate setae. Dense, short setae regularly spaced on inner and outer faces, longer fine setae on inferior and superior margin.

Maxilla (Figure 14H) bilobed, lobes ovate, serrulate setae arranged on anterior margins, becoming more dense at apex, longer on distal lobe than those on basal lobe.

Cirral segment counts are given in Table 2.

Cirrus I (Figure 15A) protopod with pappose setae basally on posterior margin. Rami unequal, anterior ramus approximately 5 times length of posterior ramus, setation lasiopod; segments with densely arranged serrulate and simple setae on mesial face.

Cirrus II (Figure 15B,C) protopod anterior margin lined with long plumose setae, posterior margin with pappose setae basally, plumose setae distally. Rami unequal, anterior ramus 1.33 times longer that posterior ramus, segments with densely arranged serrulate and simple setae on mesial face, transverse row of ctenoid scales on distal margin of each segment.

Cirrus III (Figure 15D,E) protopod anterior margin lined with long plumose setae, posterior margin with pappose setae basally, plumose setae distally. Rami subequal, anterior ramus 1.1 times longer that posterior ramus segments with serrulate and simple setae on mesial face, less densely arranged than on cirrus I and II. Anterior ramus with row of small, erect spines and ctenoid scales on anterodistal portion of all segments, except terminal segment, most prominent on medial segments.

Cirrus IV (Figure 16A–G) protopod with simple setae on anterior and posterior margins, tuft of simple, short setae at posterodistal angles of both segments; basis elongate, length 3.1–3.4 times width, anterior margin with row of 9–12 hooked teeth extending 0.75 length, evenly sized or increasing in size distally, anterodistal angle with additional upward turned teeth and erect spines. Rami subequal, setation ctenopod. Anterior ramus with 1–3 hooked teeth on first 10–11 segments, anterodistal angle with erect spines and ctenoid scales; basal segments with 1 pair of serrulate setae at anterodistal angle, intermediate segments with 2 pairs. Posterior ramus without hooked teeth, anterodistal angle with small erect spines, ctenoid scales on distal margin, 3 pairs of setae on intermediate segments.

Cirrus V (Figure 16H–J) protopod with simple setae on anterior and posterior margins, tuft of simple, short setae at posterodistal angles of both segments; basis less elongate than cirrus IV, length 2.2–2.5 times width, up to 3 teeth distally on anterior margin or teeth absent. Rami subequal, intermediate segments with 3 or 4 pairs of setae. Anterior ramus with 1 hooked tooth on 11th–18th segments; posterior ramus lacking teeth.

Cirrus VI (Figure 16L,M) similar, protopod with simple setae on anterior and posterior margins, tuft of simple, short setae at posterodistal angles of both segments; basis less elongate than cirrus IV, length 1.6–2.1 times width, respectively, without hooked teeth. Rami subequal, intermediate segments with 3 or 4 pairs of setae. Anterior rami lacking hooked teeth or short erect spinules along distal margins.

Penis (Figure 16L) shorter than cirrus VI, annulated, sparsely setose. Basidorsal point (Figure 16N), triangular, apex rounded, acute.

Hosts: *Halichondria* BAR1, *H.* NW1 (Halichondriidae).

Distribution: Western Australia: Dampier Archipelago to the Kimberley. Intertidal–9 m.

Etymology: The species epithet translates as “the flayer” and is derived from the Latin *excorior* (to flay, to skin), this is in reference to the long whip-like cirri and the strong hooked teeth on cirrus IV and V that are used to scrape away encroaching host tissues to prevent being overgrown.

Remarks: This species is characterised by several features that separate it from the remainder of the genus. In particular, the beaked tergum, the relative lengths and armature of the cirri, and mandible palp clearly define the morphological boundaries of this species. The upwardly directed teeth on the anterodistal angle of the protopod of cirrus IV also appear to be unique within the genus, as the other species have only been documented with teeth that are horizontal or hooked downward. Both *E. abnormis* and *E. tabachniki* have a tergum with a similarly beaked apex, but these species lack teeth on cirrus IV and V; the mandibular palps are not elongated; in *E. abnormis,* there are no internal parietal ribs; and *E. tabachniki* has long spines on the parietes [61,65]. In external appearance, this species is most similar to *E. zuiho* (*sensu* Hiro 1936 [45]), but this species has a typically truncated mandibular palp, shorter cirri (segment counts can be up to half of those in the present specimens), and the anterior ramus of cirrus I is approximately 2.5 times longer than the posterior, compared with 5 in *E. excoriatrix* [66]. However, the figures of *E. zuiho* given by Ren ([45] Figure 11 and Plate III 18–22) and Yu et al. ([68] Figure 14, Supplementary Figures S10 and S12) show a prominently beaked tergum, and, in the case of Ren, a mandible with a slightly produced distal angle. Their accounts still differ from the present species, having relatively short cirri and no erect spines on the protopod basis of cirrus IV. Further to this, the ribs on the inner lamina of the parietes are restricted to the basal margin, and the basidorsal point of the penis is absent in Ren's specimens. Lastly, in Yu et al., the tergal spur is distinctly separated from the basi-scutal angle. These records show some differences with those of the original description [66] and potentially also represent different species.

The armature of cirrus IV is rather constant, with only small changes in the number of teeth on the protopod and segments, but the variation seen in the protopod of cirrus V is peculiar and not symmetrical. One of the paratypes (WAM C61475) bears two small, upturned teeth on the left and three hooked teeth on the right, while the holotype bears no trace of teeth.

3.1.3. *Pectinoacasta* Kolbasov, 1993 [5]

Pectinoacasta cancellorum (Hiro, 1931) [69] (Figures 17–20)

Acasta cancellorum Hiro, 1931: p. 151, Figures 8A–C, Pl. XIII 1–1d [69]. Hiro 1937: p. 459, Figures 36, 37 [7].

Pectinoacasta cancellorum Kolbasov 1993: p. 411 [5].

Material examined: *Lectotype*: SMBL #149, Seto, Kii Province, Japan

Australia: WAM C50791, WAM C55262–4, all from Echuca Shoal, WA, 13°54′02.48″ S 123°53′36.42″ E, 20 m, Woodside Kimberley Survey 2012, stn. 108/K12, 18 Oct 2012, coll. A.M. Hosie, host: WAM Z54694 *Agelas* KMB1. WAM C57105, WAM C55302–7, all from Mermaid Reef, Rowley Shoals, WA, 17°01′35.7″ S 119°37′08.0″ E, 25 m, Woodside Kimberley Survey 2014, stn. 181/K14, 14 Oct 2014, coll. A.M. Hosie, host: *Agelas* KMB1. WAM C55340, 10.1 mm RC, Wheatstone, off Onslow, WA, 21°35′46″ S 115°00′43″ E, 12.3 m, WAMSI Onslow Survey I March 2013, stn. RVS5737/D11-T1, 27 Mar 2013, coll. C.L. Schonberg, host: WAM Z65287 *Agelas* cf. *mauritiana*. WAM C56830, WAM C55308–9, all from Clerke Reef, WA, 17°19′01.1″ S 119°23′01.6″ E, 18 m, Woodside Kimberley Survey 2014, stn. 170/K14, 10 Oct 2014, coll. A.M. Hosie, Host: *Agelas* KMB1.

Diagnosis: Shell globose, parietes permeated with narrow longitudinal incisions extending from basal rim and small membranous windows at parietal junctions; externally surfaces studded with short sharp calcareous spines; internally longitudinal ribs extend below sheath and interlock with crenate basal rim. Scutum with longitudinal ridges crossing growth ridges. Tergum with setose, yellow chitinous cuticle covering external surface of carinal side of spur furrow, growth ridges crossed with longitudinal ridges giving a latticed appearance. Cirrus IV protopod with row of 6–7 teeth on anterior margin, anterior ramus basal segments with 1–2 recurved teeth on anterior margins.

Description: *Shell* (Figure 17A–D,J,K), white or grey; orifice small relative to shell diameter, rim bluntly toothed. Parietes with longitudinal incisions extending from basal rim to over half parietal height, creating narrow, membrane-covered slits, incisions secondarily calcified in upper portions of parietes; external surfaces with numerous short, sharp, calcareous projections arranged irregularly, or in longitudinal rows where confined by incisions; parietes strongly curved toward orifice. Radii and alae not reaching basal rim, leaving small membranous windows between parietes; broad with striations perpendicular to oblique summits. Rostrum widest shell plate; internally, sheath with conspicuous horizontal growth lines; lower margin separated from internal parietal wall, extending to just above apical extent of parietal incisions.

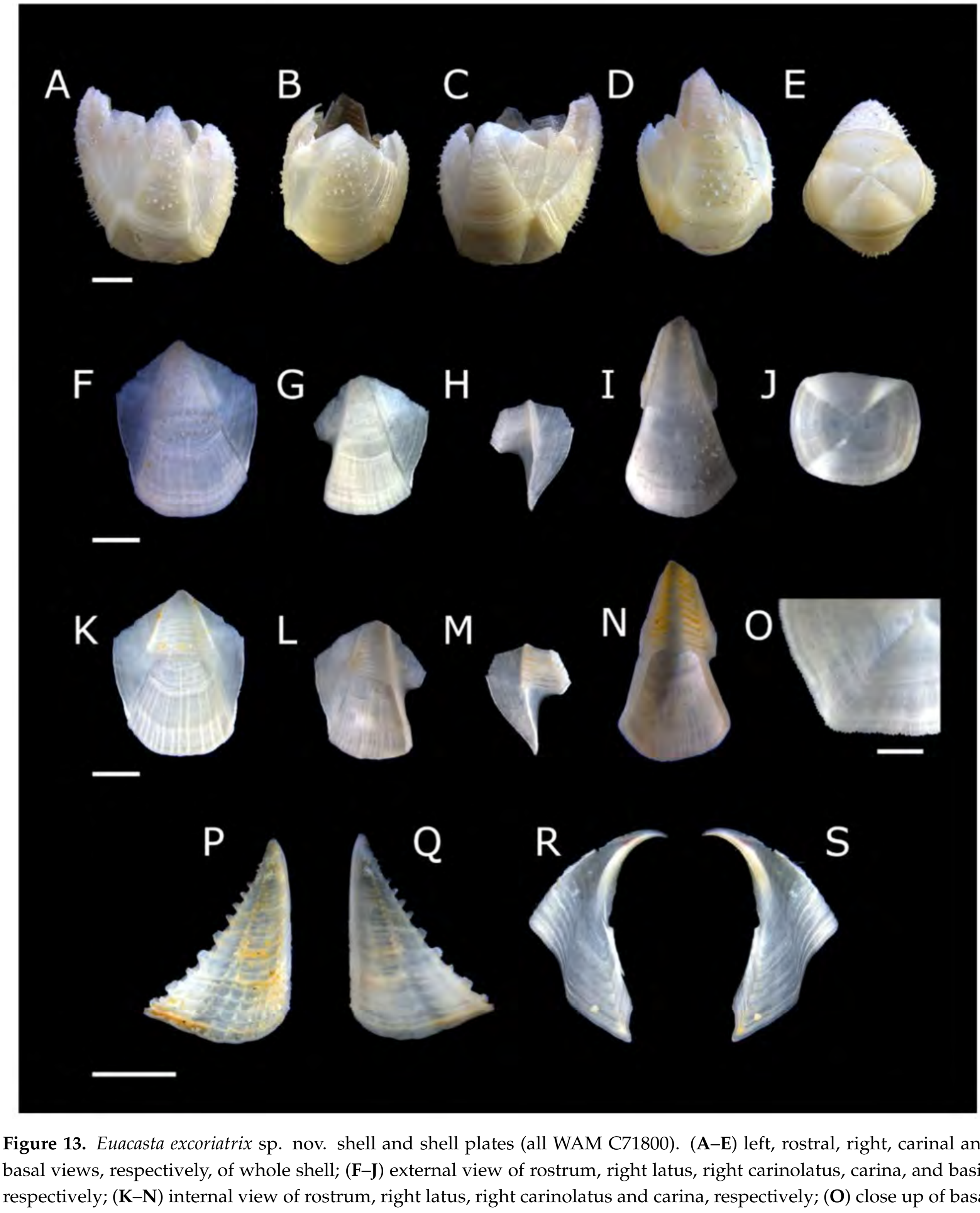

Figure 13. *Euacasta excoriatrix* sp. nov. shell and shell plates (all WAM C71800). (**A**–**E**) left, rostral, right, carinal and basal views, respectively, of whole shell; (**F**–**J**) external view of rostrum, right latus, right carinolatus, carina, and basis, respectively; (**K**–**N**) internal view of rostrum, right latus, right carinolatus and carina, respectively; (**O**) close up of basal rim; (**P**,**Q**), external and internal view of right scutum; (**R**,**S**), internal and external view of right tergum. Scale bars: A–N, P–S = 2 mm; O = 1 mm.

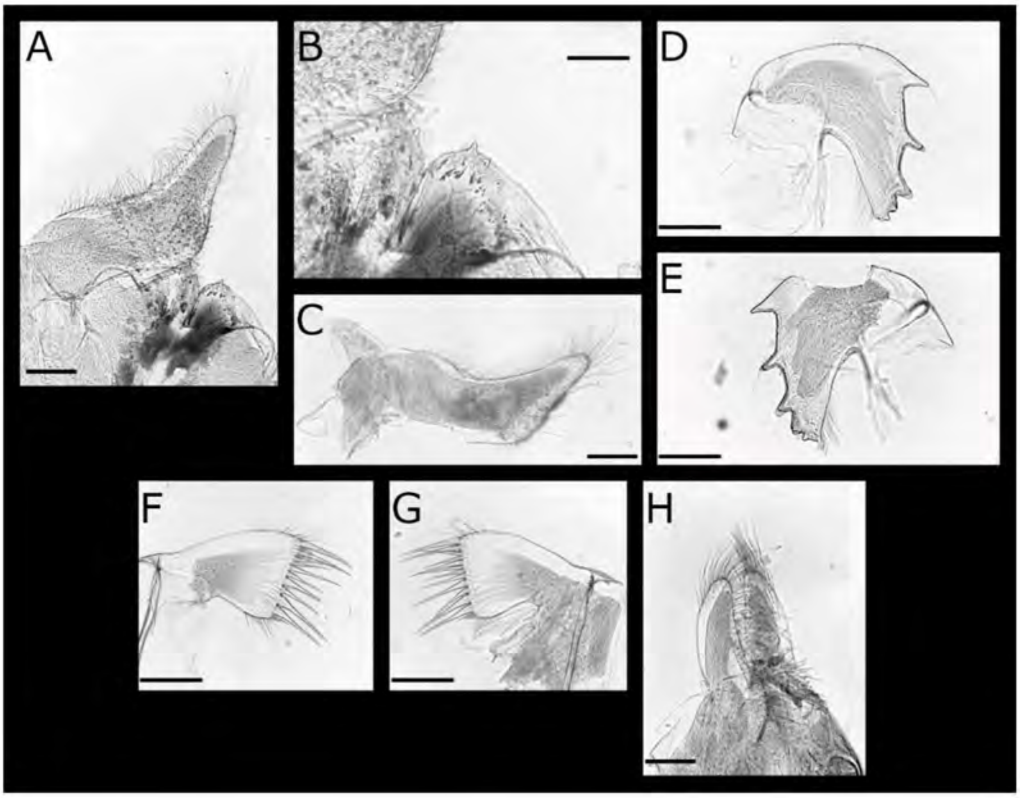

Figure 14. *Euacasta excoriatrix* sp. nov. mouthparts (A,B, WAM C71800, holotype; C–H, WAM C61475 paratype). (**A**) labrum with right mandible palp; (**B**) crest of labrum; C, right mandible palp; (**D**,**E**) left and right mandible; (**F**,**G**) left and right maxillule; (**H**) left and right maxillae. Scale bars: A, C–H = 200 µm; B = 100 µm.

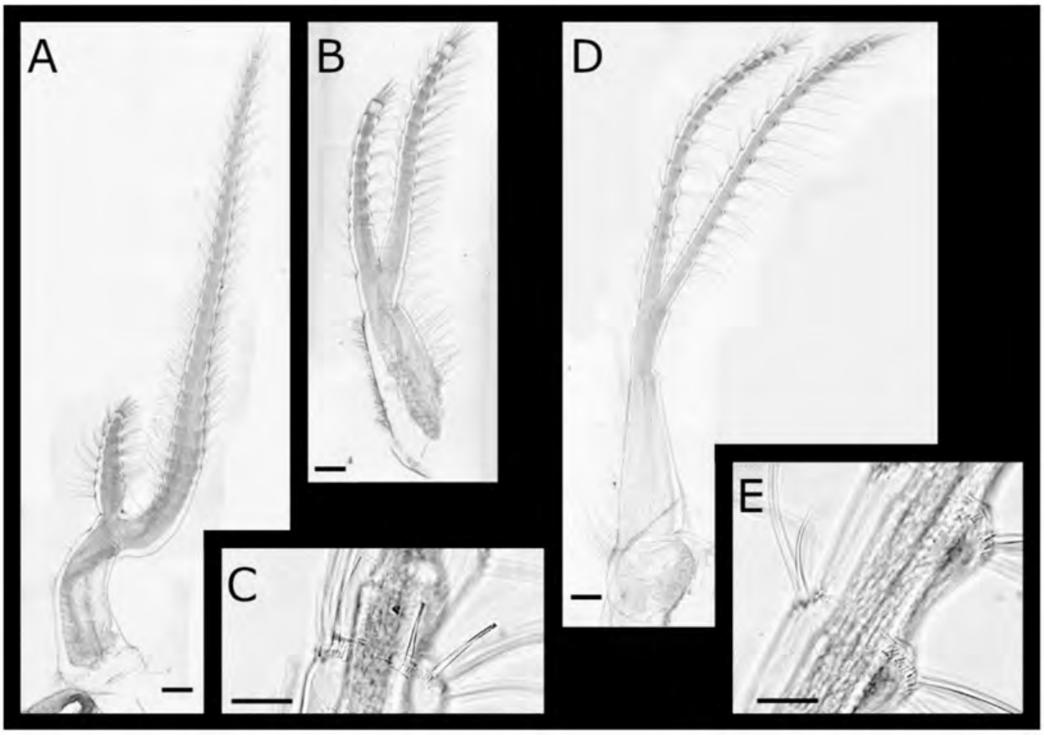

Figure 15. *Euacasta excoriatrix* sp. nov. Cirri I–III (WAM C71800, holotype). (**A**) left cirrus I; (**B**) left cirrus II; (**C**) ctenoid scales on cirrus II anterior ramus segment; (**D**) left cirrus III; (**E**) small erect spines on the anterodistal angle of cirrus III anterior ramus. Scale bars: A–B, D = 200 µm; C, E = 50 µm.

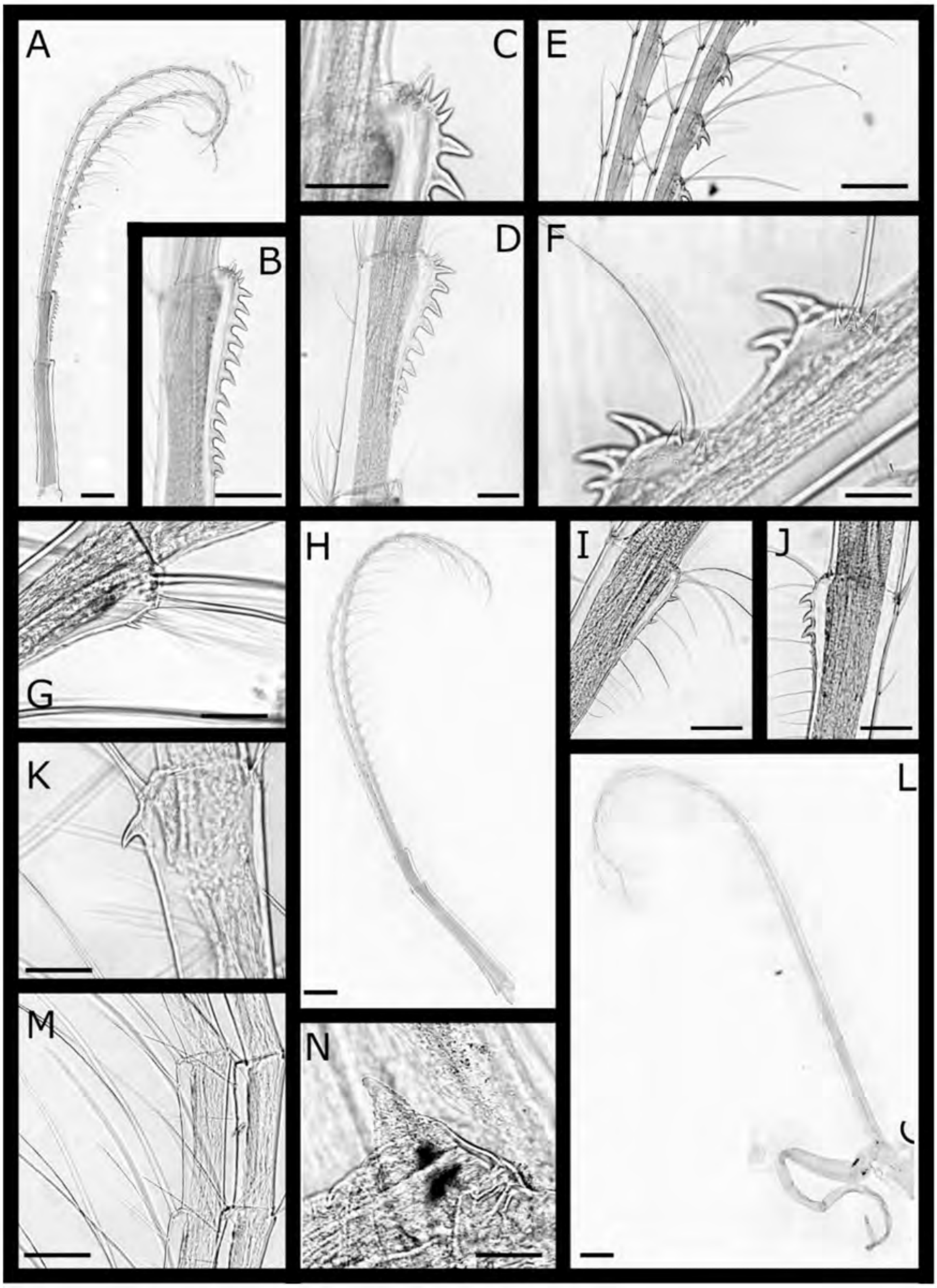

Figure 16. *Euacasta excoriatrix* sp. nov. cirri IV–VI and penis (A–C, E–M WAM C71800, holotype; D, WAM C61475, paratype). (**A**) left cirrus IV; (**B**) basis of cirrus IV protopod; (**C**) close up of anterodistal angle of same; (**D**) basis of cirrus IV protopod; (**E**) medial segments of cirrus IV anterior and posterior rami; (**F**,**G**) detail of teeth and erect spines on segments of cirrus IV anterior ramus; (**H**) left cirrus V; (**I**,**J**) teeth on distal portion of left and right cirrus V protopod; (**K**) tooth on medial segment of right cirrus V; (**L**) left cirrus VI and penis; (**M**) medial segments of cirrus VI anterior and posterior rami; (**N**) basidorsal point of penis. Scale bars: A, H, L = 400 µm; B, D–E, I–J, M = 100 µm; C, F, G, K, N = 50 µm.

Basis circular, shallow to deeply cupped, not more than half total shell height; concentric growth lines conspicuous; basal rim irregularly crenate, interlocking with internal ribs of parietes.

Scutum (Figure 17L,M) triangular, as wide as or slightly wider than high, growth ridges strongly crenate with raised points and short setae, longitudinal ridges variably pronounced; basitergal angle rounded, tergal section indistinctly separated; occludent margin strongly toothed. Internally smooth, apex with yellow chitinous cuticle, adductor and lateral depressor muscle pits present; articular ridge short, occupying 0.3 length of tergal margin, prominently protruding beyond tergal margin, with deep articular furrow, extending entire length of tergal margin.

Tergum (Figure 17N,O) apex blunt, external surface covered by yellow, setose, chitinous cuticle on carinal side of spur furrow; growth lines prominent, crossed by strong longitudinal ridges giving a lattice-like or cancellated appearance, fringed with short inconspicuous setae; articular margin concave in apical half. Carinal margin almost straight, only curved near apex; basal margin straight; spur length approximately 1.25 times width, occupying approximately 0.25 basal margin, positioned less than half own width from scutal margin; spur furrow defined by abrupt change in growth lines, margins infolded, furrow open in basal half; distal margin rounded or truncate. Internally roughened with raised tubercles in apical section, chitinous cuticle on carinal and basal margins, crests for depressor muscles prominent, particularly in larger specimens. Articular furrow broad, articular ridge low, rounded occupying 0.25 scutal margin.

Labrum (Figure 18A,B) bilobed, divided by deep, medial, v-shaped notch, each rounded lobe with 3 prominent, marginal teeth and numerous fine setae.

Mandibular palp (Figure 18A,C) rhomboid, distal end obliquely truncate, anterior margin concave, posterior margin straight; setae heavily serrulate, becoming longer and more dense distally; distal angle with long, simple setae

Mandible (Figure 18D–F) cutting margin with 4 distinct teeth, second to fourth tooth bifid, fifth tooth congruent with molariform or spinose inferior angle; superior and inferior margins with row of long, fine, simple setae, dense short setae covering inner and outer faces.

Maxillule (Figure 18G,H) cutting margin straight, with small notch between second and third setae; 10–11 cuspidate setae, upper and lower pair larger and more robust than remaining setae, 3–4 medial setae serrate on inferior margin. Dense, short setae regularly spaced on inner and outer faces, longer fine setae on inferior and superior margin.

Maxilla (Figure 18I) bilobed, lobes ovate, distal lobe elongate, length more than twice width, serrulate setae arranged on anterior margins, becoming more dense at apex, setae longer on distal lobe than on basal lobe.

Cirral segment counts are given in Table 2.

Cirrus I (Figure 19A,B) protopod with pappose setae on basal segment posterior margin, basis with tuft of setae at posterodistal angle. Rami unequal, anterior ramus 3 times length of posterior ramus, setation lasiopod, segments with densely arranged serrulate and simple setae on mesial face, tuft of simple setae on posterodistal angle.

Cirrus II (Figure 19C) protopod lined with long serrulate setae on anterior margin and pappose or plumose setae on posterior margin on basal segment; basis with long serrulate setae on anterior margin. Rami unequal, anterior ramus 1.25 times longer than posterior ramus, setation lasiopod, segments with densely arranged serrulate and simple setae on mesial face.

Cirrus III (Figure 19D–F) protopod lined with long serrulate setae on anterior margin and pappose or plumose setae on posterior margin on basal segment. Rami unequal, anterior ramus 1.25 times length of posterior ramus; setation lasiopod, segments with serrulate and simple setae on mesial face, less densely arranged than on cirrus I and II. Anterior ramus with transverse row of distally directed spines or ctenoid scales at anterodistal angle on all but distal-most segments, spines most prominent on medial segments; posterodistal angle with transverse row of ctenoid scales. Posterior ramus with similar spination but much reduced in size.

Cirrus IV (Figure 20A–F) protopod basal segment posterior margin with few plumose setae, tuft of simple, short setae at posterodistal angle; anterior margin with widely spaced plumose setae; basis elongate, length 2.09–2.15 width, with tuft of simple, long setae at posterodistal angle; anterior margin lined with up to 7 well-spaced, hooked teeth, lower third lacking teeth. Rami subequal in length, setation ctenopod. Anterior ramus with 1-2 hooked teeth on anterior margins of first 14 segments, anterodistal angles with transverse row of erect spines on all but distal-most segments; 3 pairs of serrulate setae on medial segments. Posterior ramus with similar setation as anterior ramus, with erect spines on anterodistal angles, with or without hooked teeth.

Cirrus V (Figure 20G) protopod with well-spaced, long setae and dense row of short spinules on anterior margins; posterior margin lacking setae; basis elongate, length 1.7–1.75 width, without hooked teeth, row of long simple setae on anterior margin and tuft of setae at posterodistal angle. Rami subequal, setation ctenopod, 3 pairs of serrulate setae on anterior margins; without teeth or erect spines.

Cirrus VI (Figure 20H–K) protopod and rami setation as in cirrus V; protopod basis elongate, length 1.78–1.97 width, without hooked teeth, longitudinal row of small spinules on anterior and posterior margins of basal segment. Anterior ramus without erect spines or teeth on anterior margins; both rami with 3 pairs of serrulate setae on medial segments.

Penis (Figure 20H) shorter than cirrus VI, annulated, sparsely setose; basidorsal point rounded, inconspicuous.

Distribution: Australia: oceanic coral reefs and shoals off northern WA. Southern Japan [69].

Hosts: *Agelas* KMB1, *Agelas* cf. *mauritiana* (Carter, 1883) [70] (Agelasidae).

Remarks: The presence of longitudinal slits in the parietes immediately distinguishes *P. cancellorum* from all other members of the genus except *P. sculpturata* [6], with which it also shares the chitinous cuticle on the opercular plates. The two species share an obvious morphological affinity, as recognised by Hiro [7], although what he considered to be "remarkable differences between . . . the sculpture of the opercular valves" of the two species was presumably in reference to the presence of the yellow cuticle on the tergum, which was omitted from Broch's description of *P. sculpturata* [6]. This leaves a finer morphological distinction between the two species than at first conceived. Key differences include the presence of hooked teeth on the protopod of cirrus IV of *P. cancellorum* (absent in *P. sculpturata*), the basis of which is more elongate (height/width ratio >2.0 in *P. cancellorum*, <2.0 in *P. sculpturata*), and the basidorsal point, which is rounded and inconspicuous (triangular and prominent in P. sculpturata). Furthermore, the calcareous spines on the parietes appear smaller and more numerous in *P. cancellorum* compared to the stout, blunt spines on *P. sculpturata*. This morphological affinity also corresponds with closely related host usage and a close genetic relationship (see Section 3.2).

There are no slide-mounted specimens among the extant cotypes with which to compare to our material. Only the specimen selected to serve as lectotype still has the prosoma present, which has at some point dried out. This has distorted the prosoma and makes dissection exceptionally difficult without risking further damage. However, some key characters are still observable, e.g., the teeth on cirrus IV are arranged in a similar fashion. There is some variability in the armature of cirrus IV within this species. Hiro describes the posterior ramus of cirrus IV as typically, but not always, bearing a single hooked tooth on the segments; in the present material, only one specimen was found to have this character. The number and development of the teeth on the protopod are also variable, with some specimens having few teeth restricted to the upper portion of the protopod and others having irregular spacing, and the left and right cirri do not necessarily have the same arrangement.

The type series also lacks any trace of the host and the accounts by Hiro [7,69], only mention that it was found in association with *A. sulcata* [57]. This latter species has now been recorded from three orders of sponge: Haplosclerida, Poecilosclerida, and Dictyoceratida [3,5,19]. The present specimens were all collected in species of *Agelas* (order Agelasida), the same host genus as *P. sculpturata*, albeit morphologically different species.

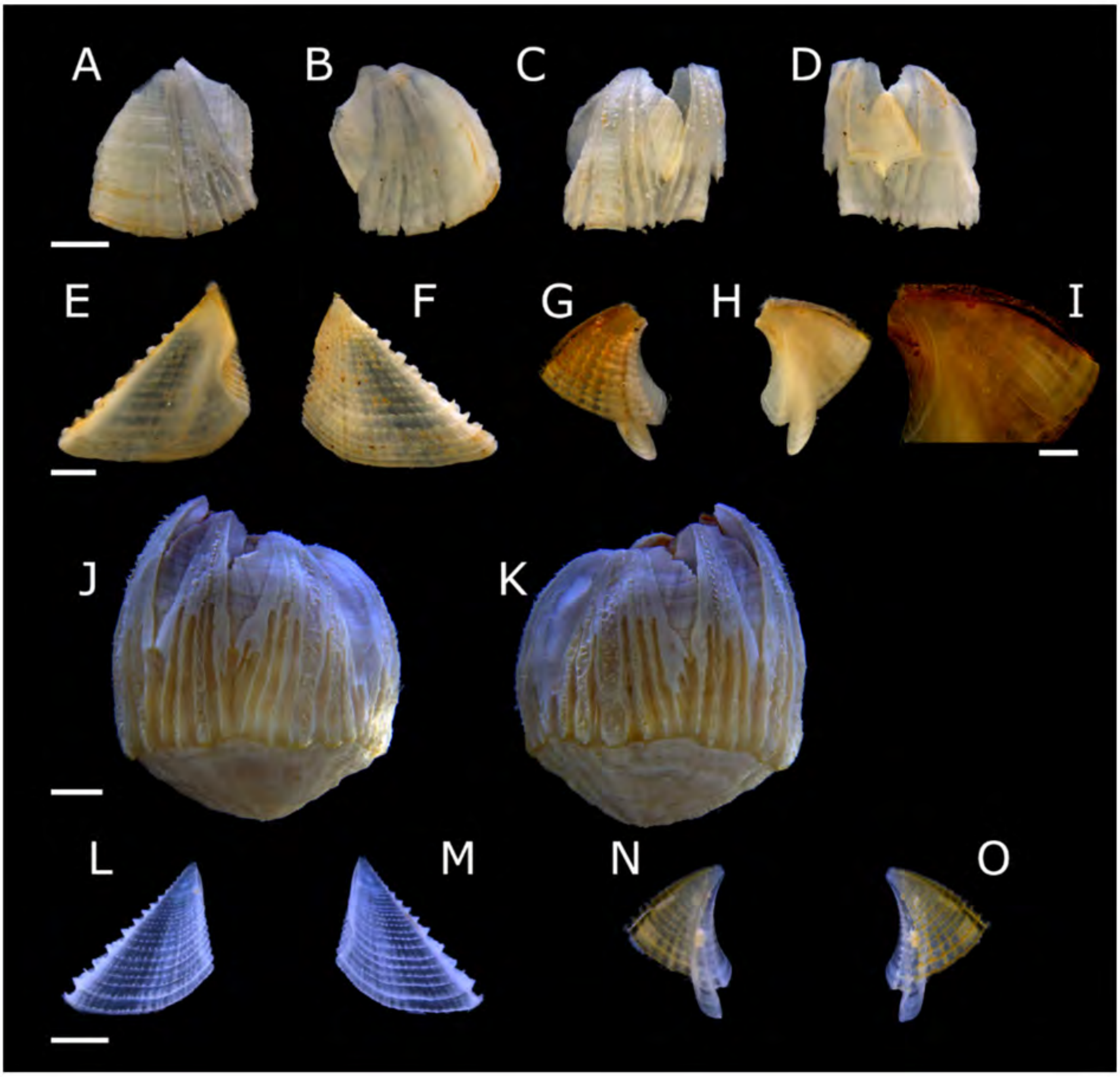

Figure 17. *Pectinoacasta cancellorum* (Hiro, 1931) shell and shell plates (A–I, Lectotype SMBL #149; J,K, WAM C55340; L–O, WAM C55305): (**A**,**B**) external and internal view of rostrum; (**C**,**D**) external and internal view of articulated right lateral and carinolateral (radius broken) plates; (**E**,**F**) internal and external view of left scutum; (**G**,**H**) external and internal view of left tergum; (**I**) close up of depressor muscle crests on right tergum; (**J**,**K**) left and right views, respectively, of whole specimen; (**L**,**M**) external and internal views of right scutum; (**N**,**O**) internal and external views of right tergum. Scale bars: A–D, J,K = 2 mm, E–H, L–O = 1 mm; I = 0.5 mm.

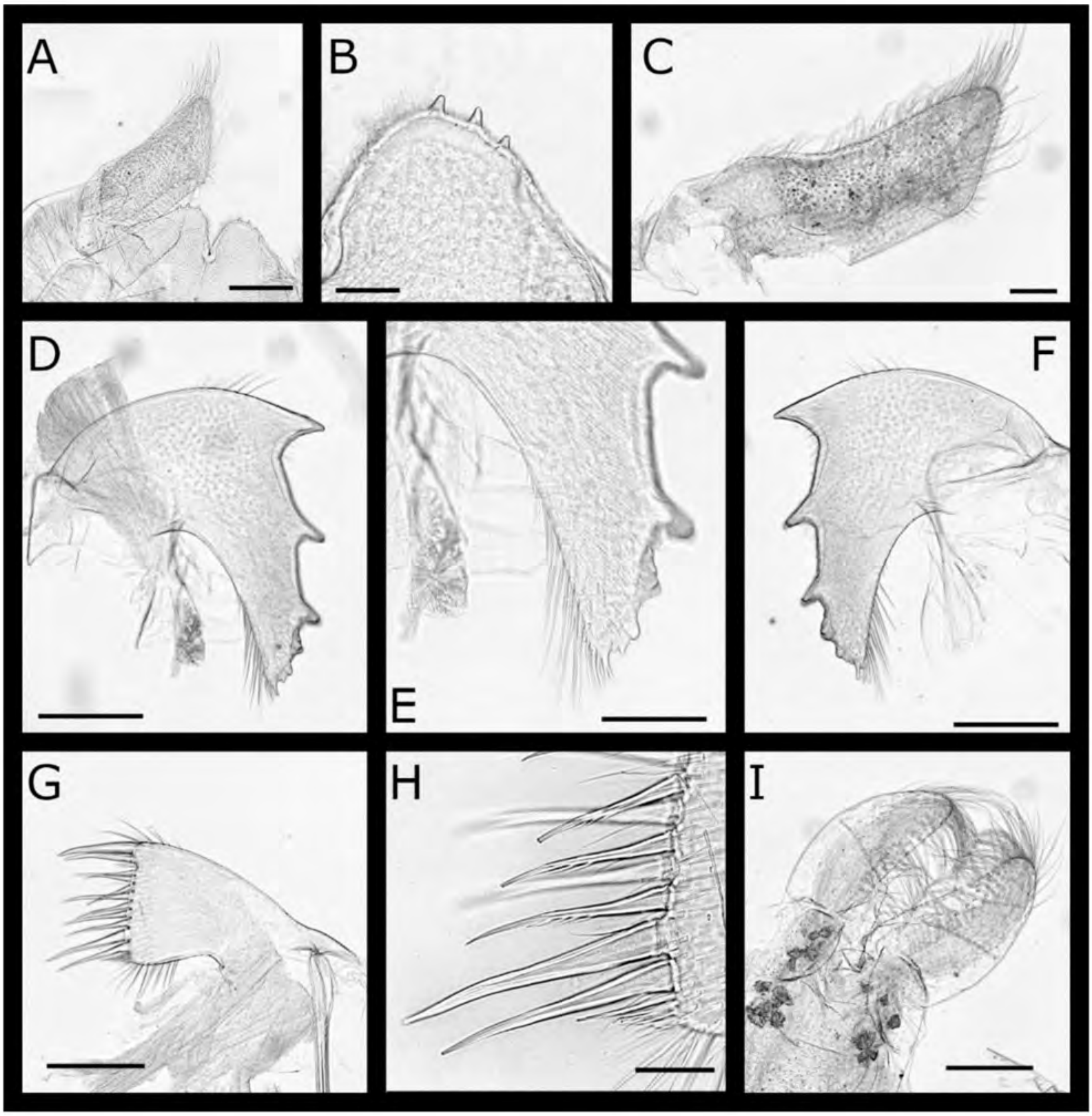

Figure 18. *Pectinoacasta cancellorum* (Hiro, 1931) mouthparts (WAM C55305): (**A**) labrum and right mandible palp; (**B**) close up of labrum crest; (**C**) left mandible palp; (**D**) left mandible; (**E**) closeup of inferior angle; (**F**) right mandible; (**G**) right maxillule; (**H**) close up of serrated setae of maxillule; (**I**) left and right maxilla. Scale bars: A, D, F, G, I = 200 µm; B = 50 µm; C = 100 µm.

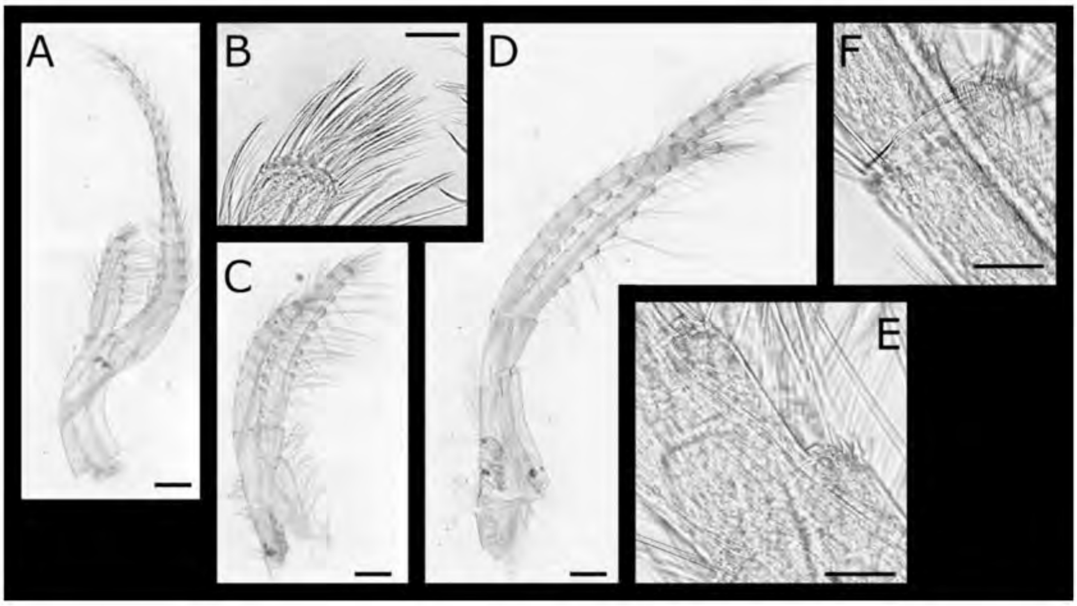

Figure 19. *Pectinoacasta cancellorum* (Hiro, 1931) cirri I–III (WAM C55340). (**A**) left cirrus I; (**B**) serrulate setae on cirrus I anterior ramus terminal segment; (**C**) cirrus II; (**D**) Cirrus III; E, erect spines on cirrus III anterior ramus; (**E**) ctenoid scales on cirrus III posterior ramus. Scale Bars: A, C–D = 200 μm; B, E–F = 50 μm.

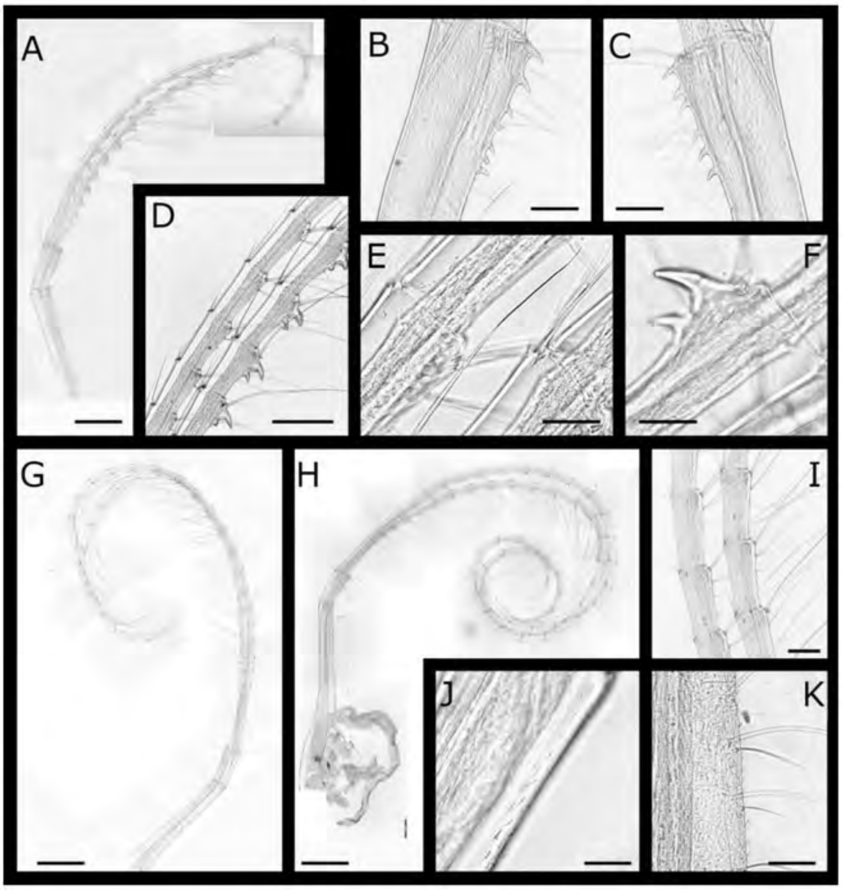

Figure 20. *Pectinoacasta cancellorum* (Hiro, 1931) cirri IV–VI (WAM C55340): (**A**) left cirrus IV; (**B**) basis of left cirrus IV protopod; (**C**) same of right cirrus IV; (**D**) medial segments of cirrus IV; (**E**) small spinules on medial segments of cirrus IV posterior ramus; (**F**) erect spines on medial segments of right cirrus IV anterior ramus; (**G**) right cirrus V; (**H**) left cirrus VI with penis; (**I**) medial segments of left cirrus VI; (**J**,**K**) close up of posterior and anterior margin of cirrus VI protopod basal segment. Scale Bars: A, G, H = 500 μm; B, C, I = 100 μm; D = 200 μm; E, F, J, K = 50 μm.

Pectinoacasta pectinipes (Pilsbry, 1912) [71] (Figures 21–24)

Acasta pectinipes Pilsbry, 1912: p. 294 [71]. Broch 1922: p. 330 [72]. Barnard 1924: p. 86 [73]. Broch 1931: p. 105 [6]. Hiro 1937: p. 463, Figure 38 [7]. Nilsson-Cantell 1938: p. 57, Figure 19 [42]. Utinomi 1962: p. 221 [74]. Zullo 1968: p. 227, Figure 6 [75]. Newman & Ross 1976: p. 54 [44]. Foster 1980: p. 219, Figure 4C. Ren 1984 [45]: p. 189, Figure 4, Pl. 2 10–18. Jones 1990: p. 222 [76] —Jones et al. 1990: p. 15 [77].

Acasta nitida Hoek, 1913: 237, Pl. 24 Figures 17–19, Pl. 25 Figures 1–3 [10].

Acasta komaii Hiro, 1931: 149, Pl. 12 Figures 1–1d [69].

Pectinoacasta pectinipes. Kolbasov, 1993: 411, Figure 14 [5]. Jones et al. 2000: p. 273 [78]. Liu & Ren 2007: [47]: Jones 2010: p. 217 [79]. Van Syoc et al. 2015: Tab. 1–2 [1]. Jones and Hosie 2016: p. 277 [50].

Material examined: WAM C48061, Cockburn Sound, WA, 32°12′ S 115°44′ E, stn. RW3 Q3 (rep 3), Aug 2008, host: *Trachytedania* L2. WAM C58141, WAM C58870, 3.4 mm RC, WAM C58871, 3 slides, WAMC 58872–3, all from South Beach, Fremantle, WA, 32°01′25.3″ S 115°45′00.1″ E, washed up on beach, 10 Jun 2015, coll. G. Raymond, host: WAM *Trachytedania* L1. WAM C66680, WAM C67748, WAM C67749, 3 slides, WAM C67750, all from west side of North Muiron Island, WA, 21°37′40″ S 114°22′25″ E, 17 m, NCB Exmouth & Muirons Expedition, stn. 7/EM16, 3 Jun 2016, coll. A. Hara, Host Z97093 *Trachytedania* MM1. WAM C66678, WAM C67772, 7.4mm RC, all from west side of North Muiron Island, WA, 21°37′40″ S 114°22′25″ E, 17 m, NCB Exmouth & Muirons 2016 Expedition, stn. 7/EM16, 3 Jun 2016, coll. A. Hara, Host Z97092 *Trachytedania* MM1. WAM C67123, South Beach, Fremantle, WA, washed up on beach, 32°04′ S 115°45′ E, 22 May 2016, coll. J. Raymond, Host: *Trachytedania* L1. WAM C70035, W of Adele Island, Lynher Bank, 63.2–64.3 m, 15°32′41.520″ S 122°12′25.680″ E to 15°32′38.760″ S 122°12′27.240″ E WAMSI Survey 4 Lynher Bank, stn. SOL23/WA112, 30 Oct 2016, coll. J. Fromont & J.A. Ritchie, host: WAM Z90726 *Tedania* sp.1. QM W27677, near Viscount Shoals, Hay Pt, Queensland, 21°25′54.9″ S 149°31′02.9″ E, 27 May 1997, host unknown.

Diagnosis: Shell globose, basis shallow to deeply cupped, small membranous slits between parietal junctions. Externally, parietes with variously pronounced longitudinal ribs lined with small, sharp points; internally with prominent longitudinal ribs interlocking with crenate rim of basis. Scutum transversely elongate, with longitudinal ridges crossing growth ridges. Tergum growth ridges crossed with strong longitudinal ridges giving a latticed appearance. Cirrus IV protopod with 14–15 curved teeth, anterior ramus basal segments with 1–4 recurved teeth on anterior margins. Cirrus V with or without 1–3 teeth on medial segments of anterior ramus.

Description: *Shell* (Figure 21A–H) globose, ranging from white to orange or pink; orifice small relative to shell diameter, rim toothed. Parietes externally with variously pronounced longitudinal ribs studded with small, sharp points; parietes strongly curved over opercular plates, creating narrow orifice. Radii and alae not reaching basal rim, leaving small membranous slits between parietes; summits oblique, broad with horizontal striations. Rostrum widest shell plate. Internally, sheath with conspicuous horizontal growth lines, vesicular structure where sheath adjoins parietes; lower margin separated from internal parietal wall, below sheath longitudinal ribs prominent.

Basis (Figure 21H) circular, shallow to deeply cupped, making up to half total shell height; concentric growth lines conspicuous; basal rim strongly crenate, interlocking with internal ribs on parietes.

Scutum (Figure 21I,J) triangular, transversely elongate, height 0.6 times width, growth lines marked by longitudinal ridges, ridges increasing in number basally; basitergal angle angular, tergal section narrow; occludent margin strongly toothed. Internally smooth, apex with yellow chitinous cuticle, adductor and lateral depressor muscle pits present; articular ridge short, occupying 0.3 length of tergal margin, prominently protruding beyond tergal margin with deep articular furrow, extending entire length of tergal margin.

Tergum (Figure 21K,L) apex blunt, growth lines prominent, crossed by strong longitudinal ridges giving a lattice-like or cancellated appearance, fringed with short, inconspicuous setae; articular margin concave in apical half. Carinal margin straight, only curved near apex; basal margin straight; spur length 0.3 times width, occupying approximately 0.4 of basal margin, positioned less than half own width from scutal margin; spur furrow defined by abrupt change in growth lines, margins infolded, furrow open in basal half; distal margin concave with disto-articular angle projecting. Internally smooth, crests for depressor muscles faint. Articular furrow broad, articular ridge low, rounded occupying 0.25 scutal margin.

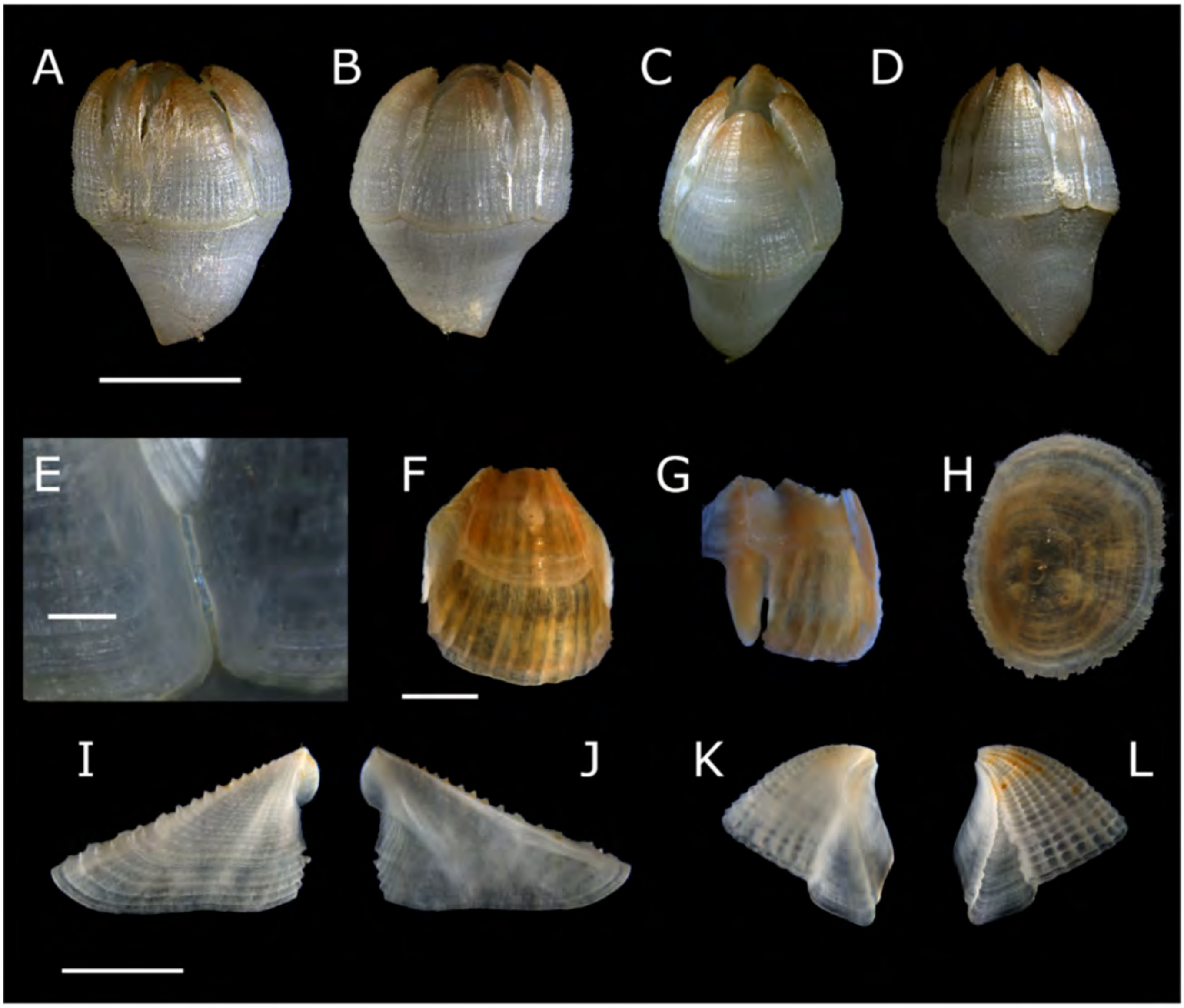

Figure 21. *Pectinoacasta pectinipes* (Pilsbry, 1916) shell and shell plates (A–E, I–L: WAM C67772; F–H: WAM C58870), (**A**–**D**) left, right, rostral and carinal views, respectively, of whole shell; (**E**) membranous slit between junction of rostrum and right lateral; (**F**) internal view of rostrum, (**G**) internal view of right lateral and carinolateral; (**H**) internal view of basis; (**I**,**J**) external and internal views of scutum; (**K**,**L**) internal and external views of tergum. Scale bars: A–D = 5 mm; E = 0.5 mm; F–H = 1 mm; I–L = 2 mm.

Labrum (Figure 22A,B) bilobed, divided by deep, medial, v-shaped notch, each rounded lobe with 2 marginal teeth and numerous fine setae.

Mandibular palp (Figure 22A,C) rhomboid, distal end obliquely truncate, anterior margin concave, posterior margin straight; setae heavily serrulate, becoming longer and more dense distally; distal angle with long, simple setae.

Mandible (Figure 22D–F) cutting margin straight with 4 distinct teeth, second to fourth tooth bifid, fifth tooth congruent with molariform or spinose inferior angle; superior and inferior margins with row of long, fine simple setae, dense short setae covering inner and outer faces.

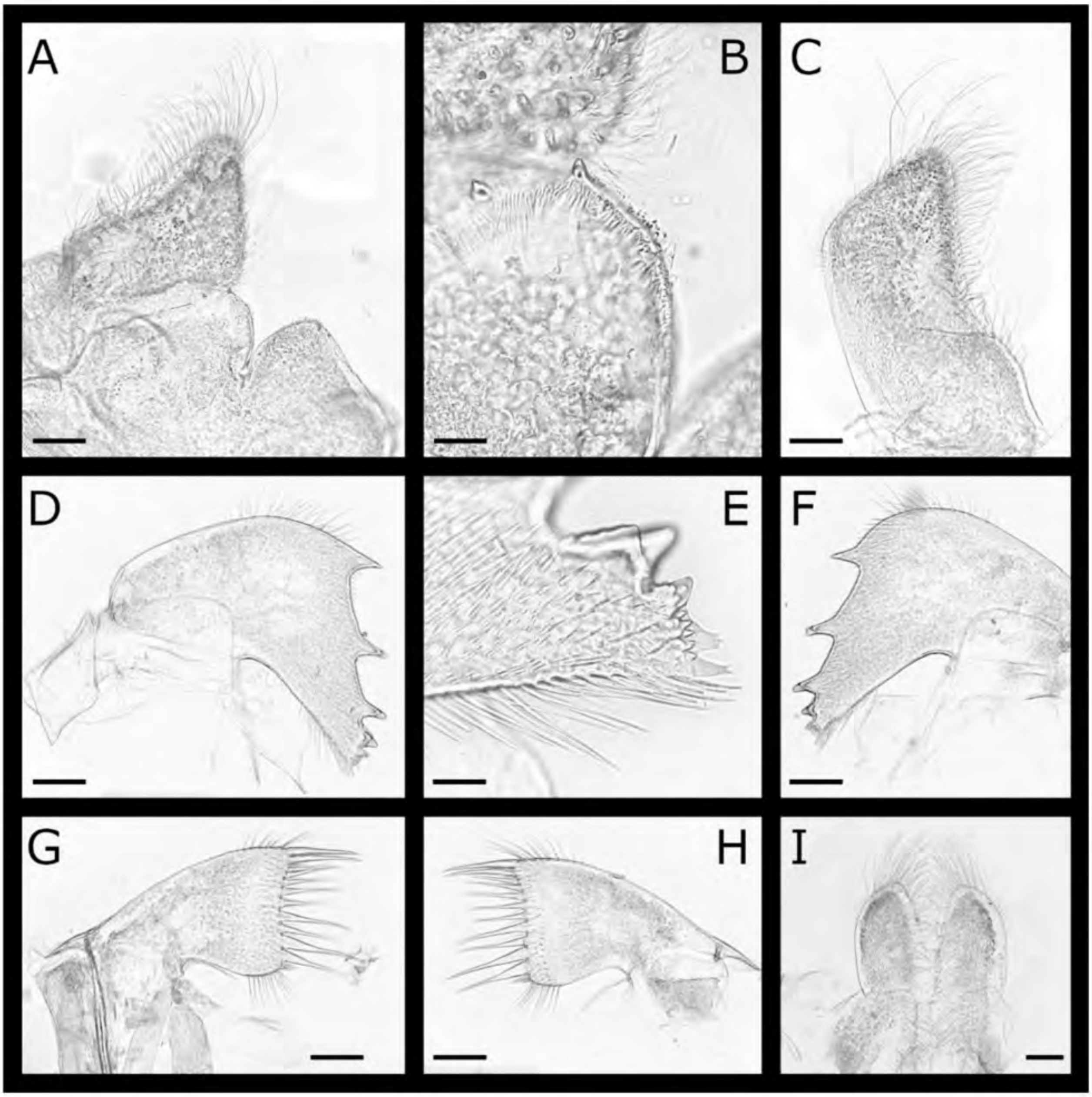

Figure 22. *Pectinoacasta pectinipes* (Pilsbry, 1916) mouthparts (WAM C58871) (**A**) labrum and right mandible palp; (**B**) crest of labrum; (**C**) left mandible palp; (**D**) right mandible; (**E**) close up of inferior angle of right mandible; (**F**) left mandible; (**G**,**H**) right and left maxillules; (**I**) right and left maxillae. Scale bars: A, C,D, F–I = 100 µm; B, E = 50 µm.

Maxillule (Figure 22G,H) cutting margin with 11 cuspidate setae, upper and lower pair larger, more robust than remaining setae. Dense, short setae regularly spaced on inner and outer faces, longer fine setae on inferior and superior margin.

Maxilla (Figure 22I) bilobed, lobes ovate, serrulate setae arranged on anterior margins, becoming more dense at apex, longer on distal lobe than those on basal lobe.

Cirral segment counts are given in Table 2.

Cirrus I (Figure 23A,B) protopod with pappose setae basally on protopod posterior margin. Rami unequal, anterior ramus 2.5 times length of posterior ramus, setation lasiopod, segments with densely arranged serrulate and simple setae on mesial face.

Cirrus II (Figure 23C,D) protopod anterior margin lined with long plumose setae, posterior margin with pappose setae basally, plumose setae distally. Rami unequal, anterior ramus 1.25 times longer that posterior ramus, setation lasiopod, segments with densely arranged serrulate and simple setae on mesial face.

Cirrus III (Figure 23E,F) protopod anterior margin lined with long plumose setae, posterior margin with pappose setae basally, plumose setae distally. Rami subequal, setation lasiopod, segments with serrulate and simple setae on mesial face, less densely arranged than on cirrus I and II. Anterior ramus with row of ctenoid scales on anterodistal portion of all segments, except terminal segment, most prominent on medial segments.

Cirrus IV (Figure 24A–E) posterior margin of protopod basal segment margin lined with plumose setae, tuft of simple, short setae at posterodistal angle; basis elongate, length 2.09–2.15 times width, with tuft of simple, short setae at posterodistal angle; anterior margin lined with 14–15 closely-spaced, hooked teeth. Rami subequal, setation ctenopod. Anterior ramus with 1-4 hooked teeth on first 8 segments, distal segments with up to 3 erect spines on anterior margins; long serrulate setae arranged in row at anterodistal angle. Posterior ramus lacking hooked teeth or erect spines on anterior margins; 3–6 pairs of long, serrulate setae arranged in row at anterodistal angle.

Cirrus V (Figure 24F–H) protopod with sparse setae on anterior margins, tufts of short, simple setae at posterodistal angles; basis elongate, length 1.7–1.75 times width, without hooked teeth. Rami subequal, setation ctenopod; anterior ramus with 1-3 teeth on segments 4–13, basal 3 segments without teeth; 2–3 pairs of serrulate setae on distal portion of anterior margins of each segment; posterior ramus setation as in anterior ramus, segments without hooked teeth or erect spines.

Cirrus VI (Figure 24I,J) protopod with sparse setae on anterior margins, tufts of short, simple setae at posterodistal angles; basis elongate, length 1.78–1.97 width, without hooked teeth. Rami equal, setation ctenopod, 2–3 pairs of long, serrulate setae on distal portion of anterior margins of each segment.

Penis long, annulated, with sparse, short setae; basidorsal point low, rounded.

Distribution: Australia, from Perth north to the Kimberley region, south to New South Wales and Victoria. South Africa, Andaman Islands, Java Sea, Sulu Archipelago, Malay Archipelago, South China Sea, Hong Kong, China, Philippines, Japan. Depth: 0–170 m.

Hosts: *Trachytedania* L1, *Trachytedania* L2, *Trachytedania* MM1, and *Tedania* sp.1 (all Tedaniidae). Previous records: *Halichondria* (*Halichondria*) *okadai* (Kadota, 1922) [80], *H.* (*H.*) *japonica* (Kadota, 1922) [7,69,80]; *Tedania* sp. [81]; and Halichondriidae [5].

Remarks: This distinctive species has been reported across the Indo-Pacific, but host identifications have been rare. Morphological variation has been reported in the armature of cirri IV and V with regards to the number of teeth present on the protopodite and anterior ramus, as well as the degree of the sculpturing on the shell plates, including the scutum [7,69]. Given the vast geographic range reported for this species, this raises the potential for more than one species to be present. These records provide the first *COI* sequences for this species. Coupling these with the description and host identifications will greatly aid further workers in identifying this species and distinguishing any potential cryptic species.

The remaining species currently assigned to the genus *Pectinoacasta* can be readily separated from *P. pectinipes.* Firstly, *P. cancellorum* and *P. sculpturata* may be considered fenestrate, but in addition to the small membranous windows between parietes are longitudinal slits within parietal sections of the wall. These two species also have a yellow chitinous cuticle on the external surface of the tergum, and their respective tergal spurs are also distinctly more elongate. *Pectinoacasta angusticalcar* (Broch, 1931) [6] does not have fenestra between the parietes, the tergal spur is elongate, and the furrow is completely closed along its length. Lastly, in *P. zevinae* (Kolbasov, 1991) [61], the orifice is large, the parietes do not curve over the opercular plates, exposing the opercular plates from above, the tergum lacks a distinct spur or spur furrow, and the armature of the posterior cirri is reduced to small erect spines, lacking the hooked teeth of *P. pectinipes*.

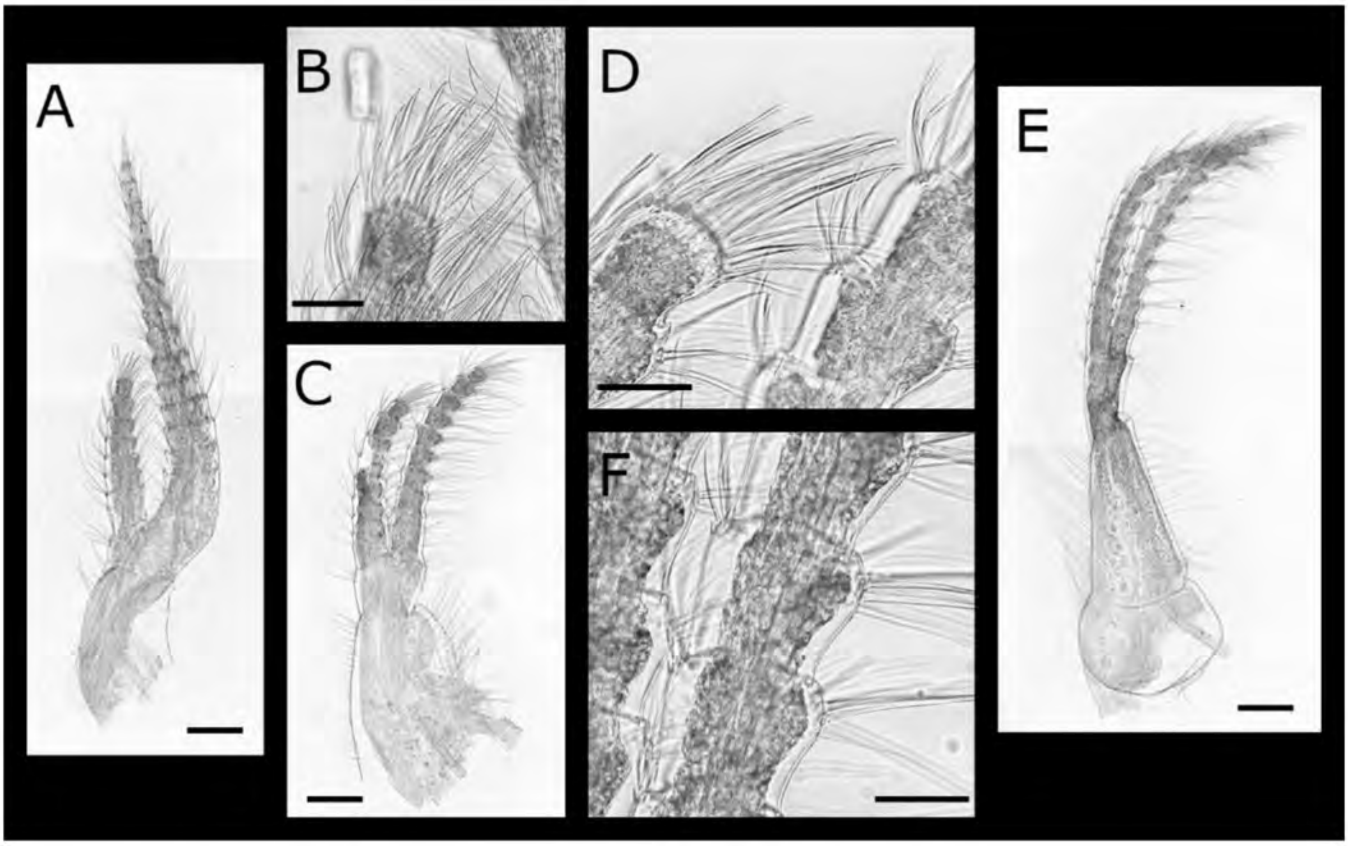

Figure 23. *Pectinoacasta pectinipes* (Pilsbry, 1916) cirri I–III (WAM C58871). (**A**) Left cirrus I; (**B**) terminal segment of cirrus I anterior ramus; (**C**) left cirrus II; (**D**) terminal segment of left cirrus II posterior ramus; (**E**) left cirrus III; (**F**) medial segments of cirrus III anterior ramus. Scale bars: A, C, E = 200 µm; B, D, F = 50 µm.

Pectinoacasta sculpturata (Broch, 1931) [6] (Figures 25–28)

Acasta sculpturata Broch, 1931: p. 101, Figure 35 [6]. Rosell 1991: p. 50 [82].

Acasta sculptura: Newman and Ross 1976: p. 54 [44].

Pectinoacasta sculpturata: Kolbasov 1993: p 411 [5]. Jones and Hosie 2016: p. 277 [50].

Pectinoacasta sculptura: Jones et al. 2000: p. 273 [78]. Yu et al. 2020: Tab. S1 [17].

Material examined: *Holotype*: ZMUC CRU9003, 8 mm RC, Indonesia, Java Sea 5°47′ S 106°7′ E, 49 m, Danish Expedition to the Kei Islands, stn. 107, 5 Aug 1922, Host: *Agelas* sp.

Paratypes: ZMUC CRU9003, 3.5 mm RC, more specimens still with host, same data as holotype.

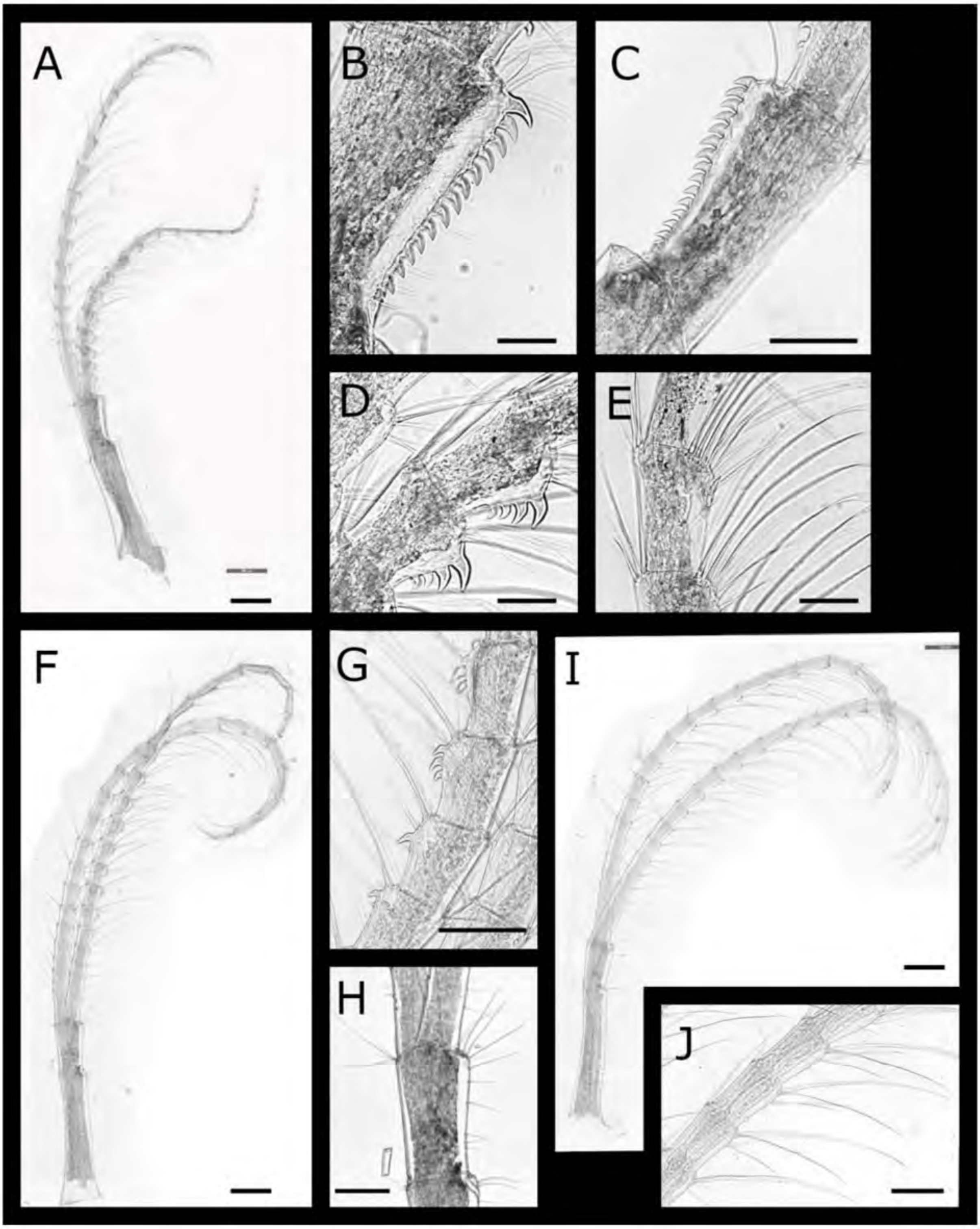

Figure 24. *Pectinoacasta pectinipes* (Pilsbry, 1916) cirri IV–VI (WAM C58871). (**A**) left cirrus IV; (**B**,**C**) left and right cirrus IV protopod basis; (**D**) hooked teeth on medial segments of left cirrus IV anterior ramus; (**E**) setation on distal segments of left cirrus IV anterior ramus; (**F**) left cirrus V; (**G**) hooked teeth on medial segments of right cirrus V anterior ramus; (**H**) protopod of left cirrus V; (**I**) left cirrus VI; (**J**) medial segments of left cirrus VI. Scale bars: A, F, I = 200 µm; B, D, E = 50 µm; C, G,H, J = 100 µm.

Other material: WAM C58282, WAM C61394, WAM C61395, 3 slides, WAM C61396, all from Pansy Island, Montebello Islands, WA, 20°21′19″ S 115°33′02″ E, 26 m, NCB Montebello and Muiron Islands Expedition, stn. 3/MM15, 15 Apr 2015, coll. A.M. Hosie & A. Hara, host: WAM *Amphinomia sulphurea*. WAM C74480, Y Island, Exmouth Gulf, WA, 9–12.8 m, 21°57′19″ S 114°24′29″ E, Bush Blitz Cape Range Expedition, stn. CR19/07, 19 Jun 2019, coll. A.M. Hosie & A. Hara, host: WAM Z88930 *Amphinomia sulphurea*. WAM C75199, Ningaloo Reef, Ningaloo Marine Park, 22°40′52.61″ S 113°36′05.76″ E, CReefs Ningaloo Expedition, stn. NR09-025, 18 May 2009, coll. J. Fromont, host: WAM Z45362 *Amphinomia sulphurea*. QM W29555, southern Great Barrier Reef, QLD, 21°46′38.3″ S 151°50′12.9″ E, 57.6 m, CSIRO SBD Project, 26 Nov 2005, coll. S.D. Cook, host: *Agelas nemoechinata*.

Diagnosis: Shell globose, parietes permeated with narrow, longitudinal incisions extending from basal rim and small windows at parietal junctions; externally surfaces studded with short, blunt, calcareous projections; internally longitudinal ribs extending below sheath and interlock with crenate basal rim. Scutum with longitudinal ridges crossing growth ridges. Tergum with setose, yellow, chitinous cuticle, growth ridges crossed with longitudinal ridges, giving a latticed appearance. Cirrus IV protopod lacking curved teeth, anterior margin with longitudinal row of small spinules, anterior ramus basal segments with 1–2 recurved teeth on anterior margins.

Description: *Shell* (Figure 25A–L) globose, white or grey; orifice small relative to shell diameter, rim toothed. Parietes with longitudinal incisions extending from basal rim to over half parietal height, creating narrow, membranous slits, incisions secondarily calcified in upper portions of parietes; external surfaces with short, blunt calcareous projections arranged irregularly, or in longitudinal rows where confined by incisions; yellow, chitinous cuticle on basal sections; parietes strongly curved toward orifice. Radii and alae not reaching basal rim, leaving small membranous slits between parietes; broad with striations perpendicular to oblique summits. Rostrum widest shell plate. Internally, sheath with conspicuous horizontal growth lines; lower margin adpressed to inner lamina, extending to just above apical extent of parietal incisions; longitudinal ribs below sheath formed either side of incisions.

Basis circular, shallow to deeply cupped; concentric growth lines conspicuous; basal rim irregularly crenate, interlocking with internal ribs of parietes.

Scutum (Figure 25M,N) triangular, approximately as high as wide, growth lines marked by longitudinal ridges, ridges increasing in number basally; basitergal angle rounded, tergal section narrow; occludent margin strongly toothed. Internally smooth, apex with yellow chitinous cuticle, adductor and lateral depressor muscle pits present; articular ridge short, occupying 0.5 length of tergal margin, prominently protruding beyond tergal margin with deep articular furrow extending entire length of tergal margin.

Tergum (Figure 25O,P) apex blunt, external surface covered by yellow, setose, chitinous cuticle; growth lines prominent, crossed by strong longitudinal ridges, giving a latticed or cancellated appearance, fringed with short, inconspicuous setae; articular margin concave in apical half. Carinal margin straight, only curved near apex; basal margin straight; spur length 2 times width, occupying approximately 0.3 basal margin, positioned less than half own width from scutal margin; spur furrow defined by abrupt change in growth lines, margins infolded, furrow open in basal half; distal margin rounded. Internally roughened, chitinous cuticle extending beyond carinal margin of calcareous part, crests for depressor muscles distinct. Articular furrow narrow, articular ridge low, rounded occupying 0.25 scutal margin.

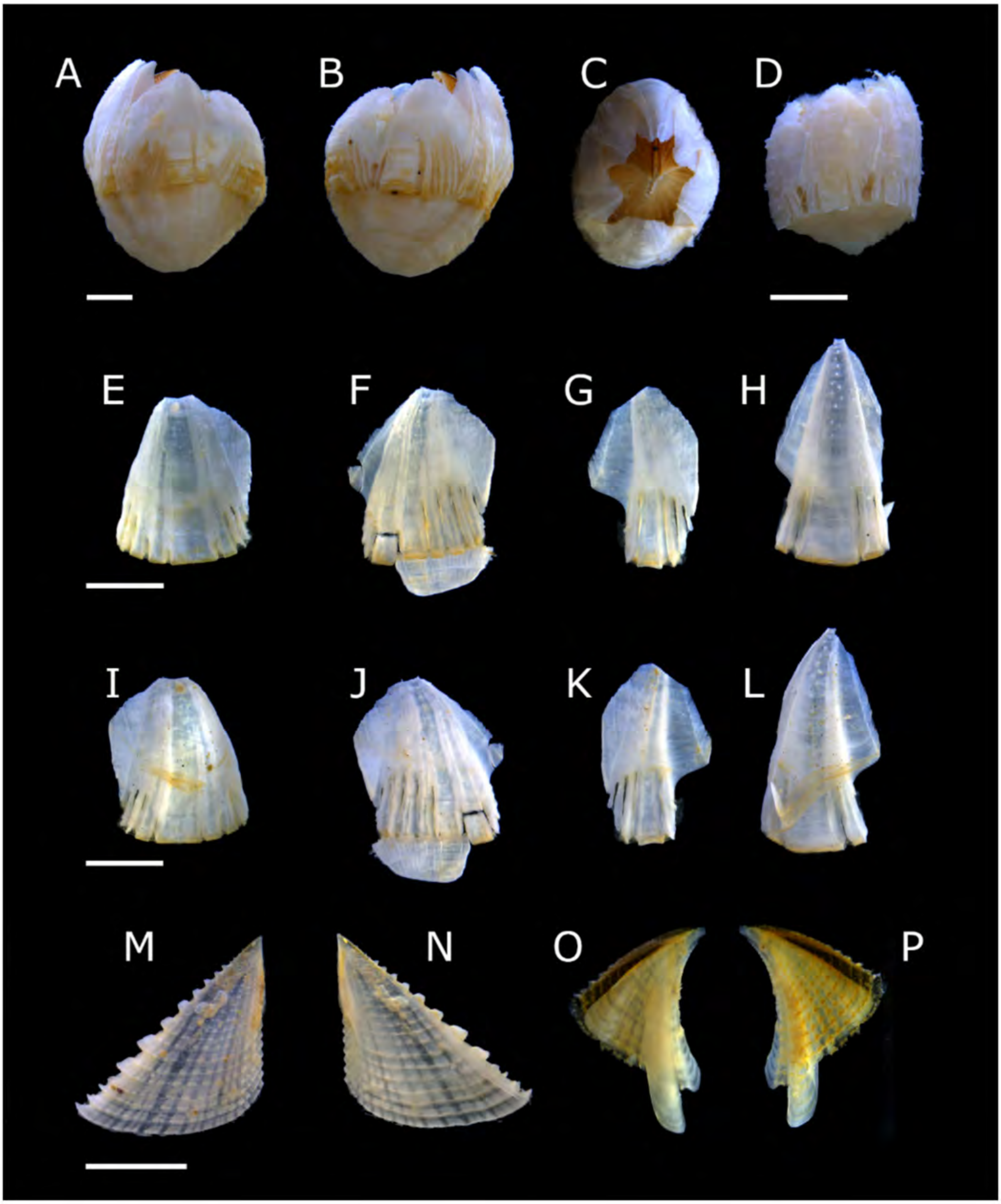

Figure 25. *Pectinoacasta sculpturata* (Broch, 1931) shell and shell plates (A–C, holotype ZMUC CRU9003; D, ZMUC CRU9003; E–L, ZMUC CRU9003; M–P, WAM C61395). (**A**–**D**) left, right and top views, respectively, of whole specimens; (**E**–**H**) external views of disarticulated rostrum, right latus, right carinolatus and carina; (**I**–**L**) internal views of same; (**M**,**N**) external and internal views of right scutum; (**O**,**P**) internal and external views of right tergum. Scale Bars: A–P = 2 mm.

Labrum (Figure 26A) bilobed, divided by deep, medial, v-shaped notch, each rounded lobe with 2 prominent, marginal teeth and numerous fine setae.

Mandibular palp (Figure 26B) rhomboid, distal end obliquely truncate, anterior margin concave, posterior margin straight; setae heavily serrulate, becoming longer and more dense distally; distal angle with long, simple setae.

Mandible (Figure 26C,D) with five teeth, second to fourth teeth bifid, fifth tooth confluent with molariform inferior angle; inferior angle with denticles. Regularly spaced, dense, short setae on inner and outer faces, longer fine setae on inferior and superior margin.

Maxillule (Figure 26E–G) cutting margin straight, with 10 cuspidate setae, upper and lower pairs longer than remaining setae; three medial, shorter setae serrulate on inferior margin; tuft of short setae at basal angle. Dense, short setae regularly spaced on inner and outer faces, longer fine setae on inferior and superior margin.

Maxilla (Figure 26H) bilobed, lobes ovate, serrulate setae arranged on anterior margins, becoming more dense at apex, longer on distal lobe than those on basal lobe.

Cirral segment counts are given in Table 2.

Cirrus I (Figure 27A) protopod with pappose setae on basal segment posterior margin, basis with tuft of setae at posterodistal angle. Rami unequal, anterior ramus 3.5 times length of posterior ramus, setation lasiopod, segments with densely arranged serrulate and simple setae on mesial face, tuft of simple setae on posterodistal angle.

Cirrus II (Figure 27B) protopod lined with long serrulate setae on anterior margin, with pappose or plumose setae on posterior margin on basal segment; basis with long serrulate setae on anterior margin. Rami unequal, anterior ramus 1.25 times longer that posterior ramus, setation lasiopod, segments with densely arranged serrulate and simple setae on mesial face.

Cirrus III (Figure 27C–E) protopod lined with long, serrulate setae on anterior margin, pappose or plumose setae on posterior margin of basal segment. Rami subequal, anterior ramus 1.1 times length of posterior ramus, setation lasiopod, segments with serrulate and simple setae on mesial face, less densely arranged than on cirrus I and II. Anterior ramus with transverse row of distally directed spines at anterodistal angle on all but distal-most segments, spines most prominent on medial segments; posterodistal angle with transverse row of ctenoid scales. Posterior ramus with similar spination but much reduced in size.

Cirrus IV (Figure 28A–F) protopod basal segment anterior and posterior margins with well-spaced row of short, simple setae; tuft of simple, short setae at posterodistal angle; dense row of short, sharp spinules on anterior margin; basis elongate, length 1.80–1.91 times width, with tuft of simple, long setae at posterodistal angle; anterior margin lined with short, simple and short, sharp spinules. Rami subequal in length, setation ctenopod. Anterior ramus with 1-2 hooked teeth on anterior margins of first 10 segments, anterodistal angles with transverse row of erect spines on all but distal-most segments; 3 pairs of serrulate setae on medial segments. Posterior ramus with similar setation to anterior ramus, with erect spines on anterodistal angles, but lacking hooked teeth.

Cirrus V (Figure 28G) and *VI* (Figure 28H,J) similar, protopod with well-spaced, long setae and dense row of short spinules on anterior margins; posterior margin lacking setae; basis elongate, cirrus V length 1.76–1.82 width, cirrus VI length 1.71–1.75 width, hooked teeth absent, row of long simple setae on anterior margin, tuft of setae at posterodistal angle. Rami subequal, setation ctenopod; 3 pairs of serrulate setae on distal portion of anterior margins of each segment; rami without teeth or erect spines.

Penis longer than cirrus VI, annulated sparsely setose. basidorsal point (Figure 28I) prominent, triangular, as wide as high.

Distribution: Australia: Ningaloo to Montebello Islands, WA; southern Great Barrier Reef, QLD. Java Sea Philippines, Taiwan. 12–97 m.

Hosts: *Agelas sp.* (type host), *A. nemoechinata* Hoshino, 1985 [83], and *Amphinomia sulphurea* Hooper, 1991 [84] (all Agelasidae). Previous records: “Alcyonarian” [6]; *Agelas nemoechinata* Hoshino, 1985 [17].

Remarks: Re-examination of the type series of this species was key in determining the identity of the Australian material, as the original description failed to mention the chitinous cuticle, a rather prominent feature of the species. The type series of this species includes mounted slide material, disarticulated shell plates, extracted whole specimens, and specimens still embedded in the host. Unfortunately, it is not possible to connect the slides to the dissected shell plates. It is also not clear which, if any, of these specimens is the one reportedly extracted from an alcyonacean. The specimen designated as "type" in Broch's figure 35a is clearly still extant and whole. It is this specimen we treat as being the holotype.

Distinguishing *P. sculpturata* from *P. cancellorum* and *P. pectinipes* has been summarised under the treatment of these latter species. The remaining species of *Pectinoacasta*, *P. angusticalcar* and *P. zevinae,* both lack the incisions in the parietes seen in *P. sculpturata*. Further to this, *P. zevinae* lacks a distinct tergal spur or teeth on the protopod or rami of cirrus IV. While in *P. angusticalcar,* the spur furrow is fully closed, the scutum is distinctly wider than high, and the protopod of cirrus IV has a row of teeth. Given Broch's omission of the chitinous cuticle in, it is not clear if it was similarly omitted from his description of *P. angusticalcar* in the same paper [6].

Examination of the type-host reveals it to be a species of *Agelas*, albeit distinct from the species inhabited by the Australian specimens, as well as the *Agelas* inhabited by *P. cancellorum*. The addition of *A. sulphurea* as a host broadens the generic range but affirms this species' affinity for sponges of the Agelasidae.

3.2. Molecular Results

The top-ranked partitions produced by the ASAP analyses suggested between 26 or 28 putative species. The three substitution models provided similar results and the first two highest-ranked partitions received close scores. Under the JC69 model and p-distance partitions of 26 species and 28 species were received an ASAP score of 2.0 and 2.50, respectively, at a distance threshold of 7% or 4%. The difference between these partitions was the lumping or splitting of *A. huangi* and *A.* sp.2, and *A. sandwichi* and *A. caveata* sp. nov. The K2P model ranked partitioning the dataset into 26 or 27 species with scores of 1.0 and 3.0, respectively, at a distance threshold of 2.9% or 3.5%. The difference between these two partitions is the lumping or splitting of *A. sandwichi* and *A. caveata* sp. nov.

The intraspecific and the interspecific K2P genetic distances ranged from 0–0.019 and 0.060−0.261, respectively across the dataset (Figure 29, Table S1). The intraspecific K2P distances of the three new species were: *A. caveata* sp. nov. 0.006, *E. acutaflava* sp. nov. 0.005, *E. excoriatrix* sp. nov. 0.002. The greatest intraspecific distance was within *P. pectinipes* (0.19), while *Acasta sandwichi* and *A. caveata* sp. nov. exhibited the closest interspecific genetic similarity (0.060).

IQTree selected the general time-reversible model with a proportion of invariant sites and gamma-distributed rate heterogeneity (GTR+I+G) as this was ranked highest under the Bayesian information criterion [85] and this was utilised in the BI analysis as well. The phylogenetic tree of sponge barnacles, with ML and BI support values, exhibited very similar topologies and statistical support (Figure 29). All new species concepts presented herein formed reciprocally monophyletic clades under all analyses; however, none of the genera were recovered as monophyletic. Although there was little support for the branching patterns observed except at nodes separating closely related species such as the nodes between *P. cancellorum* and *P. sculpturata* and the clade containing *A. undulaterga*, *A. radenta*, *A. huangi*, and *A.* sp. 2 MCY-2020.

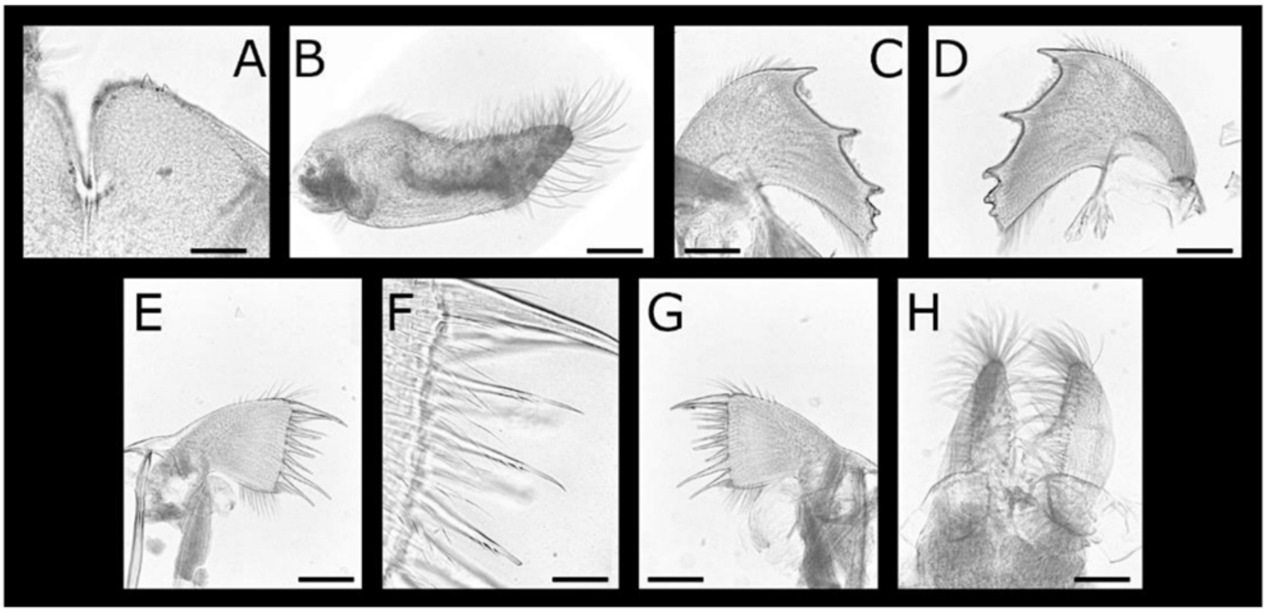

Figure 26. *Pectinoacasta sculpturata* (Broch, 1931) mouthparts (WAM C61395). (**A**) crest of labrum; (**B**) right mandibular palp; (**C**,**D**) left and right mandibles; (**E**) left maxillule; (**F**) serrated setae on left maxillule; (**G**) right maxillule; (**H**) left and right maxillae. Scale bars: A = 100 µm; B–F, H = 200 µm; G = 50 µm.

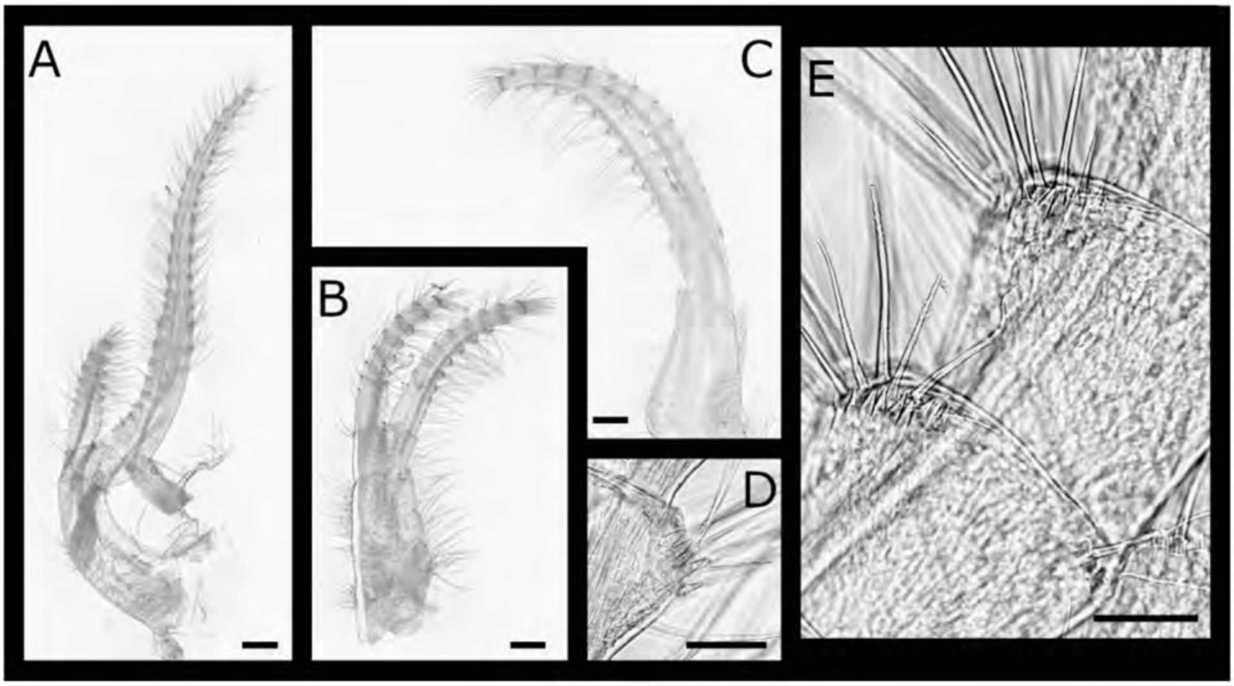

Figure 27. *Pectinoacasta sculpturata* (Broch, 1931) cirri I–III (WAM C61395). (**A**) left cirrus I; (**B**) left cirrus II; (**C**) right cirrus III; (**D**,**E**) detail of spines on medial segments of anterior ramus of left and right cirrus III, respectively. Scale bars: A–C = 200 µm; D–E = 50 µm.

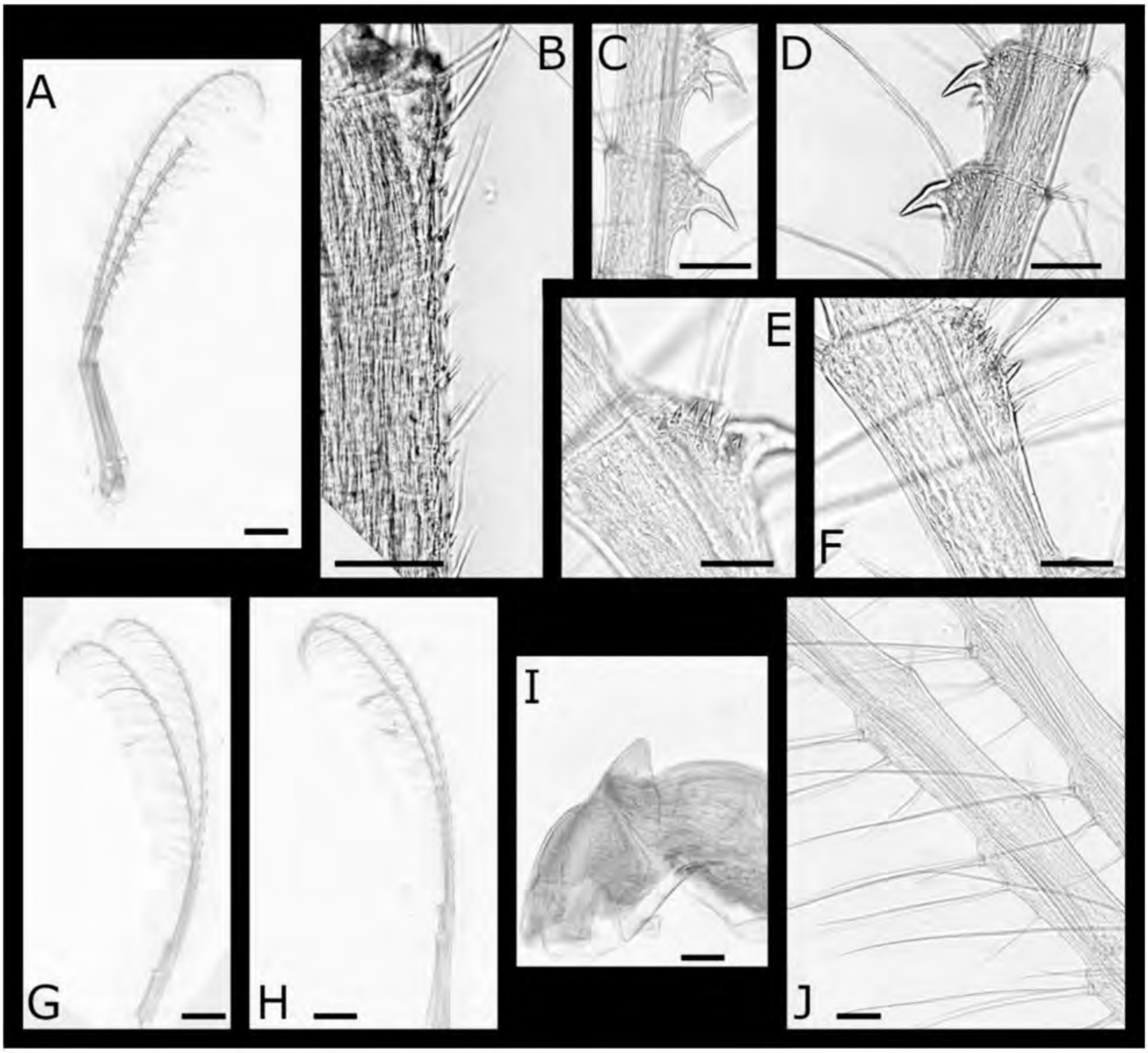

Figure 28. *Pectinoacasta sculpturata* (Broch, 1931) cirri IV–VI (WAM C61395). (**A**) left cirrus IV; (**B**) spinules on the anterior margin of cirrus IV protopod; (**C**–**E**) teeth and erect spines on basal segments of cirrus IV anterior ramus; (**F**) erect spines on medial segment of cirrus IV posterior ramus; (**G**) right cirrus V; (**H**) right cirrus VI; (**I**) basidorsal point of penis; (**J**) setation on medial segments of cirrus VI. Scale bars: A, G–H = 500 µm; B, E–F, J = 50 µm; C–D, I = 100 µm.

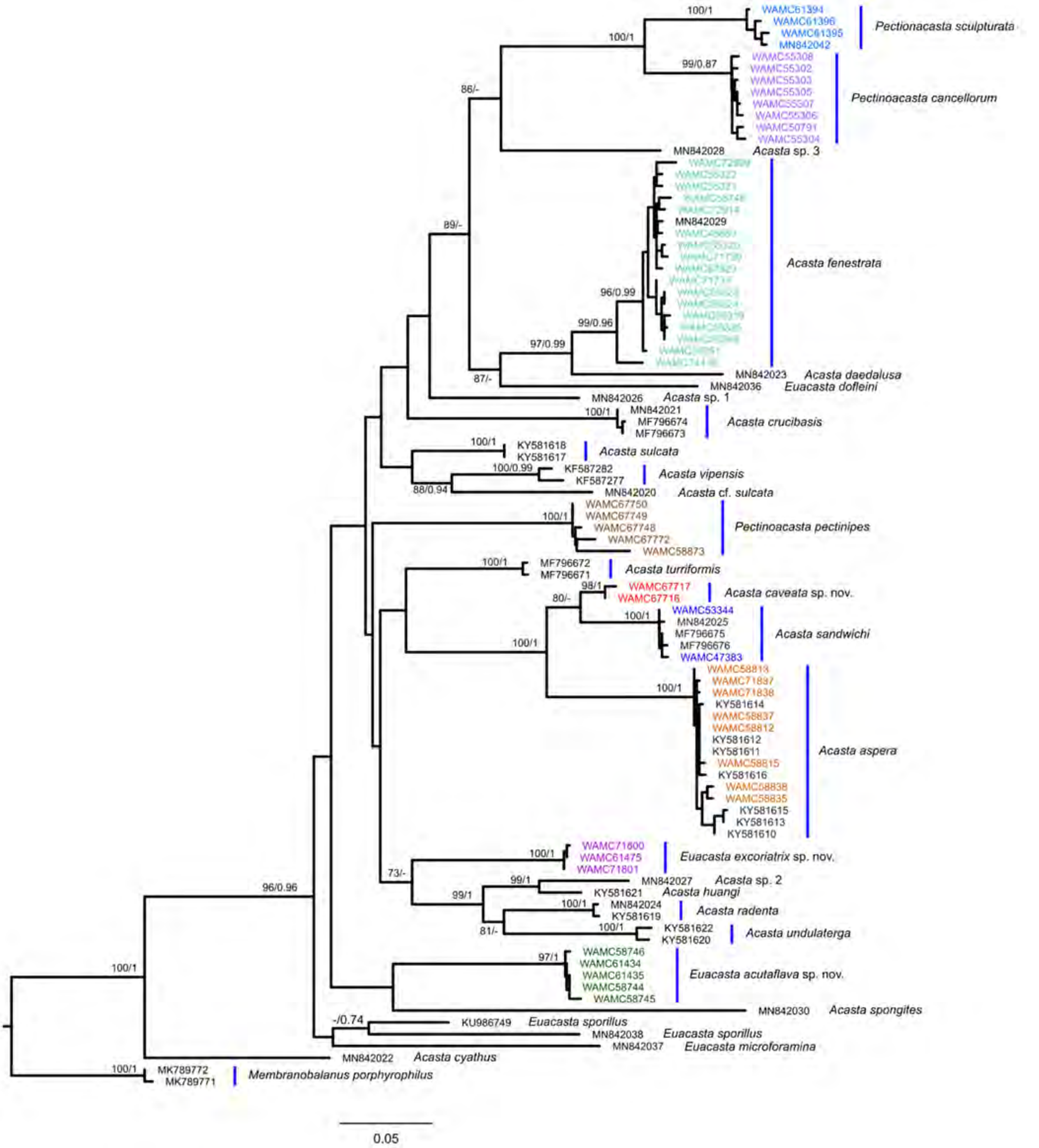

Figure 29. Maximum likelihood (ML) tree based on *COI* dataset. Tips are labelled with institutional accession numbers for newly published sequences (coloured by species) or GenBank accession numbers for previously published data (black). Node labels are supporting bootstrap (bs) and posterior probability (pp) values, respectively, with only values ≥ 70% bs or 0.7 pp shown (- indicates where only one method did not meet these thresholds). Scale bar indicates number of expected substitutions per site.

4. Discussion

The present study documents an additional six species of the Australian Acastinae; however, there are still many more species to be formally described, and the total number of species is likely to be well over 60 [4]. Hosts for most of the previously reported barnacle species are still unknown (e.g. [86,87]), and given how integral this is to understanding barnacle biodiversity and patterns of speciation [1,4,17], it is the other key gap in our knowledge.

Most of the Australian specimens documented in this study were collected from a restricted host range, typically inhabiting a single or few sponge genera. Only *A. aspera* appears to have a broad host range, with hosts from multiple families, but all from the same sponge order (Poecilosclerida). Species such as *P. pectinipes* and *A. fenestrata* have been documented from multiple host orders in other parts of their geographic range. However, once more material of *A. fenestrata* is sequenced and type specimens examined, our expectation is for a more restricted range of hosts.

In the case of *P. sculpturata*, molecular data proved that specimens reported from Taiwan [17] are conspecific with the Australian specimens, while identifying the type-host shows that this species appears to specialise in species within the genera of the Agelasidae: *Agelas* and *Amphinomia* (this latter genus is monotypic). However, the report of *P. sculpturata* inhabiting an alcyonacean coral [6] requires further investigation, as it seems unlikely for a species to specialise in one family of sponges but also embed in hosts from a different phylum. *Pectinoacasta cancellorum* was recovered as sister to *P. sculpturata* and is not only morphologically similar, but also inhabits species of *Agelas*, albeit different species. Both the genetic results and host used show these two species to be rather distantly related to *P. pectinipes*, suggesting that the morphological similarities are superficial.

The proposed new species, *A. caveata* sp. nov., *E. acutaflava* sp. nov., and *E. excoriatrix* sp. nov., were each identified from single host genera, but it is too soon to tell if they are host specialists, as they have so far been identified from only a few host individuals. The factors involved in determining the range of hosts used by individual barnacle species are unknown and would be a valuable avenue of study.

It was already known that *A. aspera* was distributed in Australia and Taiwan with no discernible genetic differentiation [3]. In an additional three species, specimens from Taiwanese waters were nested within clades of Western Australian specimens: *A. sandwichi*, *A. fenestrata* and *P. sculpturata*. Interestingly, the single sequence of *A. fenestrata* from Queensland was sister to the clade formed by the WA and Taiwanese specimens. This result suggests that there is potentially greater connectivity between WA and Taiwan than with the east coast of Australia, for this species at least, but further specimens and sequences will be needed to test this hypothesis.

The types of armature found on the fourth cirrus have long been seen as critical characters upon which to base taxonomic decisions at the species level or above [5,6]. The key morphological distinction between *A. sandwichi* and *A. caveata* sp. nov. is that the former bears a single, straight, and sharp "denticle" on each segment [2] compared to the multiple, robust, and hooked teeth of the latter. The close, but distinct, genetic relationship of these apparent sister species indicates that the evolution, or loss, of these character states may occur independently in different lineages. The ASAP analysis did not provide unequivocal support for separating these species. However, this analysis is looking for a partitioning threshold that can give predictive power to molecular identification as a starting point for assessing biological or adaptive significance [25]. The interspecific genetic distance between these two species (0.60) is still much higher than the greatest intraspecific distance (0.19) observed in this dataset and supports the hypothesis that the specimens represent separate species. Therefore, while there is more work needed on the intraspecific variation of the fourth cirrus in the Acastinae, it is considered a reliable character for delimiting species and a key support for erecting this new species and is believed to be a functional adaptation to the host [5,16]. Further evidence that supports this decision includes the separate host families (Niphatidae and Petrosiidae) suggesting ecological separation and that the Australian specimens identified as *A. sandwichi* are indistinguishable morphologically and genetically from those from Taiwan but are easily separated from those of *A. caveata* sp. nov.

Supplementary Materials: The following are available online at https://www.mdpi.com/article/10.3390/d13070290/s1, Table S1: genetic distances.

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Chapter 4. Host specificity

Synopsis

This chapter comprises a published paper that investigates the evolutionary history of host specificity in sponge-inhabiting barnacles. Chapter 2 demonstrated that the sponge-inhabiting barnacles are diverse and generally have restricted host ranges, often restricted to only a few closely related species. During that chapter the host order Dictyoceratida was proving to host a particularly diverse group of barnacles, which were forming groups of well supported clades within a larger, but poorly supported clade (Chapter 2: Figure 2.2). This order was specifically surveyed to maximise host representation to gain insight to maximal host usage by barnacles and to elucidate underlying evolutionary patterns.

Initial identification of barnacle species involved morphological and molecular data from cytochrome oxidase I (*COI*) and the 12S ribosomal small subunit (*12S*). The addition of *12S* was beneficial as the shorter fragment had greater amplification success than that of *COI* leading to the identification of 10 additional species. In total, 42 species of barnacle were identified (5 unique to *COI* and 10 unique to *12S* data) inhabiting 64 morphospecies of host sponge from across five families. Almost three quarters (74%) of barnacles were found in a single host morphospecies.

Phylogenies were reconstructed using maximum likelihood and Bayesian inference analyses. Two additional nuclear loci, histone 3 (*H3*) and the 28S ribosomal large subunit (*28S*), were sequenced to help provide better statistical support to the phylogenetic analyses. These two loci are more conserved than the mitochondrial loci and have been used to provide resolution to deeper nodes within phylogenies. Ancestral state reconstructions on these datasets explored the evolutionary history of host usage within this group of barnacles.

The results revealed six well-supported clades of species, considered to represent species complexes, with the remaining taxa dispersed between them in the phylogenetic trees. The clades had differing patterns of host usage, with three clades being restricted at family-level of host sponges. The ASR predicted that these restricted clades diversified once the most recent common ancestor (MRCA) colonised a member of the host family. Interestingly, the host for the MRCA for the group was predicted to be species of Thorectidae, but the main radiation occurred once members of the Irciniidae were colonised.

This paper did not show an over-arching pattern of host usage but did demonstrate that host usage is phylogenetically conserved in many groups of closely related species. The less host-restricted clades still were comprised of species with restricted host ranges, but evidently have been more able to colonise less-related hosts over evolutionary time.

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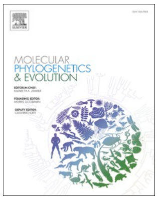

Surveying keratose sponges (Porifera, demospongiae, Dictyoceratida) reveals hidden diversity of host specialist barnacles (Crustacea, Cirripedia, Balanidae)

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Co-speciation

ABSTRACT

Sponges represent one of the most species-rich hosts for commensal barnacles yet host utilisation and diversity have not been thoroughly examined. This study investigated the diversity and phylogenetic relationships of sponge-inhabiting barnacles within a single, targeted host group, primarily from Western Australian waters. Specimens of the sponge order Dictyoceratida were surveyed and a total of 64 host morphospecies, representing four families, were identified as barnacle hosts during the study. Utilising molecular (*COI*, *12S*) and morphological methods 42 molecular operational taxonomic units (MOTUs) of barnacles, representing *Acasta*, *Archiacasta*, *Euacasta* and *Neoacasta* were identified. Comparing inter- and intra-MOTU genetic distances showed a barcode gap between 2.5% and 5% for *COI*, but between 1% and 1.5% in the *12S* dataset, thus demonstrating *COI* as a more reliable barcoding region. These sponge-inhabiting barnacles were demonstrated to show high levels of host specificity with the majority being found in a single sponge species (74%), a single genus (83%) or a single host family (93%). Phylogenetic relationships among the barnacles were reconstructed using mitochondrial (*12S*, *COI*) and nuclear (*H3*, *28S*) markers. None of the barnacle genera were recovered as monophyletic. *Euacasta* was paraphyletic in relation to the remaining Acastinae genera, which were polyphyletic. Six well-supported clades of molecular operational taxonomic units, herein considered to represent species complexes, were recovered, but relationships between them were not well supported. These complexes showed differing patterns of host usage, though most were phylogenetically conserved with sister lineages typically occupying related hosts within the same genus or family of sponge. The results show that host specialists are predominant, and the dynamics of host usage have played a significant role in the evolutionary history of the Acastinae.

1. Introduction

Ecological diversification is recognised as a significant evolutionary driver, particularly within the context of geographical sympatry, where changes in habitat, prey or behaviour lead to assortative mating and disruptive selection that subsequently lead to speciation (Rice 1987; Schluter 2001; Via 2001). For symbiotic organisms, this diversification may come in the form of a host shift or niche expansion that subsequently isolates or subdivides populations (Mestre et al. 2020). This phenomenon is well documented in terrestrial ecosystems, particularly those of phytophagous insects (see Coyne and Orr 2004), and marine examples are rapidly increasing in number, especially with the advent of molecular phylogenetics e.g. (Duffy 1996; Faucci et al. 2007; Goto et al. 2012; Hurt et al. 2013; Layton et al. 2019; Litsios et al. 2012; Munday et al. 2004; Schiaparelli et al. 2015). These studies demonstrate the effect symbiosis has on driving speciation in marine organisms.

Symbiosis has been a successful strategy for a variety of barnacle taxa, where colonisation of host groups has often led to significant speciation events. This can be seen in groups such as the Coronuloidea (Hayashi et al. 2013), which are almost exclusively found in symbiosis with marine vertebrates, the Oxynaspididae (Van Syoc and Dekelboum 2011) and Pyrgomatidae (Anderson 1992; Malay and Michonneau 2014; Simon-Blecher et al. 2007; Tsang et al. 2009; Tsang et al. 2014), symbionts of various Cnidaria, and the Rhizocephala (Glenner and Hebsgaard 2006; Høeg et al. 2019), which are highly specialised parasites of other Crustacea. Phylogenetic research on these barnacle groups shows

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significant host-driven lineages indicating the importance of host utilisation in the evolution of these taxa. The barnacles inhabiting scleractinians and hydrocorals have received much attention recently and a number of new taxa and cryptic lineages have restricted host ranges that are phylogenetically constrained (Brickner et al. 2010; Chan et al. 2013; Mokady et al. 1999; Tsang et al. 2014; Zweifler et al. 2020). The identification of the hosts is thus highly important but is often a significant barrier to understanding these interactions, which is particularly true of sponge-inhabiting barnacles.

Sponges arguably represent the most successfully-exploited host group for commensal barnacles. There are almost 100 barnacle species known to be commensal with sponges and potentially another 100 or more yet to be described (Van Syoc et al. 2015; Hosie unpub.; see results herein). The vast majority of these are classified within the family Balanidae (see Chan et al 2021 for recent changes to classification). Largely owing to the difficulty of sponge taxonomy for non-specialists, the diversity of host species utilised by barnacles in this family is poorly understood. However, where host data is more complete, the evidence indicates that restricted host usage or specialisation is a common phenomenon in sponge-inhabiting barnacles. For example, the genus *Membranobalanus* (Archaeobalaninae) and the members of Bryozobiinae are known to show high levels of host specificity, being largely restricted to a limited number of species within the sponge orders Clionaida and Poecilosclerida, respectively (Hosie et al. 2019; Van Syoc 1988; Van Syoc and Newman 2010). Historically, little attention has been given to the hosts of the much more diverse subfamily Acastinae, although recent progress has been made, and the importance of identifying the hosts is being recognised (e.g. Ilan et al. 1999; Kolbasov 1993; Van Syoc et al. 2015; Yu et al. 2020; Yu et al. 2017).

The present study investigates the biodiversity of barnacles inhabiting the sponge order Dictyoceratida using mitochondrial and nuclear DNA markers. Dictyoceratida is a diverse, predominantly shallow water group, abundant in Australian waters. Species of this order do not possess a mineralised skeleton, but instead skeletal elements are made of collagen-like proteins called spongin (de Cook and Bergquist 2002). The key aims of this study were to enumerate the diversity of barnacles inhabiting the Dictyoceratida, identify the hosts, assess host specificity, and investigate evolutionary relationships.

2. Methods

2.1. Sampling

Barnacles and sponge hosts were collected from various locations in Western Australia and preserved in 100% ethanol (see Supplementary File 1 for locality data). The sponge collections of the Western Australian Museum (WAM) were surveyed for species hosting barnacles, with additional specimens sourced from the Queensland Museum (QM) and the South Australian Museum, Adelaide (SAMA). Barnacles were manually extracted using scalpel and forceps. The free-living *Striatobalanus amaryllis* (Darwin, 1854), was selected to serve as an outgroup and although the relationships between the subfamilies of the Balanidae are ambiguous (Chan et al. 2021; Perez-Losada et al. 2014) our data has consistently shown this species to be phylogenetically close to, but outside of the Acastinae (Hosie et al. unpub.)

2.2. Morphological analysis

For direct morphological examination of barnacle shell plates and arthropodal characters, the body and associated soft tissues were removed from the shell. The remnants of the barnacle tissue and host sponge on the surfaces of the parietes, scutum and tergum were removed using forceps. The shell was then immersed in 2% bleach for less than 2 hrs hours to completely digest the organic tissue and subsequently rinsed in water. Any remaining debris or contaminants were then removed by cleaning in an ultrasonic cleaner for less than 5 s. The specimens were examined under a Leica M205 C (Leica, Germany) stereomicroscope and digital photographs produced with a Leica DMC4500. All images were processed using GIMP 2.10 (www.gimp.org) or Inkscape (www.inkscape.org).

Sponge identifications were partly facilitated by examining gross morphology, surface characteristics and microscopic skeletal characteristics of specimens. Subsamples of sponge tissue were sectioned at right angles to the surface of the sponge and processed for microscopic examination using a Shandon Elliott tissue processor. This included ethanol dehydration, histolene to clear the tissue and subsequent paraffin impregnation. Thick sections (~90 μm) were cut with a Leitz slide microtome from wax blocks. Sections were de-waxed in histolene and mounted using Shandon EZ-Mountant. Skeletal slides were examined with an Olympus BX50. Further to the morphological identifications, specimens were sequenced within a concurrent project investigating a subfamily of the Dictyoceratida, but the scope of species examined was only a subset of this study (see Abdul Wahab et al. 2020).

2.3. Molecular analysis

Specimens in hosts collected pre-2000 were not included as sequencing success was too low. Adductor or depressor muscle tissues of barnacles were subsampled from specimens, and genomic DNA was extracted using either a Bioline Isolate II or Qiagen DNeasy extraction kit following the manufacturer's instructions. Partial fragments of the cytochrome *c* oxidase I (*COI*), 12S ribosomal subunit (*12S*), Histone 3 (*H3*) and 28S ribosomal subunit genes (*28S*) were amplified (see Table 1 for primers) in a 25 μL reaction volume and consisting of 2 μL DNA extract, 1 unit MyTaq DNA polymerase, 1x MyTaq PCR buffer and 0.5 μL (0.1 μM) of each primer. The following Polymerase Chain Reaction conditions were used: 2 min at 95 °C for initial denaturing, then 35 cycles of 30 s at 95 °C, 30 s at 46 °C or 50 °C (see Table 1), 45 s at 72 °C, and a final extension for 7 min at 72 °C. The resulting amplicons were sequenced at the Australian Genome Research Facility, Perth, using the same primers via Sanger (cycle) sequencing.

The sequences were assembled and trimmed using Geneious Prime and submitted to GenBank (Supplementary File 1, https://www.ncbi.nlm.nih.gov/genbank/). Quality control of sequences involved inspecting for stop codons in protein coding genes, checking matches on BLAST and re-examination of original specimens.

Molecular operational taxonomic units (MOTUs) were inferred using both maximum likelihood and Bayesian Poisson Tree Processes (PTP and bPTP; Zhang et al. 2013) and Assemble Species by Automatic Partitioning (ASAP; Puillandre et al. 2020). Parameters for PTP and bPTP were set to 500,000 MCMC generations, a thinning value of 100, 10% burn-in and with the remaining settings on default. Completed analyses were checked for convergence by examining the trace files. ASAP analyses were run using all three distance methods available (Jukes-Cantor, Kimura 2-parameter and simple *p*-distances), under default parameters, to compare results. The data for *COI* and *12S* were analysed separately to compare the results and to maximise coverage of individuals and potential MOTUs. To avoid potential issues in using the different sequence lengths generated by the different *12S* primers used in this study, the *12S* alignment was trimmed to 353 bp, representing the shortest read, and then implemented in the delimitation analyses.

To examine relationships between MOTUs, concatenated sequences were aligned from all specimens where at least two of the four genes were successfully sequenced. The concatenated alignment was analysed using maximum likelihood (ML) and Bayesian inference (BI) methods. Data for both analyses were partitioned by gene, with the *COI* sequences also partitioned by codon position. The ML analysis and model selection was implemented with the IQ-TREE webserver (Trifinopoulos et al. 2016). Tree support was calculated by conducting 1000 ultra-fast bootstraps (Minh et al., 2013).

The BI analysis was conducted in MrBayes 3.2.6 (Ronquist et al. 2012) utilising the CIPRES webserver (Miller et al. 2015) with 4 heated

Table 1
The primers used in this study.

Primer	Direction	Sequence (5′–3′)	Annealing temperature (°C)	Reference
12S			50	
F1	Forward	GAAACCAGGATTAGATACCC		Mokady et al., 1994
FB	Forward	GTGCCAGCAGCTGCGGTTA		Tsang et al. 2009
R1	Reverse	TTTCCCGCGAGCGACGGGCG		Mokady et al., 1994
R2	Reverse	CCTACTTTGTTACGACTTATCTC		Tsang et al. 2009
COI			46	
dgLCO1490	Forward	GGTCAACAAATCATAAAGAYATYGG		Meyer, 2003
COL6b	Forward	ACAAATCATAAAGATATYGG		Schubart & Huber 2006
dgHCO2198	Reverse	TAAACTTCAGGGTGACCAAARAAYCA		Meyer, 2003
H3			50	
AF	Forward	ATGGCTCGTACCAAGCAGACVGC		Colgan et al. 1998
AR	Reverse	ATATCCTTRGGCATRATRGTGAC		Colgan et al. 1998
28S			50	
LSU5	Forward	ACCCGCTGAAYTTAAGCA		Littlewood 1994
LSU3	Reverse	TCCTGAGGGAAACTTCGG		Littlewood 1994

chains, a reversible-jump (Nst = mixed) MCMC of 11 million generations, and a burn-in of 10% (Ronquist and Huelsenbeck 2003). Full details of BI data block are provided in Supplementary File 2.

Ancestral state reconstruction (ASR) analyses to infer ancestral host families were conducted in RASP (Yu et al. 2015) using the Bayesian binary MCMC (BBM) method, under default parameters, utilising the final ML and BI trees. Character states were unordered and equally weighted.

3. Results

Over 240 barnacles were subsampled and either *12S* s or *COI* was successfully sequenced from 186 of them (supplementary File 1). These barnacles were extracted from 99 individual sponge hosts, representing 64 morphospecies (in 19 genera) across four families. Over 300 morphospecies were surveyed during this project, predominantly from tropical and temperate Australian waters. Barnacles from only two hosts outside of this range were included *Ircinia variabilis* and *Phyllospongia foliascens* from the Mediterranean and Red Seas, respectively.

3.1. *Barnacle diversity*

Results for the species delimitation analyses are summarised in Table 2 and presented graphically in Figs. 1 and 2. For the *COI* dataset, ASAP proposed the same 31 MOTUs across all distance metrics. The bPTP and PTP analyses gave highly congruent results, but split off an additional three and two MOTUs, respectively. The *12S* dataset gave less consistent results. Using the Kimura 2-parameter model ASAP proposed 40 and 36 MOTUs with equal rank, while the other two distance metrics proposed 37 MOTUs. The bPTP analysis proposed 94 (see Supplementary File 1). The PTP results proposed 35 MOTUs many of which were congruent with the ASAP analyses, but where there was incongruence it was a mixture of lumping (e.g. D14, D17, D19, D21 into one MOTU) or splitting (e.g. D22 into six MOTUS).

Ultimately, the results from the ASAP analysis were adopted to divide the barnacles in individual biological units for the purposes of this study, as it provided the most consistent MOTUs after comparing all the results across both datasets. The bPTP delimitation is rejected outright as it proposed almost triple the MOTUs of other methods. Specimens of five *COI* MOTUs were not represented by corresponding *12S* sequences and specimens of ten *12S* MOTUs were similarly not represented by corresponding *COI* sequences. Where overlap occurred the results from the two genes were completely congruent utilising the ASAP analysis. This is not the case with bPTP and PTP (e.g. D14, Figs. 1 and 2). Thus, a total of 42 MOTUs are herein identified as inhabiting the sponge order Dictyoceratida (Table 2). The range of inter- and intra-MOTU K2P distances shown in Fig. 3. Comparing minimum inter-MOTU and maximum intra-MOTU distances show a barcode gap of ~ 2.5% (between 2.5% and 5%) for *COI*, while the *12S* dataset this gap was ~ 0.5% (between 1% and 1.5%).

Generally, clear morphological distinctions could be made between the MOTUs using standard shell and arthropodal characters e.g sculpture and shape of the shell plates, armature of the cirri but cryptic lineages are present where closely-related sister lineages may represent population structure (e.g. Fig. 1: D1, D2 and D31; Fig. 2: D12 and D41; D11 and D42). The MOTUs were morphologically assigned to four genera: *Acasta* (8 MOTUs), *Archiacasta* (6 MOTUs), *Euacasta* (3 MOTUs) and *Neoacasta* (25 MOTUs), following the diagnoses given by Kolbasov (1993). Figs. 4–7 show representative images that demonstrate the range of morphology present within the barnacles studied and further comparisons are discussed in sections 4.1.1 to 4.1.7.

3.2. *Phylogenetic relationships*

The final concatenated dataset of four genes consisted of 2508 base pairs from 36 barnacle MOTUs (Table 2, Supplementary File 1). Congruence between the ML and BI analyses was demonstrated in several areas, notably that a set of key clades with high support, with identical member MOTUS were recovered (Figs. 8 and 9). Four of these key clades could be morphologically identified with a known described species: *Neoacasta laevigata* (Gray, 1825), *Neoacasta coriobasis* (Broch, 1947), *Acasta flexuosa* (Nilsson-Cantell, 1931) and *Acasta spongites* (Poli, 1791) and will be referred to as species complexes hereafter. The identities for the two remaining clades were more ambiguous or heterogenous and will be referred to as Clade A and B. The *A. spongites* complex and the members of *Euacasta* (D26, D15 and D6) were recovered in the same positions in both analyses. However, the relationships among the other clades were poorly resolved with low support values and the topology differed between the two trees. Firstly, 11 MOTUs did not form part of the six key clades but were dispersed between them and their relative positions differed between the analyses (e.g. D30 and D34). Secondly, the *A. flexuosa* complex was sister to the remaining, predominantly *Neoacasta*, MOTUs in the BI analysis (Fig. 9), but this position was occupied by Clade B in the ML analysis (Fig. 8). For the purposes of this study these clades will be the focus of the discussion in section 4.1.

3.3. *Host utilisation*

Barnacles inhabiting multiple host morphospecies was very rare with 31 (74%) MOTUs found within only a single host morphospecies, 35 (83%) MOTUs within a single host genus and 39 (93%) MOTUs restricted to a single host family. The barnacles with the largest number of host morphospecies were *Neoacasta* D14 (6), *Neoacasta* D13 (5) and *Neoacasta* D22 (5), but were restricted to a single host family. Only three instances of host-sharing by multiple barnacle MOTUs were

Table 2
Details of barnacle host diversity identified during this study, sorted by barnacle MOTU.

MOTU Designation	Host family	Host species
Neoacasta D1	Thorectidae (Phyllospongiinae)	*Phyllospongia foliascens* (Pallas, 1766) *Phyllospongia papyracea* (Esper, 1806) *Phyllospongia* cf *papyracea* (Esper, 1806)
Neoacasta D2	Thorectidae (Phyllospongiinae)	*Phyllospongia foliascens* (Pallas, 1766)
Neoacasta D3	Thorectidae (Phyllospongiinae)	*Polyfibrospongia flabellifera* Bowerbank, 1877 *Polyfibrospongia* KMB6 *Polyfibrospongia kulit* Abdul Wahab & Fromont, 2020, in Abdul Wahab et al, 2020
Acasta D4	Dysideidae	*Dysidea* sp.3 *Dysidea MM2*
Acasta D5	Thorectidae Dysideidae	*Luffariella* SS11? *Dysidea* cf *granulosa* Bergquist, 1965
Euacasta D6	Dysideidae	*Dysidea* cf *granulosa* Bergquist, 1965
Neoacasta D7	Irciniidae	*Ircinia* KMB2
Acasta D8	Dysideidae	*Dysidea* sp.4 *Dysidea* MM1
Archiacasta hainanensis (Ren, 1984) D9	Thorectidae (Thorectinae)	*Hyrtios erectus* (Keller, 1889) *Hyrtios* KMB1 *Hyrtios* SS2
Acasta D10	Dysideidae	*Lamellodysidea* KB1
Neoacasta D11	Spongiidae	*Spongia* (*Heterofibria*) SS1 *Spongia* CERF 1
Neoacasta D12	Spongiidae	*Hyattella* SS2
Neoacasta D13	Thorectidae (Phyllospongiinae) Thorectidae (Thorectinae)	*Strepsichordaia lendenfeldi* Bergquist, Ayling & Wilkinson, 1988 *Cacospongia* P1 *Luffariella* SS10 *Luffariella* cf SS10 *Luffariella* SS11
Neoacasta D14	Thorectidae (Thorectinae)	*Cacospongia* NG1 *Cacospongia* PB2 ?*Cacospongia* DA1 *Fascaplysinopsis reticulata* (Hentschel, 1912) *Hyrtios* SS4 *Luffariella* PB1
Euacasta D15	Thorectidae (Thorectinae)	*Hyrtios* sp.1
Archiacasta D16	Spongiidae Thorectidae (Thorectinae)	*Spongia* (*Heterofibria*) cf NG1 *Dactylospongia elegans* (Thiele, 1899)
Neoacasta D17	Thorectidae (Thorectinae)	*Hyrtios* SS2
Acasta D18	Dysideidae	*Dysidea* P1
Neoacasta D19	Spongiidae	*Spongia* (*Australospongia*) KMB1
Acasta spongites (Poli, 1791) D20	Irciniidae	*Ircinia variabilis* (Schmidt, 1862)
Neoacasta D21	Spongiidae	*Hippospongia* P1
Neoacasta D22	Irciniidae	*Psammocinia* sp.6 *Sarcotragus* PB1 *Sarcotragus* PB2 *Sarcotragus* SS8 *Sarcotragus* DA1
Neoacasta D23	Irciniidae	*Sarcotragus* SS7
Neoacasta D24	Irciniidae	*Sarcotragus* SS14
Neoacasta D25	Irciniidae	*Sarcotragus* SS11
Euacasta D26	Thorectidae (Thorectinae)	*Thorectandra* NG1
Neoacasta D27	Spongiidae	*Spongia* cf PB1
Neoacasta D28	Spongiidae	*Hippospongia* SS1
Neoacasta D29	Irciniidae	*Sarcotragus* KMB5
Acasta D30	Dysideidae	*Candidaspongia flabellata* Bergquist, Sorokin & Karuso, 1999
Neoacasta D31	Thorectidae (Thorectinae)	*Phyllospongia foliascens* (Pallas, 1766)
Neoacasta D32	Thorectidae (Thorectinae)	*Thorectandra* sp.
Neoacasta D33	Irciniidae	*Ircinia* sp.5 *Sarcotragus* JB1
Acasta D34	Spongiidae	*Spongia* (*Australospongia*) cf sp.1
Neoacasta D35	Spongiidae	*Spongia* (*Australospongia*) sp.1
Archiacasta fragilis (Ren, 1984) D36	Irciniidae	*Sarcotragus* cf sp.2
Archiacasta D37	Irciniidae	*Sarcotragus* sp.2
Neoacasta D38	Irciniidae	*Ircinia* KGR1
Archiacasta D39	Irciniidae	*Sarcotragus* NG1
Archiacasta D40	Spongiidae	*Leiosella* sp.1 *Spongia* (*Heterofibria*) RA1
Neoacasta D41	Spongiidae	*Hyattella intestinalis* (Lamarck, 1814)
Neoacasta D42	Spongiidae	*Spongia* (*Heterofibria*) NG1

encountered: *Acasta* D5 and *Euacasta* D6 inhabiting *Dysidea* cf. *granulosa*, *Neoacasta* D1, D2 and D31 in *Phyllospongia foliascens,* and *Archiacasta hainanensis* D9 and *Neoacasta* D17 in *Hyrtios* SS2.

Of the six key clades recovered in the analyses the members of *A. flexuosa, N. coriobasis* and *N. laevigata* complexes were found to inhabit a single family of sponge, the Dysideidae, Irciniidae and Thorectidae, respectively. Members of both Clade A and B inhabited species of the Irciniidae, Spongiidae and Thorectidae. Lastly, the *A. spongites* MOTUs have been recorded from all four host families documented in this study (this includes literature records of *A. spongites*).

3.4. Ancestral State reconstruction (ASR)

The ASR analyses provided similar results across both the ML and BI phylogenetic trees (Figs. 8 and 9). The trees provided generally clear predictions of the likely host family for the most recent common ancestor (MRCA) at most nodes. The MRCAs for the basal-most nodes of both analyses were inferred to have inhabited members of the Thorectidae. In the ML analysis (Fig. 8), most key nodes distal from the *A. spongites* complex showed that the family Irciniidae was the likely host family from which subsequent MOTUs radiated. The single host families of the complexes *A. flexuosa*, *N. coriobasis* and *N. laevigata* were confirmed as the likely host of the MRCA.

There was significant uncertainty at the node for the MRCA between the *A. flexuosa* complex and the remaining MOTUs in the BI analysis (Fig. 9). At this node, the probability of the MRCA inhabiting the Dysideidae was only 48% on the BI tree (the Irciniidae and Thorectidae were the next likely host families at 22% and 17%, respectively). This uncertainty was not present in the ML analysis, which differed by having recovered the clade of D34 and D30 as sister to the *A. flexuosa* complex. The MRCA of these two clades was predicted as 86% likely to be a dysideid.

The probability of an MRCA inhabiting multiple host families exceeded 15% at only two nodes. The probability that the MRCA for Clade A (D39 + D16 + D11 + D12 + D27) inhabited members of both the Irciniidae and Spongiidae was given at ~ 25% (25% ML, 26% BI). This dropped to 18% and 20% for the node D39 + D16. In both cases the MRCA inhabiting just an irciniid was inferred the most probable ranging from 47 to 67% across the analyses.

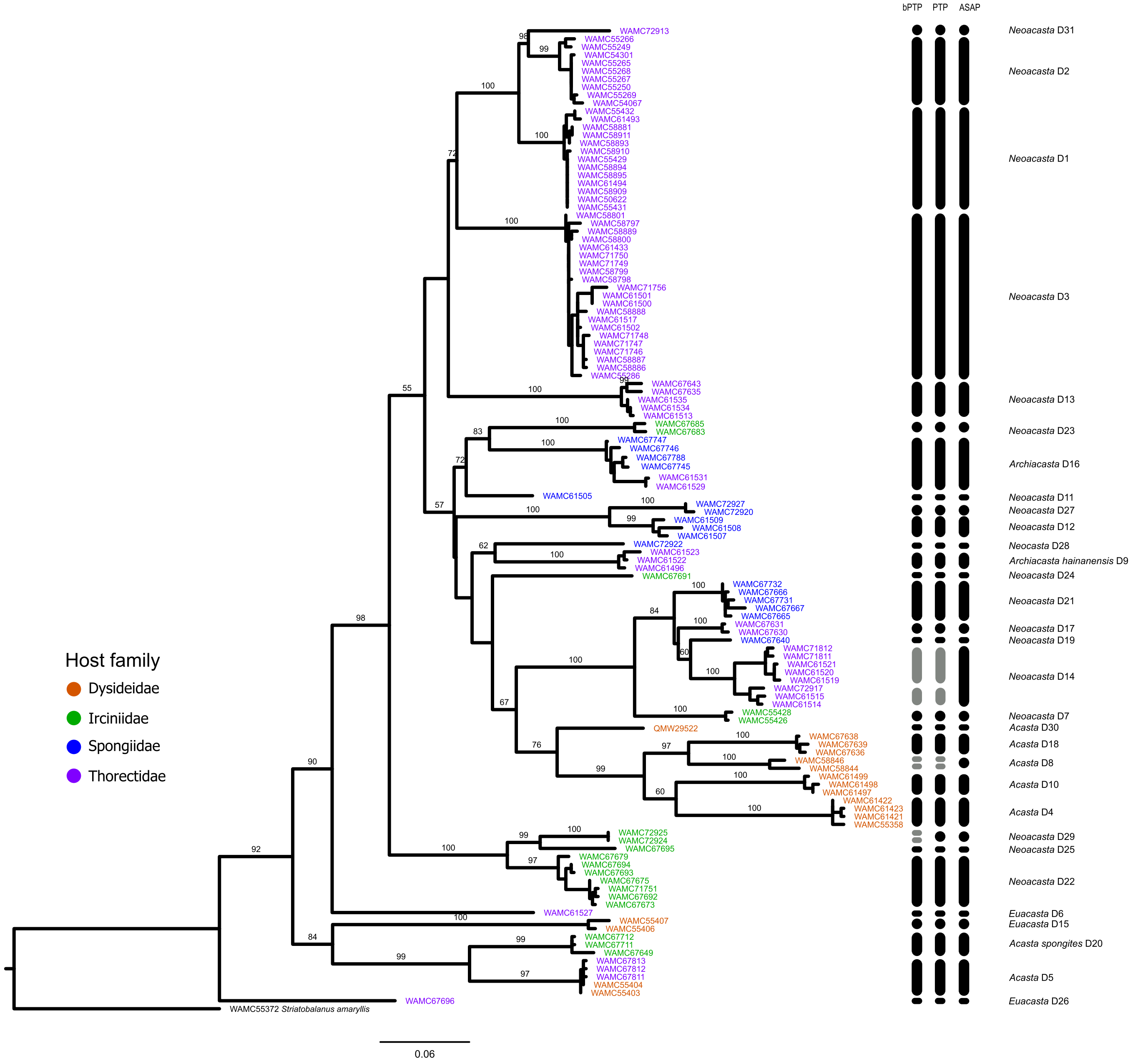

Fig. 1. Maximum likelihood tree showing results of the molecular species delimitation analyses based on the *COI* dataset. Tips are labelled with specimen registration number and coloured by host family. Grey bars highlight incongruence with the accepted ASAP delimitation results. Bootstrap values are only given on nodes with more than 50% support. This figure is available in colour in the electronic version.

4. Discussion

The results of the present study revealed that dictyoceratid sponges are widely utilised by a high diversity of barnacles. The demonstrated high level of host specificity indicates that sponge-inhabiting barnacles are segregated in their environment and emphasizes the need to document host identifications when dealing with this group of sponge-inhabiting barnacles.

4.1. Barnacle diversity

The clades of MOTUs are indicative of species complexes that inhabit closely-related host species, but overlap in host range was rarely encountered. Many of the MOTUs discussed below are difficult to separate morphologically, or confidently assign to known species. This is a problem exacerbated by the paucity of knowledge on host use in the literature (Van Syoc et al. 2015). There is the possibility that the delimitation methods used have over-split the more closely related barnacles due to significant population structure caused by assortative mating within separate hosts or geographic distance in the case of *A. spongites* and *N. laevigata* (see Carstens et al. 2013; Dellicour and Flot 2018; Sukumaran and Knowles 2017; Zhang et al. 2011 for discussions on delimitation limitations). However, the differences in the intra- and inter-MOTU distances showed that *COI* has a potential barcode gap at about the 5% threshold, but in *12S* this is much smaller, meaning that the delimitation methods are less effective as seen by the varying number of species proposed by these methods.

The potential that the 42 MOTUs identified in this study could constitute species supports the Acastinae as being one of the most speciose groups of barnacles (Van Syoc et al. 2015). In Australian waters

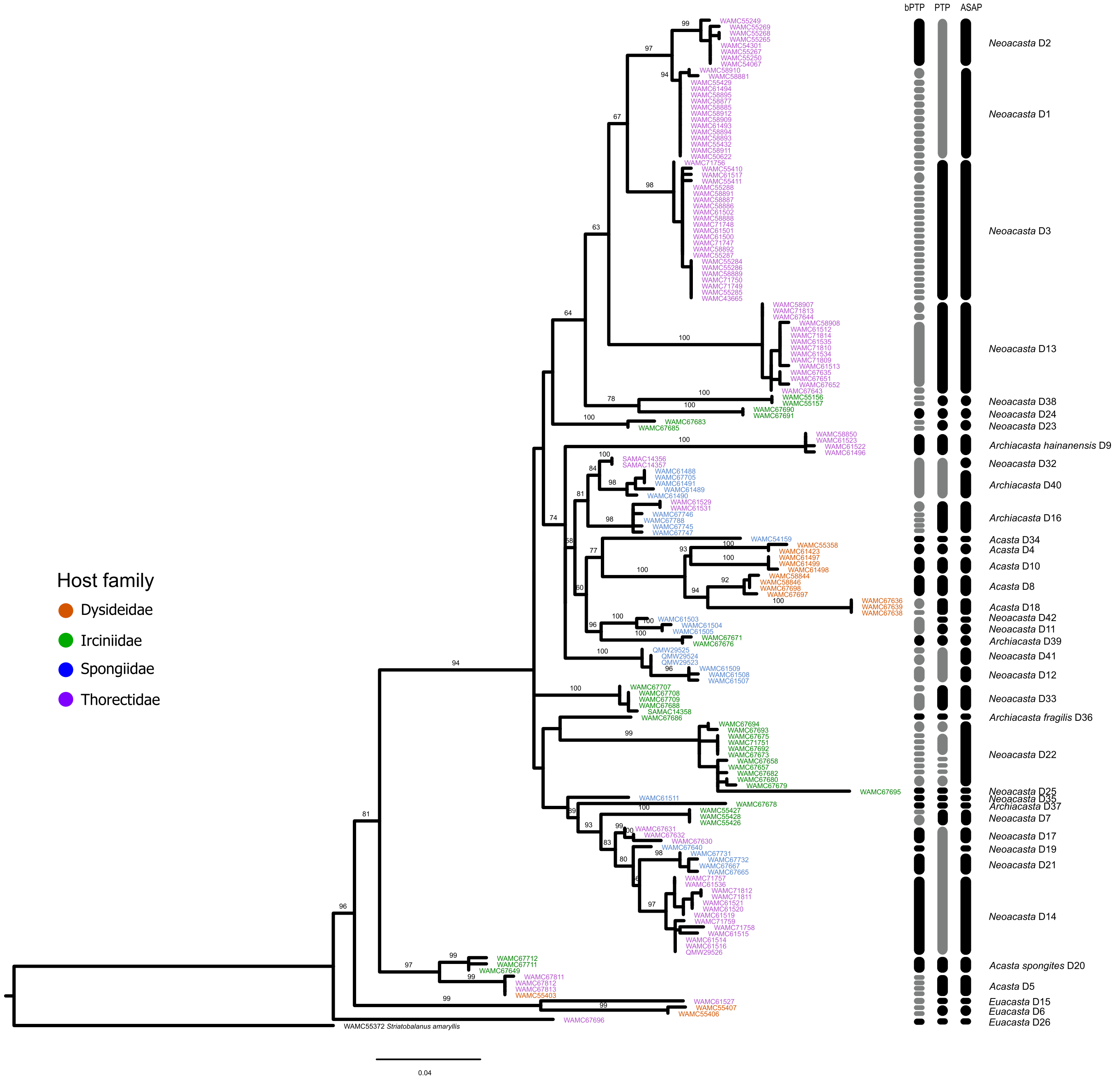

Fig. 2. Maximum likelihood tree showing results of the molecular species delimitation analyses based on the *12S* dataset. Tips are labelled with specimen registration number and coloured by host family. Grey bars highlight incongruence with the accepted ASAP delimitation results. Bootstrap values are only given on nodes with more than 50% support. This figure is available in colour in the electronic version.

there are currently 19 species recorded (Jones 2012; Yu et al. 2016) and these results more than double this total. The genus *Neoacasta* accounts for half of the MOTUs, indicating that this genus is significantly more diverse than the seven presently recognised species. It is possible that the colonisation of dictyoceratid sponges as hosts has enabled a major adaptive radiation for this genus.

Future taxonomic work will require additional lines of evidence to determine if the proposed MOTUs represent species. This would include identifying the hosts of the type specimens of the known barnacle species, where available in museum collections. In addition, it will be useful to collect barnacle specimens, and their hosts, from type localities to connect historical collections to contemporary data, to aid in resolving species boundaries and distributions.

The analyses did not recover any of the barnacle genera as reciprocally monophyletic. The three MOTUs assigned to *Euacasta* form a paraphyletic grade to the remaining taxa. The two clades of *Acasta spongites* and *A. flexuosa* are paraphyletic in relation to the clade of *Neoacasta* + *Archiacasta* and the placement of *Archiacasta* leaves *Neoacasta* polyphyletic under the current taxonomic arrangement. The original diagnoses of these latter three genera did not provide synapomorphies and many of the proposed characters overlap e.g. extent of calcification and depth of basis, meaning these genera were paraphyletic when they were first erected (see Kolbasov 1993, Fig 17; Van Syoc & Winther 1999). However, nomenclatural acts such as changes to the generic arrangement of the Acastinae is beyond the scope of the present paper as the poor backbone support and topological differences do not provide a clear alternative hypothesis. Further molecular and morphological data, particularly of the type species for all five genera within the

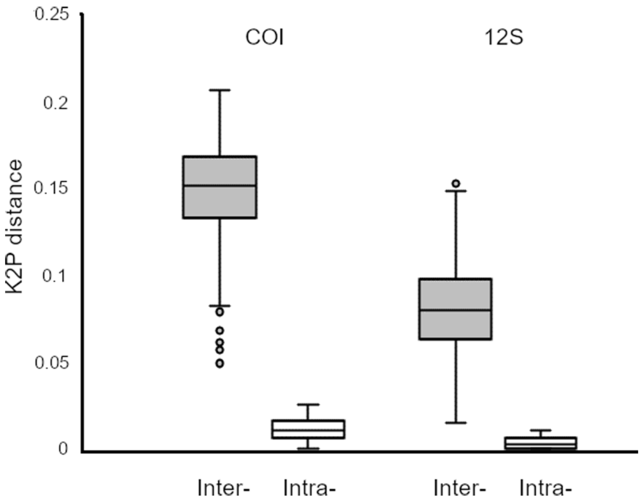

Fig. 3. Box and whisker plot showing the distribution of the K2P distances between and within the final MOTUs for the *COI* and *12S* sequence data. Dots represent outliers that were beyond the quartiles by >1.5x the interquartile range.

Acastinae, would be required for such a review.

4.1.1. *Neoacasta laevigata* species complex

Neoacasta laevigata (Gray, 1825) has been widely reported across the Indo-West Pacific (see Jones and Hosie 2016). Members of this complex have a similar outward appearance, being generally squat with a varying density of short spines projecting from the parietes (Fig. 4A). The specimens of D13 and D3 have distinct morphologies and can be separated from each other and the remaining three MOTUs by shape of the opercular plates (Fig. 6A–C, 7A, B). Variation within D13 show that the depth of the basis is not a reliable taxonomic character as it can be almost flat to making up half of the total shell height (Fig. 4B). D1, D2 & D31 are much more similar in appearance and could all be assigned morphologically to the species *N. laevigata*. The genetic distances within the clade containing D1, D2 and D31 are relatively small compared to the distances between them and D3, and based on the localities and shared host species (*Phyllospongia foliascens*), it may be that this split is indicative of the geographic distance between coastal Western Australia, Ashmore Reef and the Red Sea. A recent molecular study on the host *P. foliascens* has also documented similar breaks between eastern and western Indian Ocean localities (Abdul Wahab et al. 2020)

All five MOTUs in this clade were found inhabiting sponges classified within Thorectidae, four of which were restricted to the subfamily Phyllospongiinae. Sister to these, MOTU D13 inhabits a broader range of species from both Phyllospongiinae and Thorectinae. The first host species identified for *N. laevigata* was *Phyllospongia foliascens* (Ilan et al. 1999) from the Red Sea. However, Kolbasov (1993) had previously reported Spongiidae and Dysideidae as host families but given recent research on dictyoceratids it is likely that these latter family-level identifications need to be re-visited (see section 4.2).

4.1.2. *Neoacasta coriobasis* species complex

Neoacasta coriobasis (Broch, 1947) has been reported from Japan, China and Vietnam (Broch 1947; Ren 1984; Utinomi 1953). The morphology of the basis is characteristic of the MOTUs in this complex. The deep basal cup is composed of a framework of numerous concentric ribs and six radial ridges between which are rectangular areas that are finely porous and have the appearance of sintered glass (Fig. 5H) and described as being leathery in texture (Broch 1947; Utinomi 1953). The function of this structure is unknown, but it provides a significant amount of vertical flexibility to the base. The host sponges are also very soft, so potentially this flexibility reduces damage to the barnacle should the host flex or be compressed due to current or wave action. The articulation of the rostrum and lateral plates (i.e. radii and alae) in this group are very narrow and the apices of these plates are adjoined, whereas the carinolateral and carina stand apart (Fig. 4G, 5A). This feature is also present in some members of the *Archiacasta* (see 4.1.7) and morphological intermediates are seen in Clade B (Fig. 5B).

The present specimens are all recorded from separate species of the Irciniidae and the only previous attempts at host identifications are those of Broch's (1947) original description describing the host as large and soft, and Utinomi's (1953) record states that the host was a tetraxon sponge indicating it belonged to an order other than Dictyoceratida. This latter host is deemed unlikely given the restricted host range evidenced in the present study.

4.1.3. *Acasta flexuosa* species complex

Acasta flexuosa (Nilsson-Cantell, 1931) has been reported from Japan, the South China Sea and Thailand (Hiro 1931; Kolbasov 1993; Nilsson-Cantell 1931). The type and only specimen seen by Nilsson-Cantell (1931) was an empty shell without a trace of the host; the remains of type material of *Acasta amakusana* Hiro, 1931, a subjective synonym, are similarly disarticulated shell plates. The parietes, particularly the laterals and carinolaterals, have their apices directed towards the rostrum, with the rostrum itself being recurved, giving this group a distinctive external appearance (Fig. 4H, I). Of the opercular plates, the scuta are weakly sculptured and the weak growth ridges are not fringed with setae (Fig. 7G).

The only previous host record attributed to *A. flexuosa* was by Kolbasov (1993) for the family Dysideidae. The four MOTUs sampled were found inhabiting four separate species of Dysideidae in the genera *Dysidea* and *Lamellodysidea.* Definitively assigning one of these MOTUs to *Acasta flexuosa* is not yet possible as it would require sampling and sequencing specimens from Japan. Given the geographic proximity of the present MOTUs within Western Australia there is the potential for further cryptic species throughout the documented range of this species.

4.1.4. *Acasta spongites* species complex

Acasta spongites (Poli, 1791) was originally described from Sicily and now has one of the widest reported distributions in the subfamily Acastinae, with records from the Atlantic, Indian and Pacific Oceans (e.g. Darwin 1854; Jones 1990; Kolbasov 1993; Ren 1984; Stebbing 1910; Utinomi 1958). The two MOTUs in this clade were collected from the Mediterranean Sea and Eastern Indian Ocean and share some key morphological features in that both have near identical opercular plates with a heavily striated scutum (Fig. 7 H), weak spines on cirrus IV, and a calcareous basal plate with a variously developed lattice-work of perforations that penetrate into the interior of the shell.

Acasta spongites has been recorded inhabiting a range of species within the Dysideidae, Irciniidae, Spongiidae and Thorectidae in the Mediterranean and north eastern Atlantic (Uriz et al. 1992; Voultsiadou-Koukoura and Koukouras, 1993; Zintzen and Kerckhof 2009) and the present specimens inhabited *Ircinia variabilis* from near Marseille. The closely related *Acasta* D5 from Australian waters inhabits Spongiidae and Thorectidae, thus supporting the concept that *A. spongites* is a relative host generalist. Prior to this study, the only host information for this species outside of European waters was an unidentified *Dysidea* from near the Seychelles (Kolbasov 1993).

Given the results of the present study, molecular analysis of specimens spanning the reported geographic and host range would likely reveal additional MOTUs in this complex. Further study of this group is also important for nomenclatural reasons as *A. spongites* is the type species for the genus, and consequently the subfamily Acastinae. Clarifying the identity of this species is important for stabilising the taxonomy of sponge-inhabiting barnacles.

4.1.5. Clade A

Clade A contains MOTUs that are assigned to *Archiacasta* (D16 and

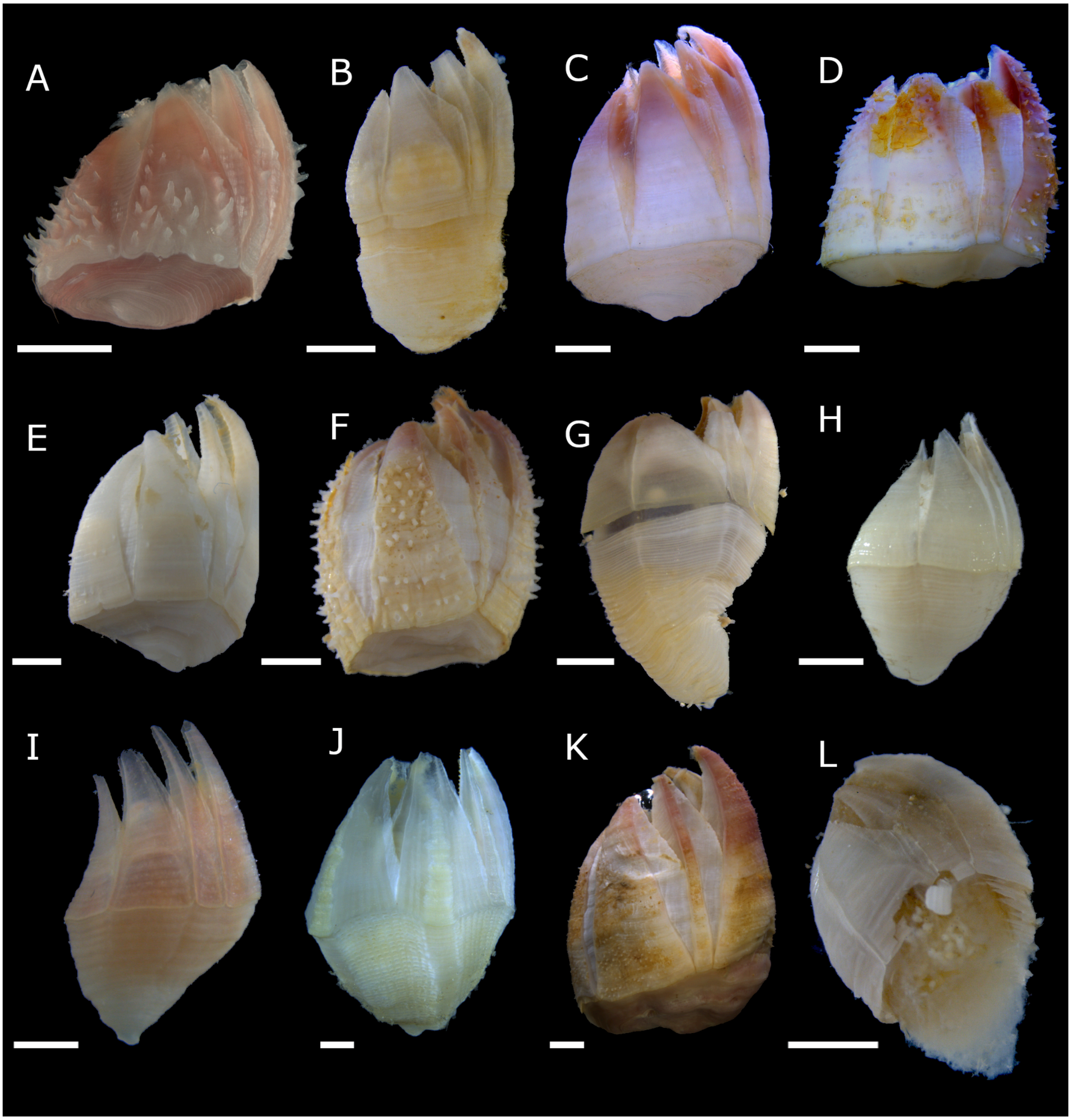

Fig. 4. Representative images of whole specimens in lateral view to demonstrate morphological diversity of the MOTUs. *Neoacasta laevigata* complex: A, D3 WAM C58797; B, D3 WAM C61517; C, D13 WAMC61535. Clade A: D, D11 WAM C61504. Clade B: E, D17 WAM C67631; F, D14 WAM C61514. *Neoacasta coriobasis* complex: G, D22 WAM C67674. *Acasta flexuosa* complex: H, D10 WAM C61497; I, D18 WAM C67638. *Acasta spongites* complex: J, D5 WAM C67812. K, *Neoacasta* D28 WAM C72922; L, *Archiacasta hainanensis* D9 WAM C61523. Scale bars: A–L = 2 mm.

D39) and *Neoacasta* (D11, D12 and D27). The basis of D16 and D39 is flat and can be either membranous or calcareous among different individuals within each MOTU, while in D11, D12 and D27 it is always calcareous and cupped. As such this clade challenges the utility of the morphological characters upon which the generic classification of *Archiacasta* and *Neoacasta* is based (see 4.1.7).

Within this clade host usage is varied with D16 inhabiting two species, one each from Spongiidae and Thorectidae. D11 inhabited two morphospecies of *Spongia*, while the remaining MOTUs were restricted to single host species of Irciniidae (D39) or Spongiidae (D12 and D27).

4.1.6. Clade B

This group of barnacles is united morphologically by the opercular plates and the form of the rostrum and lateral plates. The scuta are concave along the apicobasal axis, with radial striation of varying development (Fig. 7D–F). The terga are narrow, have setose growth lines and are arcuate, with a pronounced beaked apex that projects beyond the scutum when articulated (Fig. 6F, G, 7E). These characters give this clade an affinity with *Acasta japonica* Pilsbry, 1911, however, the present specimens' parietes lack internal ribs and the basis in some have six radial ridges and corresponding teeth around the margin (Fig. 5D, E), giving them a closer affinity with the members of *Neoacasta* with which they have been tentatively assigned.

This complex inhabits the widest range of hosts of the complexes examined, inhabiting ten species found in seven genera belonging to Irciniidae, Spongiidae and Thorectidae. However, all MOTUs were restricted to a single host species, except D14, which was recovered from three species of *Cacospongia* and one species of *Fascaplysinopsis*, *Hyrtios*

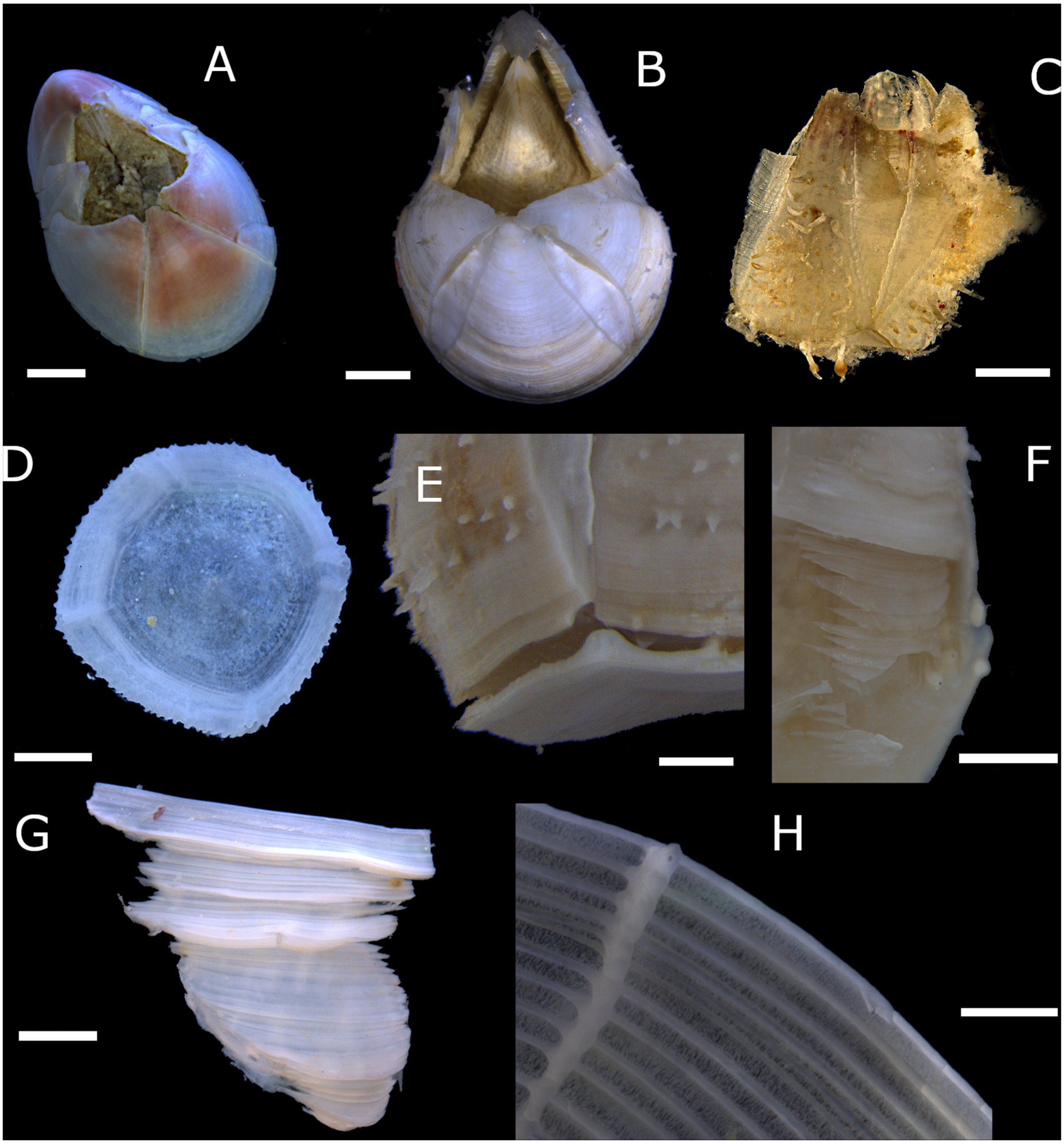

Fig. 5. Representative images of shell plates to demonstrate range of morphological diversity of the MOTUs. *Neoacasta coriobasis* complex: A, D29 WAM C72925, ventral view. Clade B: B, D17 WAM C67630, ventral view. C, *Euacasta* D6 WAM C55406, lateral view of articulated lateral, carinolateral and carina. Clade B: D, D14 WAM C72917, internal view of basis; E, D14 WAM C67640, junction of rostrum, lateral and basis. F, *Archiacasta hainanensis* D9 WAM C61523, junction between carina and basis. G, *Archiacasta fragilis* D36 WAM C67686, partially calcified basis. *Neoacasta coriobasis* complex: H, D22 WAM C71751, rim of basis. Scale Bars: A, B = 2 mm; C–G = 1 mm; H = 0.5 mm.

and *Luffariella* (all Thorectidae).

4.1.7. Remaining species groups

Many MOTUs could not be unambiguously resolved in a clade, but still warrant discussion. Five MOTUs were identified as belonging to the genus *Archiacasta* based on having a membranous or partially calcified basis (D9, D16, D36, D39 and D40). *Archiacasta hainanensis* (Ren, 1984) and *A. fragilis* (Ren, 1984), represented here by D9 and D36, have a distinctive basis, which is only partly calcified, being represented by separate rostral and carinal calcified portions (Fig. 5F, G). The calcareous aspect is made up of crescent-shaped pieces, deposited in two longitudinal series below the carina and rostrum. These arc towards the lateral plates but do not meet. This contrasts with the remaining *Archiacasta* D16, D39 and D40, which have a simple flat basis that is fully, partially or completely uncalcified, and this can vary within a MOTU. The phylogenetic results show that D16 and D39 are closely related, as are *A. hainanensis* and *A. fragilis*, but both pairs show closer relationships with other MOTUs assigned to the genus *Neoacasta* i.e. Clade A and D28, respectively. This study demonstrates the need to re-evaluate the current classification of the group, as much of the morphological generic diagnoses hinge on the nature of the basis.

The three MOTU's assigned to *Euacasta* are typical of the genus and characterised by exceptionally narrow carinolateral plates (Fig. 5C) and prominent hooked teeth on cirrus IV. This latter character is also

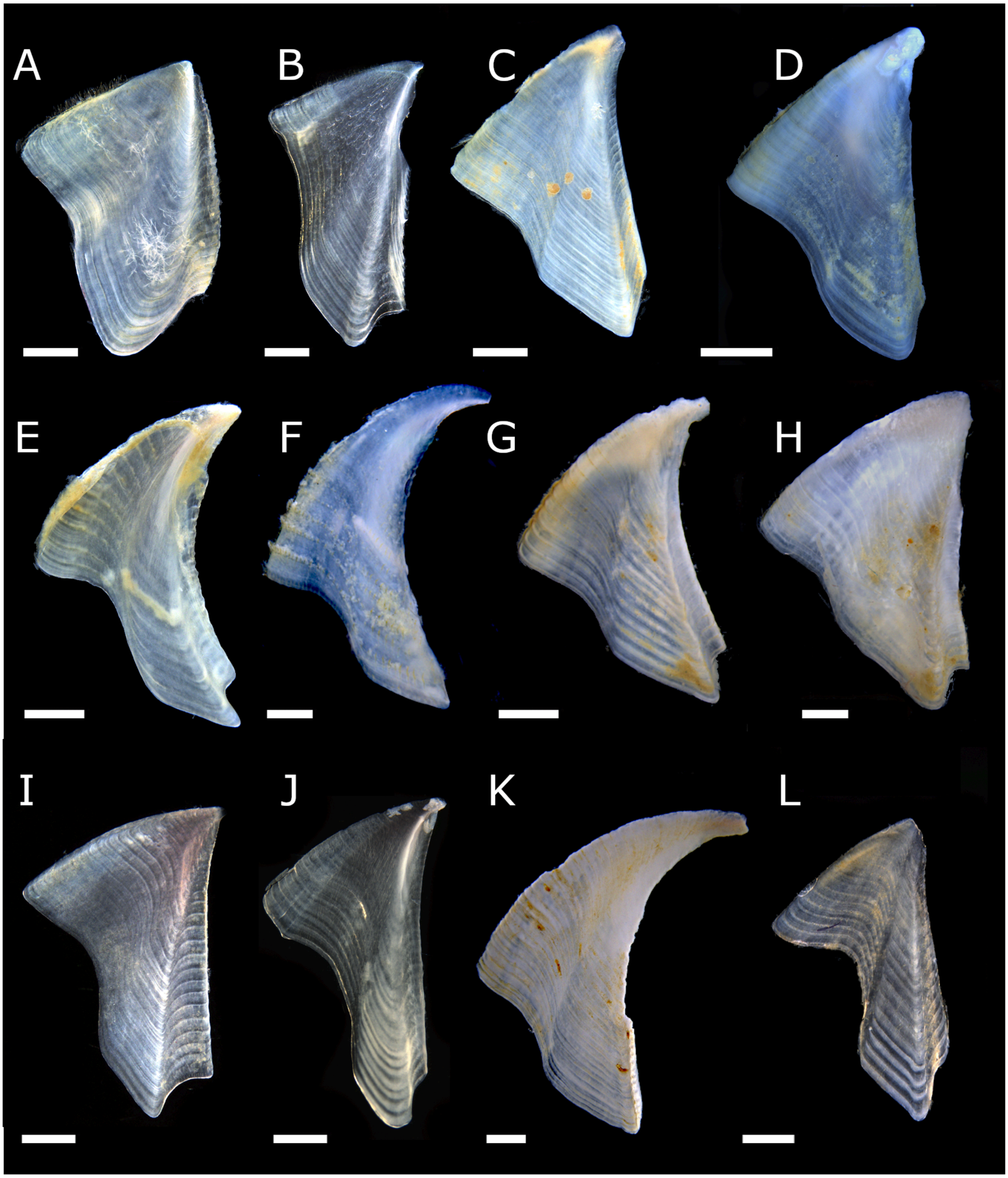

Fig. 6. Representative images of terga demonstrating morphological diversity of MOTUs. *Neoacasta laevigata* complex: A, D1 WAM C55429; B, D3 WAM C58800; C, D13 WAM C61535. Clade A: D, D11 WAM C61504. Clade B: E, D7 WAM C55428; F, D14 WAM C72917. *Neoacasta coriobasis* complex: G, D25 WAM C67695; H, D29 WAM C72924. *Acasta flexuosa* complex: I, D8 WAM C67691. *Acasta spongites* complex: J, D5 WAM C67812. K, *Neoacasta* D28 WAM C72922. *Archiacasta hainanensis* D9 WAM C61523. Scale bars: A, B, F, I, J, L = 0.5 mm; C, D, E, G, H, K = 1 mm.

common in *Acasta* but was not present in any of the other MOTUs in this study. These hooked teeth are used to prevent the host from overgrowing the orifice of the barnacles. It has been hypothesised that barnacles that have the most prominent teeth inhabit hosts with tough tissues or fast growth (Van Syoc and Winther 1999).

4.2. Host utilisation and relationships

This study found that 19 of the 32 dictyoceratid genera recorded from Australian waters (39 genera occur globally, excluding the Verticillitidae) are hosts to barnacles. It is expected that barnacles will be found in more genera as additional specimens are collected and examined from across their geographic ranges. It seems possible that Acastinae barnacles may be found in all dictyoceratid genera, if not all species in Australia. However, it was outside the scope of this paper to determine if any dictyoceratid sponge taxa are definitively barnacle-free.

Van Syoc et al. (2015) documented 23 Acastinae morphospecies inhabiting 12 sponge genera (only 11 host species were identified) of

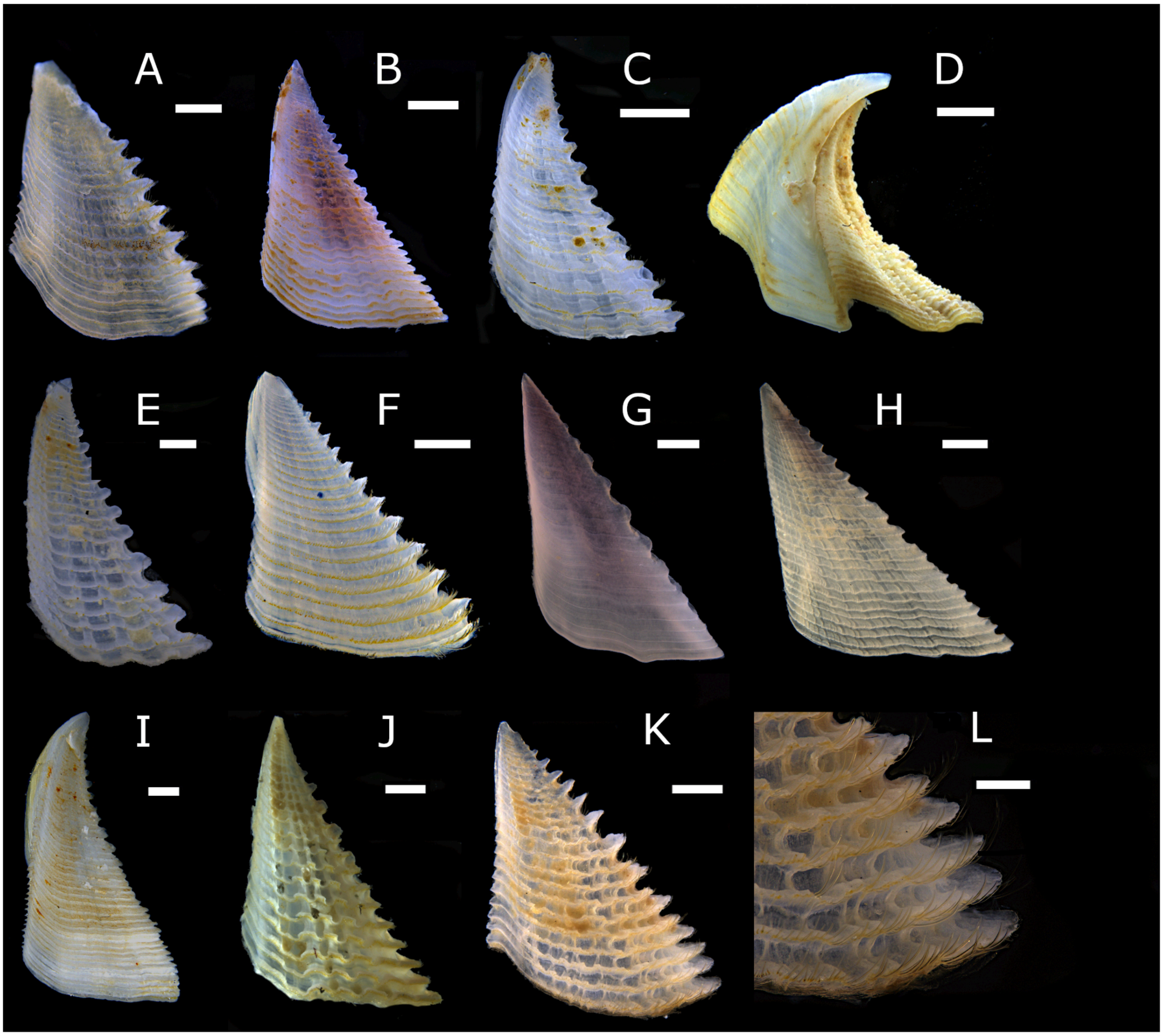

Fig. 7. Representative images of scuta to demonstrate morphological diversity of MOTUs. *Neoacasta laevigata* complex: A, D1 WAM C55429; B, D13 WAM C61435. *Neoacasta coriobasis* complex: C, D23 WAM C67683. Clade B: D, D12 WAMC75120; E, articulated tergum and scutum of D19 WAM C67640; F, D14 WAM C72917. *Acasta flexuosa* complex: G, D8 WAM C67697. *Acasta spongites* complex: H, D5 WAM C67812. I, *Neoacasta* D28 WAM C72922. *Archiacasta*: J, D36 WAM C67686; K, D9 WAM C61523; L, close up of same showing setae lining growth ridges. Scale bars: A, E–H, K = 0.5 mm; B, C, J = 1 mm; D = 2 mm; L = 0.25 mm.

dictyoceratid sponges, based on the known hosts of all sponge-inhabiting barnacles at that time as well as a suite of new morphospecies documented from various museum collections. The 39 barnacle MOTUs documented in the present study were extracted from members of all genera documented by Van Syoc et al. (2015) except *Thorecta*. They did not discuss relationships between the morphospecies and related hosts, and with the data available it is difficult to make direct comparisons to determine which, if any, are conspecific with those in the present study. One key finding shared between these studies is that the Acastinae are much more diverse than currently is known and, as a general trend, inhabit only a few sponge species, which are largely confamilials or congeners.

The Dictyoceratida has been demonstrated to be monophyletic, but the evolutionary relationships amongst the host sponges documented in this study are still unclear after several phylogenetic studies involving the Dictyoceratida (Abdul Wahab et al. 2014; Abdul Wahab et al. 2020; Erpenbeck et al. 2020; Erpenbeck et al. 2012; Galitz et al. 2018; Redmond et al. 2013; Thacker et al. 2013). These recent phylogenetic studies show that specific and generic assignments within families need to be reassessed, but broadly speaking, Dysideidae forms a distinct clade sister to the monophyletic Irciniidae and the remaining families. The fossil family Verticillitidae with the single extant genus *Vaceletia*, is the only dictyoceratid group to have a mineral skeleton (Erpenbeck et al. 2020; Wörheide 2008) and is not known to host barnacles. The genera currently in Spongiidae and Thorectidae were not resolved at the family level in any of those studies. Although, evidence suggests that the Phyllospongiinae (Thorectidae) and Spongiidae are reciprocally monophyletic but nested within the remaining thorectids (Erpenbeck et al. 2020). The genera of the Phyllospongiinae have historically been considered as a distinct family or placed in the Spongiidae but were transferred to the Thorectidae by Bergquist et al. (1999).

Although host families were distributed across the barnacle trees, aspects of the evolutionary relationships of the Dictyoceratida are reflected in portions of the barnacle phylogeny. A phylogenetic signal is most prominent in the barnacle complexes found to specialise on a single family e.g. *A. flexuosa* in Dysideidae, *N. coriobasis* in Irciniidae. These examples indicate the potential for an adaptive radiation event where the initial colonisation of the respective family by the MRCA enabled the spread and subsequent specialisation within confamilial species.

Potentially the strongest example of this is the barnacles of the *N. laevigata* complex, which were found inhabiting sponge genera assigned to the Phyllospongiinae. *Neoacasta* D13 is sister to the

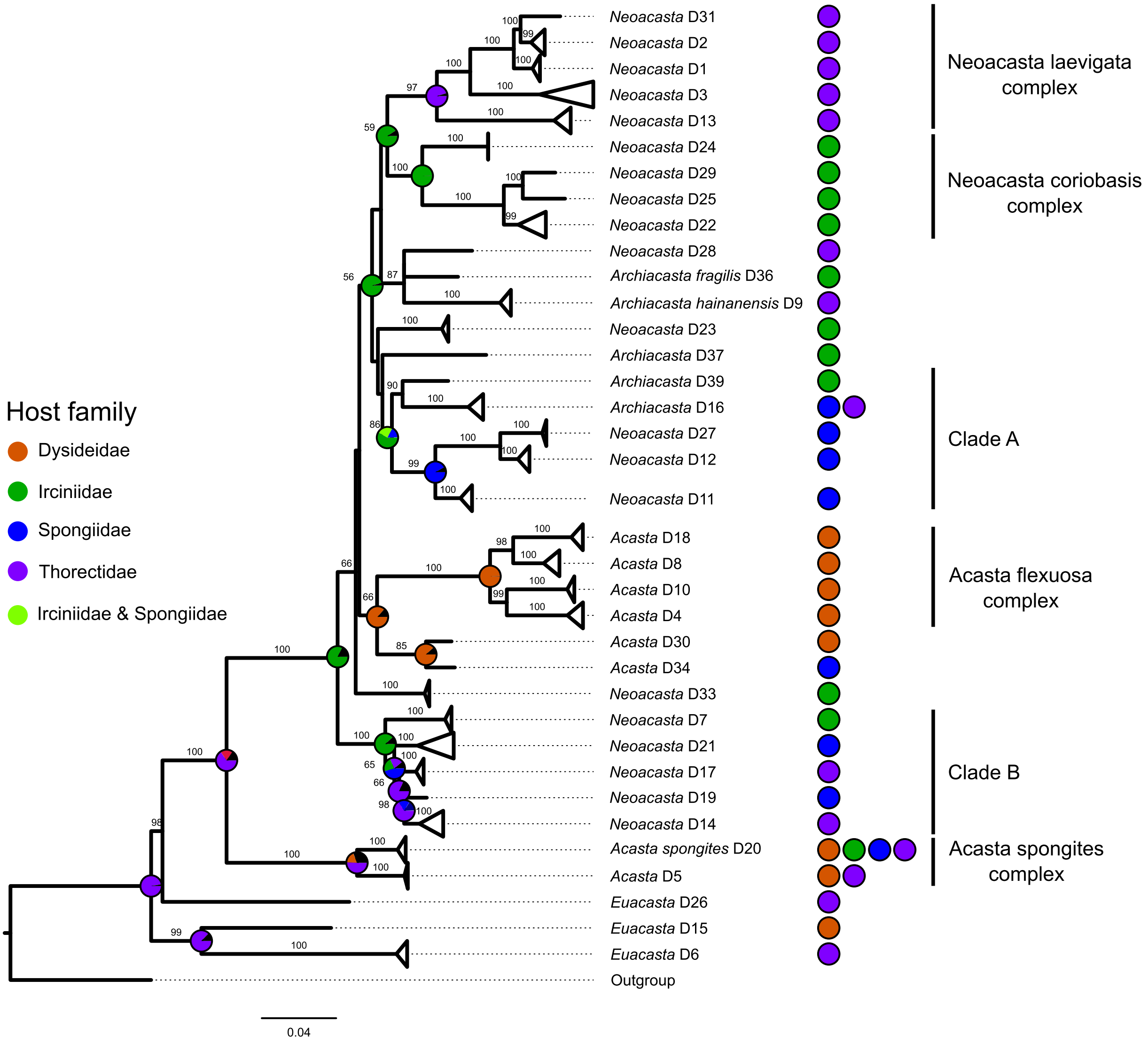

Fig. 8. Phylogenetic relationships of barnacles based on maximum likelihood analysis of the concatenated sequence data (*12S*, *COI*, *H3*, *28S*). Pie charts at nodes represent results of the Ancestral State Reconstruction, host suggestions of less than 15% were collapsed and represented by black wedges. Host family of each MOTU is indicated by coloured circles. Bootstrap values are only shown at nodes where support was higher than 50%. This figure is available in colour in the electronic version.

remaining members of the clade and is a relative generalist, inhabiting genera from both Thorectinae and Phyllospongiinae with the remaining MOTUs (D1, D2, D3 and D31) restricted to members of Phyllospongiinae. The MOTUs *Neoacasta* D1, D2 and D31 all inhabit *P. foliascens*, with D31 collected in the Red Sea. As discussed, these breaks correspond with breaks shown in a recent taxonomic revision of Phyllospongiinae (Abdul Wahab et al. 2020). Furthermore, under the new taxonomic arrangement presented by Abdul Wahab et al. (2020), D3 is restricted to members of *Polyfibrospongia* while the remaining D1, D2 and D31 are found in the genera *Phyllospongia* and are thus segregated at the host genus-level. Application of the principle of niche conservatism, where symbionts should inhabit closely-related hosts (Wiens et al. 2010), to this group is thus strengthened, as prior to this revision these barnacles were considered to have an overlap in host genera.

Even the unresolved relationships between some genera of Spongiidae and Thorectinae is mirrored in this study. *Archiacasta* D16 is found inhabiting *Dactylospongia elegans* (Thorectidae) and *Spongia* (Spongiidae). Molecular studies indicate *Dactylospongia* has an equivocal relationship, either being placed within a Spongiidae/Phyllospongiinae clade or in a clade that includes genera of the Thorectinae (Thacker et al. 2013; Erpenbeck et al. 2020). The prevalence of family-level host specificity would lend support to the hypothesis that *Dactylospongia* is more closely related to Spongiidae than the Thorectidae within which it is presently classified. A second example is the host usage by members of Clade B, after having initially colonised irciniid hosts members of this clade colonised the thorectid genera *Hyrtios* and *Cacospongia* (*Neoacasta* D17 and D14), and the spongiids *Hippospongia*, *Hyattella* and *Spongia* (*Neoacasta* D21 and D19) and could be viewed as reflecting the uncertainty in the host classification.

4.3. Potential drivers for diversification

How species diversity evolves and is maintained is subject to much debate, but a general explanation is that diversity reflects the level of environmental heterogeneity (Kassen 2002). The sponge communities of north Western Australia, where much of the specimens studied were sourced, can be deemed as very heterogenous in the sense that they are highly diverse and with centres of apparent endemism (Fromont et al. 2016). The abundance and diversity of potential hosts certainly explains the diversity of barnacles in part, but what maintains the high diversity

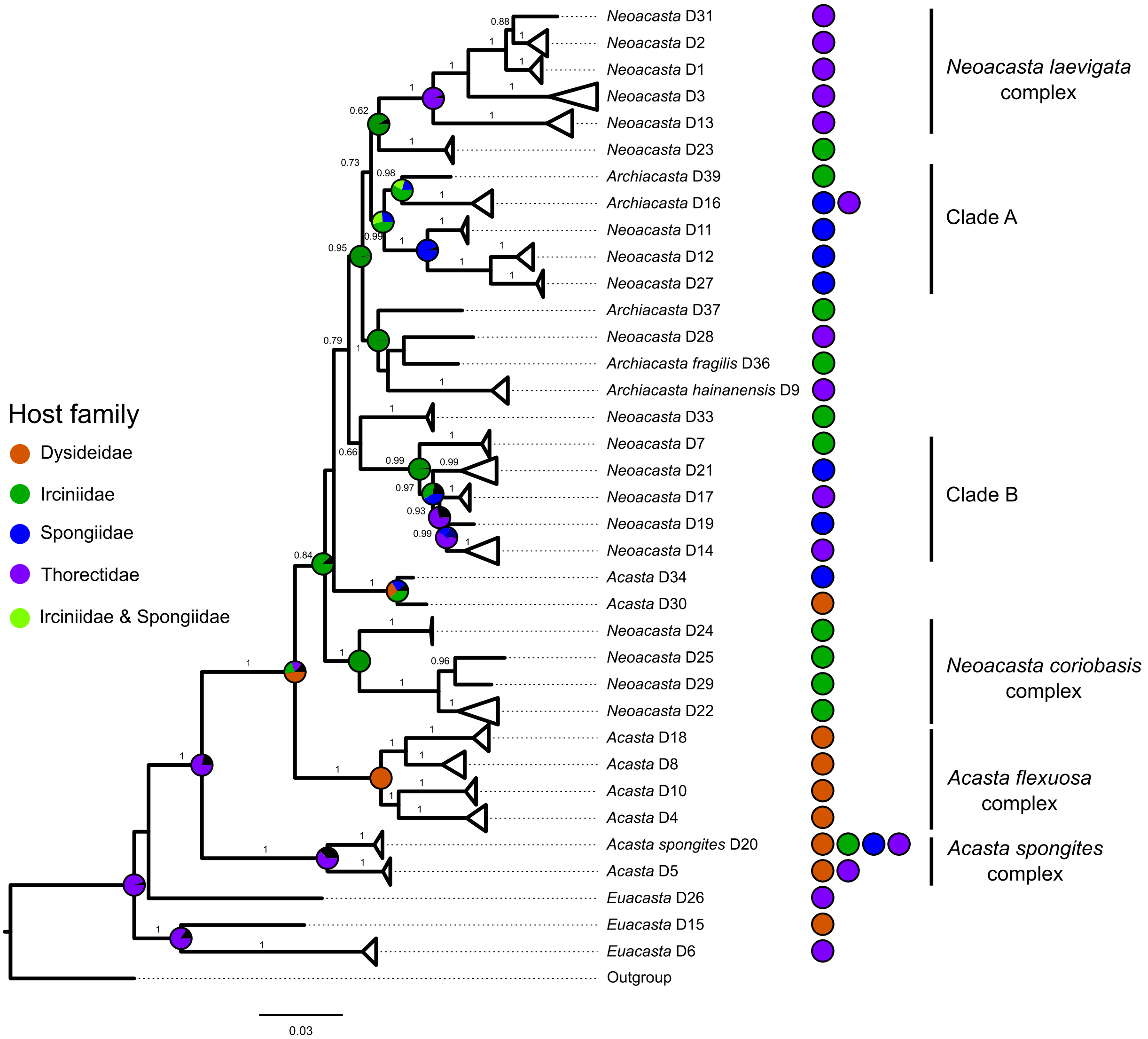

Fig. 9. Phylogenetic relationships of barnacles based on Bayesian inference analysis of the concatenated sequence data (*12S*, *COI*, *H3*, *28S*). Pie charts at nodes represent results of the Ancestral State Reconstruction, host suggestions of less than 15% were collapsed and represented by black wedges. Host family of each MOTU is indicated by coloured circles. Posterior probability values are only shown at nodes where support was higher than 0.5. This figure is available in colour in the electronic version.

of host specialists as opposed to having fewer generalists?

The Acastinae adhere to the typical barnacle reproductive strategies of hermaphroditism and internal fertilisation through copulation, followed by a free-living, planktonic larval stage. Although, successful breeding via broadcasting sperm into the water column has been documented in a few free-living species these are currently considered to be exceptional cases (Barazandeh et al. 2013; Barazandeh et al. 2014). Coupled with their sessile mode of life, mating opportunities for sponge-inhabiting barnacles are restricted to those individuals within reach of their male reproductive organ. Ultimately this means that breeding will only ever occur between individuals from within the same host individual and thus establishes assortative mating (Rice 1987; Schluter 2001; Via 2001).

Although the mechanisms preventing cross breeding between inhabitants of different sponge species is presently clear cut, maintaining this assortative mating over successive generations requires larval recruitment to also be restricted. In free-living barnacles, the gregarious nature of barnacle settlement is induced by several pheromones released by conspecific adults and newly settled cyprids (see Clare & Matsumura 2000 for review). In substrata without conspecifics cues are related to biofilms present on the substrata (see Hadfield 2011). In the case of symbiotic barnacles, the cyprid larvae have been shown to locate potential hosts via waterborne cues (Pasternak et al. 2004a; Pasternak et al. 2004b). New cohorts of larvae will always be attracted to hosts with living members of previous generations, but what drives the colonisation of a novel host remains unknown.

In a recent study, a range of novel morphological adaptations on the antennule, the limbs responsible for settlement and attachment to the substrata, were discovered on sponge barnacle cyprid larvae (Yu et al. 2020). These features, which are not seen in other free-living or symbiotic groups, show some correlation with host spicule morphology and density and are perhaps the key innovation that precipitated the adaptive radiation in sponge inhabiting barnacles (Yu et al. 2020). Although further work is needed to test this, their study suggests that host utilisation has become restricted by the functional capability of the settling cyprid, having evolved beyond the initial behavioural changes associated with choosing a host.

4.4. Conclusions

This study is the first in-depth investigation into the diversity of barnacles inhabiting a single, targeted, host sponge group. The results revealed a highly diverse group of sponge-inhabiting barnacles that has radiated from at least one successful colonisation of the Dictyoceratida. Host usage is generally restricted to a few species within a genus or family, indicating that host selection is non-random and demonstrated the evolutionary success of ecological specialists in nature.

Although the geographic scope of these specimens was predominantly limited to northern Western Australia, this helped reduce the chance of geographic distance confounding the effect of host specificity and helped understand the likelihood of co-habitation. The presented data show that co-habitation is rare, with the barnacles being segregated by host when in relative sympatry. The barnacle MOTUs found co-inhabiting host species were either not closely related or separated geographically (Western Australia to the Red Sea).

Future work on dictyoceratid-inhabiting barnacles should expand the geographic scope of specimens sampled. A particular focus could be on host species with wide ranging distributions. Increased sampling will benefit future attempts at differentiating between species and population-level distinctions among the documented MOTUs. Additionally, utilising molecular data to aid sponge identifications and infer host phylogeny would greatly improve understanding of sponge-barnacle symbiosis.

CRediT authorship contribution statement

Andrew M. Hosie: Conceptualization, Funding acquisition, Investigation, Data curation, Formal analysis, Methodology, Writing - original draft, Writing - review & editing. **Jane Fromont:** Supervision, Conceptualization, Data curation, Funding acquisition, Writing - review & editing, Investigation, Project administration. **Kylie Munyard:** Supervision, Conceptualization, Project administration, Writing - review & editing. **Nerida G. Wilson:** Data curation, Project administration, Resources, Writing - review & editing. **Diana S. Jones:** Supervision, Writing - review & editing, Funding acquisition.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ympev.2021.107179.

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Chapter 5. Origins of sponge symbiosis and phylogenetic placement of the sponge-inhabiting barnacles.

Synopsis

Molecular phylogenetic research over the last two decades has culminated in a significant rearrangement of balanomorph barnacle classification. This has largely occurred because traditionally used macro-morphological characters (such as the number of shell plates, diversity of parietal tubes and the nature of the basal plate) have been shown to be either plesiomorphic or homoplastic when compared to molecular-derived phylogenetic trees. For symbiotic groups, adaptations to the hosts can confound the results of morphological based analyses as the phenotypes are often characterised by the loss of characters compared with free-living relatives. Also, they are under similar selection pressure to unrelated species that inhabit similar hosts, leading to convergent evolution of the remaining characters. The underlying assumption is that symbiosis stemmed from a free-living ancestor, with "regressing" to a free-living mode being improbable. Many groups of balanomorph barnacles have been subject to comprehensive phylogenetic study. However, inclusion of sponge-inhabiting barnacles has been sparse. This chapter aims to place the various sponge-inhabiting groups into the broader phylogenetic framework that has already been established and in the process pinpoint the origin, or origins, of the symbiotic relationship.

5.1. Introduction

The last two decades have seen extensive molecular and morphology-based phylogenetic research that has reshaped barnacle evolution and systematics (Glenner & Hebsgaard, 2006; Hayashi et al., 2013; Høeg et al., 2019; Kolbasov et al., 2016; Kolbasov & Newman, 2005; Lin et al., 2016; Linse et al., 2013; Malay & Michonneau, 2014; Pérez-Losada et al., 2008; Pérez-Losada et al., 2014; Simon-Blecher et al., 2007; Tsang et al., 2014; Van Syoc & Newman, 2010). Most recently Chan et al. (2021) synthesised the findings of previous studies and overhauled the Linnean hierarchy from the family level and above to create a new base structure. One of the big changes they made was synonymising the Archaeobalanidae Newman and Ross, 1976 under the Balanidae Leach, 1817 on the grounds that no molecular phylogeny had thus far provided support for the reciprocal monophyly of the two families. It should be noted that the Archaeobalanidae was thought to be paraphyletic when established, a practice common at the time, by Newman and Ross (1976), as they considered this family to contain the ancestral forms from which members of the Balanidae and Pyrgomatidae Gray, 1825 evolved.

The Balanidae is now one of the largest barnacle families with over 350 species distributed in 10 extant subfamilies and 38 extant genera. The Balanidae contains some of the most familiar barnacle groups such as those common on intertidal rock platforms, but there is also a significant diversity of poorly known symbiotic groups. In fact, these are likely to make up the majority of balanid species (see Chapter 1; Hosie et al., 2021; Van Syoc et al., 2015). The nature of many of these relationships may only be facultative epibiotic species that cement to a host species, much like free-living species on rocks, without much else in the way of morphological adaptation. Examples are species of *Solidobalanus* Hoek, 1913 found on urchin spines or species of *Amphibalanus* Pitombo, 2004 and *Fistulobalanus* Zullo, 1984 associated with mangroves. The other extreme is seen in obligate symbionts like *Wanella* Anderson, 1993, found embedded within the fire coral, *Millepora* spp. (Cnidaria, Hydrozoa). The fused wall plates and the form of the opercular valves had this genus placed within the Pyrgomatidae, symbionts of scleractinian corals (Cnidaria, Hexacorallia) until molecular phylogenies showed that the similarities were a case of convergent evolution (Malay & Michonneau, 2014; Simon-Blecher et al., 2016; Tsang et al., 2014).

In Chapter 2 it was further demonstrated that sponges, particularly the class Demospongiae, are the most successfully exploited host group in terms of the number of barnacle species as indicated by previous morphological studies (Kolbasov, 1993; Van Syoc et al., 2015). The nature of the relationship is presently considered commensal, with the barnacle gaining habitat and potential protection from predators or competitors. There is no evidence to suggest that there is a significant trophic interaction, or that the host sponge is affected by the embedded barnacles (Kolbasov, 1993). The sponge-inhabiting barnacles are distributed in three subfamilies (Acastinae Kolbasov, 1993, Archaeobalaninae Newman and Ross, 1976 and the Bryozobiinae Van Syoc and Newman, 2010) and exhibit a diverse array of morphologies. The Acastinae and *Membranobalanus* Hoek, 1913 (Archaeobalaninae) are always embedded within the sponge, while the Bryozobiinae and some species of *Armatobalanus* (Archaeobalaninae) are considered to need to cement to the substrate but are always covered by a thin layer of encrusting sponge (Van Syoc & Newman, 2010).

The key molecular phylogenetic studies that have examined balanoid evolution have had limited taxonomic coverage of these symbiotic groups from the former Archaeobalanidae (Pérez-Losada et al., 2008; Pérez-Losada et al., 2014; Simon-Blecher et al., 2007). The results of Pérez-Losada et al (2014) show the Acastinae as being polyphyletic and this was corroborated by Yu et al. (2020a), with both studies showing that some species have a sister relationship with the Megabalaninae Newman, 1979 and/or the Amphibalaninae Pitombo, 2004. Both studies have also shown that the phylogenetic placement of other symbiotic genera such as *Conopea* Say, 1822 and *Membranobalanus* should also be re-examined.

The primary focus of this chapter is to examine the phylogenetic relationships between the Acastinae genera, *Membranobalanus* and *Conopea* in relation to those of other genera and subfamilies of the Balanidae through the reconstruction of a multi-locus phylogeny. Through this the origins of symbiosis with sponges can be determined.

5.2. Methods

5.2.1. Taxon sampling

In this study the majority of material examined was collected from Western Australia with additional material from New Zealand, Europe, the Red Sea and South Africa (See Appendix I for full material examined). The molecular datasets and identifications generated in Chapters 2–4 (Hosie et al., 2021) were expanded in this chapter by sequencing additional loci of representative species. The primary species hypotheses and the molecular operational taxonomic units from previous chapters have been incorporated into the identifications for this chapter e.g. *Archiacasta hanainensis* D9 20. Other members of the Balanomorpha were either newly sequenced or publicly available and downloaded from GenBank (www.ncbi.nlm.nih.gov/genbank; see Appendices II for full list of sequences downloaded from GenBank). Representatives of the Pyrgomatidae, Coronuloidea and Elminioidea were included in the analyses to provide broader context and to “catch” any potential rogue taxa. Representative members of the Chthamaloidea were selected as the outgroup due to their longstanding position as sister to the remaining balanomorph barnacles (Darwin, 1854; Newman & Ross, 1976; Pérez-Losada et al., 2008; Pérez-Losada et al., 2014).

5.2.2. Molecular data and analysis

5.2.2.1. Data acquisition

Adductor or depressor muscle tissues of barnacles were subsampled from specimens, and genomic DNA was extracted using either a Bioline Isolate II or Qiagen DNeasy extraction kit following the manufacturer’s instructions. Partial fragments of the cytochrome c oxidase I (*COI*), 12S ribosomal subunit (*12S*), Histone 3 (*H3*), RNA polymerase subunit II (*RPII*) and 28S ribosomal subunit genes (*28S*) were amplified (see Table 5.1 for primers and annealing temperatures) in a 25 µL reaction and consisting of 2 µL DNA extract, 1 unit MyTaq DNA polymerase, 1x MyTaq PCR buffer and 0.5 µL (0.1

µM) of each primer. The following Polymerase Chain Reaction conditions were used: 2 min at 95 ◦C for initial denaturing, then 35 cycles of 30 s at 95 ◦C, 30 s at 46 ◦C, 50 ◦C or 58 °C, 45 s at 72 ◦C, and a final extension for 7 min at 72 ◦C. The resulting amplicons were sequenced at the Australian Genome Research Facility, Perth, using the same primers, via Sanger (cycle) sequencing.

The sequences were assembled and trimmed using Geneious Prime. Quality control of sequences involved inspecting for stop codons in protein coding genes, checking matches on BLAST and re-examination of original specimens to detect and remove potentially contaminated sequences. The assembled consensus sequences were aligned using MAFFT (Katoh & Standley, 2013) implemented in Geneious Prime using the auto option (coding genes) and the E-ISI-i option (rRNA genes). The aligned loci were then concatenated: *12S-H3-COI-RPII-28s.*

5.2.2.2. Phylogenetic analyses

The concatenated alignment was analysed using maximum likelihood (ML) and Bayesian inference (BI) methods to construct phylogenetic trees. Data for both analyses were partitioned by gene, with the *COI* sequences also partitioned by codon position. The ML analysis and model selection was implemented with the IQ-TREE webserver (Kalyaanamoorthy et al., 2017; Trifinopoulos et al., 2016). Tree support was calculated by conducting 1000 ultra-fast bootstraps (BS, Minh et al., 2013). The BI analysis was conducted in MrBayes 3.2.6 (Ronquist et al., 2012) utilising the CIPRES webserver (Miller et al., 2015) with 4 heated chains, a reversible-jump (Nst = mixed) Markov chain Monte Carlo (MCMC) of 11 million generations, and a burn-in of 25% (Ronquist & Huelsenbeck, 2003). Support values were calculated as posterior probability (PP). Full details of the BI data block and model selection are provided in this chapter's supplementary information (S5.1 and S5.2). The BI results were checked for convergence using Tracer 1.7 (Rambaut et al., 2018).

5.2.2.3. Ancestral states

Ancestral state reconstruction (ASR) analyses, to infer ancestral host phyla and the origins of sponge symbiosis, were conducted in RASP (Yu et al., 2020b) using the Bayesian binary MCMC (BBM) method, under default parameters, utilising the final ML and BI trees. Each balanoid taxon was coded by host group: Porifera (sponges), Scleractinia (hard corals), Alcyonacea (soft corals), Antipatharia (black corals) and Hydrozoa (fire corals). Character states were unordered and equally weighted.

5.2.2.4. Divergence time estimation

The origins of sponge symbiosis within the Balanoidea were explored using molecular clock analyses in BEAST 2.6.4 (Bouckaert et al., 2019). The dataset of 145 sequences for this was based on the alignment of the concatenated sequences of *12S-H3-COI-RPII-28S* from a single representative of each species from the main phylogenetic analysis. Individual specimens were selected for having the most complete dataset for their respective species. Rates were calculated using a relaxed lognormal clock under the Hasegawa, Kishino, and Yano (HKY, 1985) model, using a gamma distributed rate (+G) and proportion of invariant sites (+I), was used for each of the 6 gene partitions, which were unlinked, under the Yule model of speciation. The use of the simple HKY model was implemented to increase efficiency of the overall analysis as recommended by Barido et al. (2018). Tree Nodes were calibrated using two fossils and three ages (Table 5.2). The fossil calibrations were introduced as described by Pérez-Losada et al. (2014) with minimum ages using lognormal priors with the lower bound (offset) implemented as the lower end of the epoch containing the first fossil occurrence and a size (mean) adjusted to the duration of the epoch where necessary. Nodes that were calibrated based ages from the results of Pérez-Losada et al. (2014) were introduced as the mean age with a normal distribution prior and the sigma was adjusted to reflect their 95% confidence limits. Five independent MCMC runs of $5x10^8$ generations, sampling every 50,000th generation. Output log files were checked for convergence using Tracer 1.6 i.e. effective sample sizes (ESS) values >200 and unimodal parameter distributions, stable trace plots. Tree files for the respective analysis were combined using Log Combiner version 2.6.6 (Bouckaert et al., 2019) with 25% discarded as burn in. TreeAnnotator 2.6.4

was used to summarise the combined trees into a single maximum clade credibility tree, with common ancestor node heights and a posterior probability height limit of 0.0.

Table 5.1. Primers and annealing temperatures used in this chapter.

Primer	**Direction**	**Sequence (5’–3’)**	**Annealing temperature (°C)**	**Reference**
12S				
F1	Forward	GAAACCAGGATTAGATACCC	50	Mokady et al. 1994
FB	Forward	GTGCCAGCAGCTGCGGTTA		Tsang et al. 2009
R1	Reverse	TTTCCCGCGAGCGACGGGCG		Mokady et al. 1994
R2	Reverse	CCTACTTTGTTACGACTTATCTC		Tsang et al. 2009
COI				
dgLCO1490	Forward	GGTCAACAAATCATAAAGAYATYGG	46	Meyer et al. 2003
COL6b	Forward	ACAAATCATAAAGATATYGG		Schubart & Huber 2006
dgHCO2198	Reverse	GGTCAACAAATCATAAAGAYATYGG		Meyer et al. 2003
H3				
AF	Forward	ATGGCTCGTACCAAGCAGACVGC	50	Colgan et al. 1998
AR	Reverse	ATATCCTTRGGCATRATRGTGAC		Colgan et al. 1998
28s				
LSU5	Forward	ACCCGCTGAAYTTAAGCA	50	Littlewood 1994
LSU3	Reverse	TCCTGAGGGAAACTTCGG		Littlewood 1994
RPII				
RP-for1	Forward	CACAAGATGAGTATGATGGG	58	Tsang et al. 2014
RP-rev1	Reverse	CGTGCCGTCGTAGTTGACCAT		Tsang et al. 2014

Table 5.2. Fossil species and nodes used to calibrate divergence time estimations. Ages based on Pérez-Losada et al. (2014) are given as the mean age and those based on fossils are given as an age range of the deposits. Calibrated nodes are indicated on Figure 5.3.

Species	**Geological Age**	**Node**	**Reference**
Balanomorpha MRCA	Early Cretaceous (105)	C1	Pérez-Losada et al., 2014
Amphibalaninae MRCA	Late Eocene (35)	C2	Pérez-Losada et al., 2014
Pyrgomatidae MRCA	Eocene (52)	C3	Pérez-Losada et al., 2014
Austromegabalanus victoriensis	Late Miocene (23-11.6)	C4	Buckeridge, 1983
Austrobalanus antarcticus	Mid-Eocene (47.8-38)	C5	Buckeridge & Newman, 2010

5.3. Results

5.3.1. Phylogenetic relationships

A total of 145 species representing seven families were included in the analyses. The taxonomic distribution of species used for analyses described in this chapter is given in Table 5.3. The final alignment was 3569 base pairs long (*12S*: 518; *H3*: 327; *COI*: 655; *RPII*: 924; *28S*: 1145).

Nodes across both analyses varied from poorly (BS<75% or PP<0.90) to well (BS>75% or PP>0.90) supported, and the level of support was not always consistent between the analyses (Figures 5.1 and 5.2). The species presently assigned to the Balanoidea constituted a well-supported clade, with the exception of *Notobalanus vestitus* (Darwin*,*1854), which was placed within the Coronuloidea. However, neither the Pyrgomatidae nor the Balanidae were supported as reciprocally monophyletic clades in the analyses. At the subfamily level only the Amphibalaninae, Megabalaninae and Semibalaninae Newman & Ross, 1976 formed well supported monophyletic clades in both analyses, but not the symbiotic groups where one or more representative species is present in separate clades (Acastinae, Archaeobalaninae, Pyrgomatinae). Many of the genera of the symbiotic groups were also found to be polyphyletic.

The sponge inhabiting barnacles were distributed across five well-supported clades (indicated at nodes A–E in Figures 5.1 and 5.2). In Clade A, *Membranobalanus* was recovered in a clade containing the pyrgomatid genus *Pyrgospongia* Achituv & Simon-Blecher, 2006 and species identified as *Archiacasta tenuivalvata* (Broch, 1947). In both analyses this clade was recovered as sister to the clade containing the Pyrgomatidae and some members of the soft coral-inhabiting *Conopea.* However, this was poorly supported in the BI analysis (PP = 0.46, BS = 78%). Host use in Clade A includes the sponge orders Biemnida, Clionaida and Haplosclerida.

Clade B contained the bulk of the Acastinae as well as including *Multatria filigranus* (Broch, 1916) and three species of *Armatobalanus* Hoek, 1913*.* Acastinae were found in three sub clades (C–E), each well supported in both analyses (Figures 5.1 and 5.2). Both clades C and E contained an intermixture of taxa identifiable to current genera, while clade D contained only species identifiable as *Euacasta* Kolbasov, 1993 i.e. the parietal section of the carinolatus is reduced to a narrow strip. Clade B contains *Acasta* Leach, 1817, *Archiacasta* Kolbasov, 1993 and *Neoacasta* Kolbasov, 1993 including the type species of these genera: *Acasta spongites* (Poli, 1791), *Archiacasta membranacea* (Barnard, 1924) and *Neoacasta glans* (Lamarck, 1818)*.* Clade E contained species currently assigned to *Acasta, Euacasta* and *Pectinoacasta* Kolbasov, 1993*,* most notably the type species *Pectinoacasta pectinipes* (Pilsbry, 1912)*.* All species in these clades inhabit sponges except for *A.* cf. *vipensis* (Van Syoc et al., 2014) and *A. spinitergum* (Broch, 1931) in Clade E, both of which inhabit alcyonaceans*.*

A clade containing two species, *Acasta cyathus* Darwin, 1854 and *A.* cf *cyathus* was recovered sister to a clade containing members of the Concavinae (Zullo, 1992), Balaninae and Semibalaninae (PP = 0.82, BS = 78). *Acasta cyathus* inhabits sponges of the order Haplosclerida and is sister to the morphologically similar *A.* cf. *cyathus* that inhabits the soft coral family Alcyoniidae (Alcyonacea).

The genus *Conopea* was polyphyletic with one species recovered in one clade sister to the Megabalaninae and six species nested within a clade containing the scleractinian-inhabiting Pyrgomatidae and *Armatobalanus allium* (Darwin, 1854; Archaeobalaninae)*.* The relationship between *C.* cf. *calceola* (Ellis, 1758) and the Megabalaninae was well supported in both analyses, but the relationship between the remaining species and the Pyrgomatidae was more ambiguous.

Table 5.3. Taxonomic distribution of species included in the phylogenetic analyses.

Family	**Subfamily**	**# of species**
Chthamalidae		3
Catophragmidae		1
Coronulidae		1
Tetraclitidae		4
Elminiidae		2
Balanidae	Acastinae	84
Balanidae	Amphibalaninae	6
Balanidae	Archaeobalaninae	20
Balanidae	Balaninae	3
Balanidae	Concaviinae	2
Balanidae	Megabalaninae	6
Balanidae	Semibalaninae	2
Pyrgomatidae	Pyrgomatinae	9

5.3.2. Ancestral State Reconstructions

The ASR analyses on the ML and BI trees gave similar results and provided mostly clear predictions for the ancestral host group (Figures 5.1 and 5.2). The transition from free-living to sponge symbiosis was predicted to have occurred three times. These were most likely to have occurred at the MRCA of the clade containing *A. cyathus*, Clade A, and Clade B. For the *A. cyathus* clade the MRCA was predicted as 53% likely to have inhabited a sponge host and 34% to have inhabited an alcyonacean host in the ML analysis, compared with 41% and 30% in the BI analysis.

The host for the MRCA of Clade A was predicted to be a sponge (100% for both analyses), while the prior node at the clade containing the Pyrgomatidae and *Conopea* was less clear and predicted to either inhabit a sponge, (57%), or be free-living (39%) in the ML analysis, but 77% likely to be free-living and only 17% to inhabit a sponge in the BI analysis. The MRCA of the clade containing the Pyrgomatidae and *Conopea* was inferred to have been symbiotic with the scleractinian hard corals (74% ML, 77% BI) before shifting to inhabiting alcyonaceans and antipatharians for the MRCA of nodes within the *Conopea* clade.

The host MRCA of Clade B was also predicted to have been a sponge (100% for both analyses). Two species within Clade E, *A.* cf. *vipensis* and *A. spinitergum,* were collected from alcyonacean hosts (Gorgoniidae and Subergorgiidae), forming a clade with an MRCA predicted to inhabit an alcyonacean host (99% for both analyses).

For symbiotic species found within clades of otherwise free-living species such as *Conopea* cf. *calceola* and the hydrozoan inhabiting *Wanella milleporae* and *Megabalanus ajax* (Darwin, 1854), the transition to symbiosis occurred at some point after the MRCA with their nearest relative.

5.3.3. Divergence times

The chronogram produced by the BEAST analysis gave a slightly different topology to the analyses above, primarily the ML analysis (Figure 5.3). The only difference with respect to the main symbiotic clades was within clade B. The position of the clade of *Multatria* Van Syoc and Newman, 2010 and *Armatobalanus* was nested between Clades D and E, instead of being sister to them, but was otherwise similar. Many of the symbiotic balanoid lineages emerge in the early Paleogene (or possibly late Cretaceous), with the sponge barnacles of Clade B appearing in the early Paleogene at 62.95 (56–71) mya, the MRCA of Clade A at 57.58 (50–65) mya, the pyrgomatids 52.31 (46–58) mya. Based on the branching patterns the radiation that resulted in the present-day Australian sponge-inhabiting barnacles was particularly rapid in the late Eocene through to the early Miocene (approximately 40–20 mya). The 95% high posterior density intervals were quite variable between nodes, but were relatively narrow around (<15 mya) nodes of interest in this study.

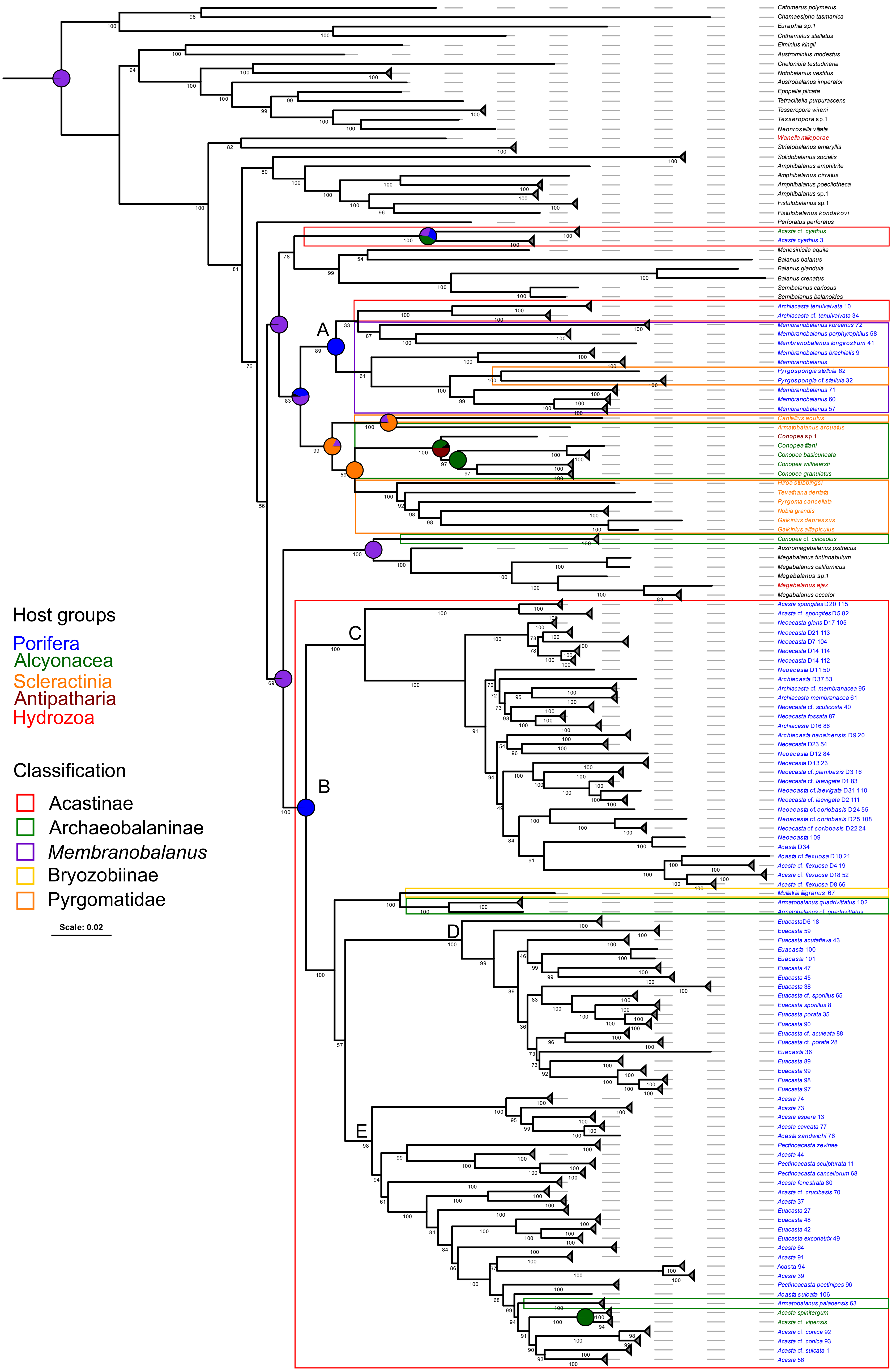

Figure 5.1. Maximum likelihood phylogeny of the Balanomorpha showing results of the ancestral state analyses. Branch lengths are proportional to substitutions per site. Boxes indicate the current classification of symbiotic lineages. Pie charts are placed at nodes to indicate where host transitions occur. Coloured tip labels indicate host group, and these colours correspond to the predicted ancestral state reconstructions as indicated by the pie charts at key nodes. Scale is represented by substitutions per site.

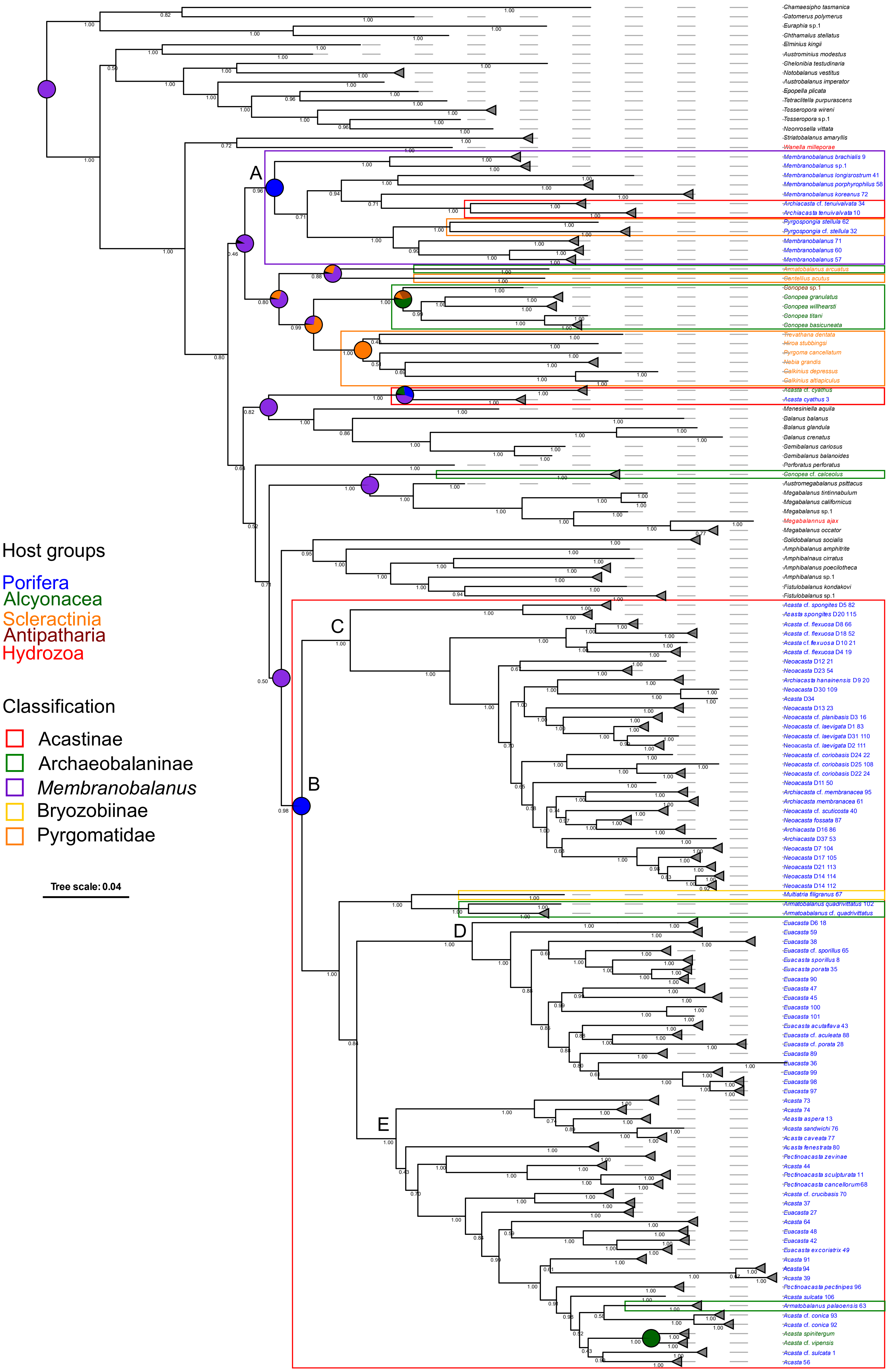

Figure 5.2. Bayesian inference phylogeny of the Balanomorpha showing results of ancestral state reconstructions. Branch lengths are proportional to substitutions per site. Boxes indicate the current classification of symbiotic lineages. Pie charts are placed at nodes to indicate where host transitions occur. Coloured tip labels indicate host group, and these colours correspond to the predicted ancestral state reconstructions as indicated by the pie charts at key nodes. Scale is represented by substitutions per site.

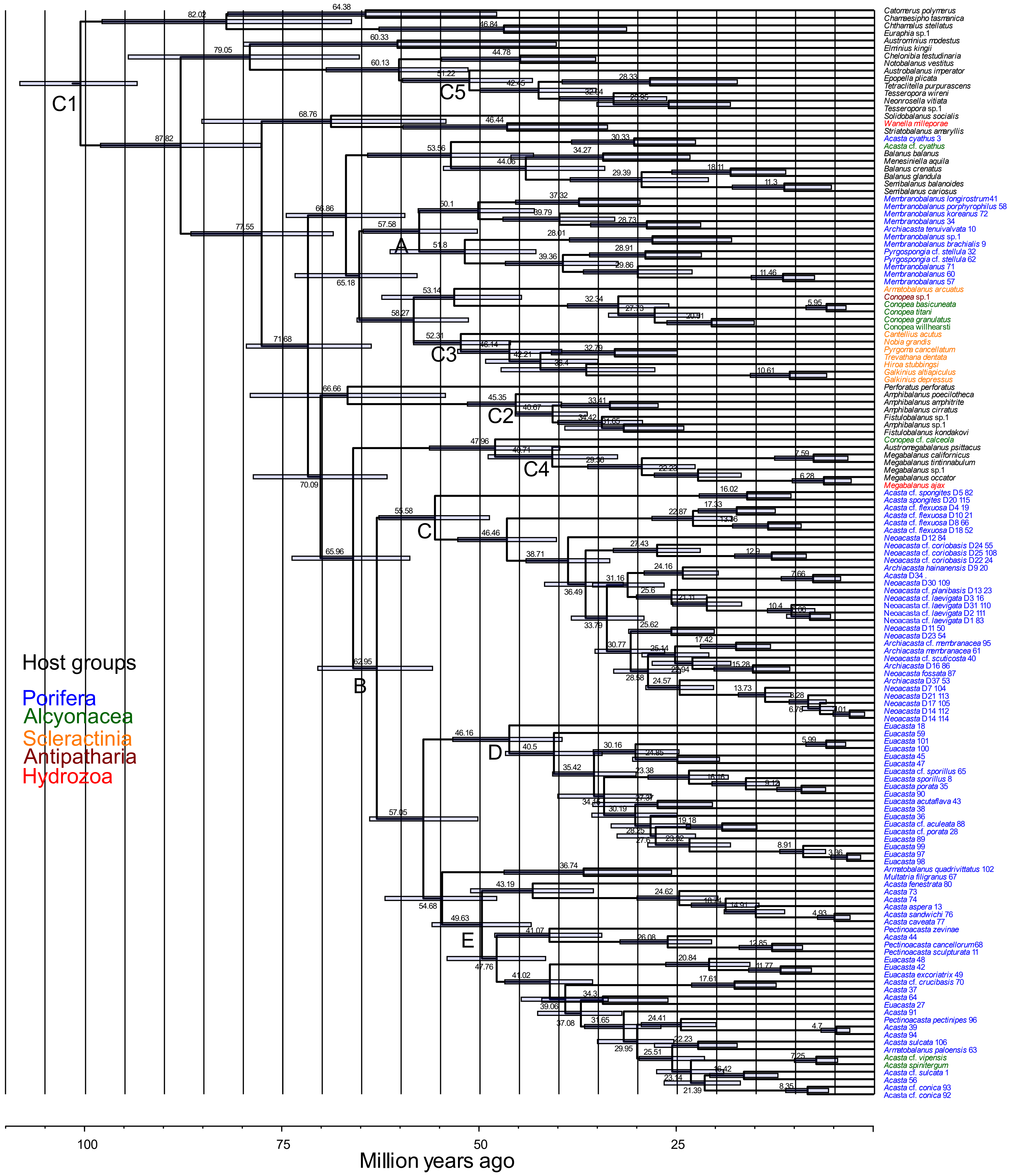

Figure 5.3. Bayesian chronogram of balanomorph radiation based on concatenated dataset. Node bars represent 95% high posterior density intervals. Calibrations at nodes C1–C5 are detailed in Table 5.2, nodes A–E represent clades as in Figures 5.1 and 5.2. Coloured tip labels indicate host group.

5.4. Discussion

The BI, ML and BEAST trees provided similar sets of well supported clades that group the sponge-inhabiting barnacles in three well-supported clades, two of which correspond with significant radiation events. The separation of *Membranobalanus* from the Acastinae is here justified and the two lineages are even shown to be widely separated. Various relationships inferred from the analyses including monophyly of subfamilies such as Megabalaninae and Amphibalaninae, and the paraphyly of *Semibalanus* and *Balanus* are congruent with previous molecular and morphological analyses (Pérez-Losada et al., 2008; Pérez-Losada et al., 2014; Pitombo, 2004).

5.4.1. Host usage

The analyses show that sponges have been independently colonised by barnacles three times, but only two of these have resulted in significant speciation events. The clade of *Acasta cyathus* and *A.* cf. *cyathus* may expand as morphologically similar species from the eastern Pacific and Atlantic Oceans are studied. As many representative genera of the Bryozobiinae were not sampled in this study additional colonisation events may also be yet to be discovered. The species within Clade A are found primarily in the Clionaida, but also the Haplosclerida and Biemnida. While a pattern with host phylogeny is not apparent, all hosts sampled here were soft and/or easily crumbled. *Membranobalanus* has previously been considered to be restricted to the Clionaida (Hosie et al., 2019; Van Syoc, 1988) and it is only the species that are assigned to the *Archiacasta* that have been identified from the other orders (but see section 5.4.3). A re-examination of the hosts from other studies is warranted to determine how broad the host range is for this group (e.g. Ilan et al., 1999; Pitriana et al., 2020; Wibowo et al., 2011).

Clade C contains the species inhabiting the order Dictyoceratida which were studied in Chapter 4, with the exception of the *Euacasta* species that are here found in Clade D. These *Euacasta* species are demonstrated here to inhabit multiple host orders and can be considered as relative generalists. Clade C has expanded beyond species just inhabiting dictyoceratids and now includes hosts of the orders Suberitida, Tethyida and Tetractinellida. Support for the internal nodes of this clade are not strong enough to draw conclusions on how these additional hosts impact on the trends documented in Chapter 4, but the clades restricted to the Dysideidae (*A. flexuosa* complex), Irciniidae (*N. coriobasis* complex) and Thorectidae (*N. laevigata* complex) still form well-supported clades. This indicates that sponge barnacle evolution has followed a pattern of an initial colonisation followed by a subsequent adaptive radiation across related hosts, prior to another jump that was documented in Chapter 4.

The members of Clades D and E inhabit a wider variety of sponge orders as well as two species found in soft corals (both in Clade E). Unfortunately, species inhabiting alcyonacean suborders Alcyoniina, such as *Acasta echinata* Hiro, 1937 have not been sampled during this study and the inclusion of more of the species transferred from *Conopea* by Kolbasov et al. (2016) in future studies will be necessary to conclude if the host shift from sponge to soft coral within the Acastinae happened just once or if the colonisation of different orders or families of Alcyonacea happened independently from different sponge-inhabiting groups.

5.4.2. Origins of symbiosis

Fossils attributed to the Acastinae have been found in European deposits dated to the Oligocene through to the Pliocene (Carriol, 2008) with the earliest known fossil, *Acasta sarda* De Alessandri, 1895*,* found in Sicily. The only recorded of fossil *Acasta* in Australia is that of *Acasta* cf. *cyathus*, which was identified from Miocene deposits in south eastern Australia (Buckeridge, 1985). The genus *Membranobalanus* is known from the Pliocene of the USA (Ross, 1999a), *Conopea* from the Miocene in Europe and Australia (Carriol & Schneider, 2016) and *Armatobalanus* fossils have been identified from lower Miocene deposits in New Zealand (Buckeridge, 1983). These fossil records are often disassociated shells with no indication of potential hosts, with the exception of the tentatively identified *Armatobalanus* sp. indet. found embedded in *Turbinaria* coral (Buckeridge, 1983), although the deposits where *A.* cf. *cyathus* was found has had a number of sponge species from the class Calcarea identified (McSweeney et al., 2019).

The phylogenetic results presented here made placing these fossils at appropriate nodes to calibrate the molecular clock problematic. The key issue is that the fossil remains do not allow for an accurate enough identification, relative to the phylogeny presented here. The estimated divergence dates based on the applied calibrations indicate that the Balanoidea diverged from the Coronuloidea and Eliminoidea approximately 88 mya (97–77 mya) in the late Cretaceous with the major balanoid groups diverging from each other by the beginning of the Palaeocene. The emergence of the Balanoidea, and the 'modern' sessile barnacles do not appear in the fossil record until the Eocene, approximately 20 my later, with groups such as *Solidobalanus*, *Kathpalmeria* and *Palaeobalanus* (Buckeridge, 1983; Ross, 1965). An estimated emergence of the Acastinae *sensu lato* of 63 mya, with a subsequent radiation beginning ~40 mya, predates the predominantly Miocene-Pliocene fossil record by over 30 million years. Clade A appears to be younger having an MRCA dated at approximately 58 mya, but fossils are only known from the Pliocene, 2.5 mya (Ross, 1999a). The main clade of *Conopea* is proposed to be even younger emerging approximately 32 mya in the early Oligocene.

The earliest balanomorph fossil is that of *Pachydiadema cretacea* (Withers, 1935) from the upper Cretaceous (83.6–72.1 mya) and is morphologically far removed from the balanoid forms that first appear in the Eocene (56–33.9 mya; Buckeridge, 1983; Chan et al., 2021). The proposed divergence dates are treated with caution in light of the present incongruence between them and that of the published fossil record. Additional data from both extant and extinct species record is needed to test the timing of the radiation that has led to the present-day diversity. However, the relative order in which groups emerged through time is congruent with the current knowledge of the fossil record.

The Acastinae appear to predate some groups such as the Balaninae, Megabalaninae and Amphibalaninae which are dated here as emerging 40–44 mya. Thus, demonstrating that the Acastinae are not a recently derived group but the result of a relatively early divergence event during the balanoid radiation. Interestingly, these latter two subfamilies are each sister to a lineage that contains a member of the Archaeobalaninae (*Conopea* cf. *calceola* and *Solidobalanus socialis*, respectively).

The emergence of the sponge barnacles coincides approximately with the radiation of other balanoid lineages such as the Pyrgomatidae. Fossil pyrgomatids first appear in the late Oligocene in the Western Atlantic and later in the Mediterranean, leading to the hypothesis that they originated in the Western Tethys during the Paleogene and spread through the Tethys seaway to what is now the Indo-Pacific (Baarli et al., 2017; Ross & Newman, 2000). Given the distribution of fossil Acastinae in Europe, perhaps a similar origin for the sponge-inhabiting barnacles is possible (Carriol, 2008). This hypothesis is supported in the present analysis by the lineage of the *A. spongites* complex, which diverged from other members of Clade C ~55.5 mya at the beginning of the Eocene and the Australian species shared an MRCA with the Mediterranean *A. spongites* ~16 mya. This coincides roughly with the closure of the Tethys Seaway, 20–14 mya (Bialik et al., 2019), which would have prevented geneflow and divided the population. As *A. spongites* has been reported from southern Africa and the western Pacific (Barnard, 1924; Ren, 1984), analysis of more specimens from across the range will be needed prior to a final conclusion. Including specimens of the other Atlantic and Eastern Pacific species, *A. cyathus*, *A. newmani* Van Syoc & Winther, 1999 and *N. scuticosta* (Weltner, 1887) may also show a similar biogeographic pattern and could support this hypothesis.

The jump from sponge to alcyonacean hosts has occurred at least once within the broader Acastinae, and this occurred ~7.25 mya. Expanded sampling of alcyonacean-inhabiting Acastinae is needed to ascertain if this host jump was the only such transition or if it has occurred independently multiple times. The clade of the *Acasta cyathus* complex is of similar age as that of *Conopea at* ~30 mya.

The examined symbiotic lineages demonstrate examples of colonisation followed by diversification. That the Pyrgomatidae radiated after colonising scleractinian corals has long been known (e.g. Anderson, 1992; Darwin, 1854; Ross & Newman, 1973), but prior to the extreme morphological adaptations seen in genera such as *Nobia* Sowerby, 1839 and *Galkinius* Perrault, 2014, a jump to colonising other cnidarians (Antipatharia and Alcyonacea) by one lineage led to a clade of species currently assigned to *Conopea* that has retained the so-called balanoid form of a 6-plated shell and opercular valves. This group diverged from the pyrgomatids approximately 58 mya and had jumped host groups by 32 mya and have subsequently radiated. Additional representation of pyrgomatid species particularly from *Cantellius* Ross & Newman, 1973 from the Megatrematinae Holthuis, 1982 and Ceratoconchiinae Newman & Ross, 1976 in future analyses would be needed when reassessing the classification of *Conopea* within the Pyrgomatidae.

The position of *Membranobalanus* is not clear within the current analyses as the relationship of this genus to the other lineages was only well supported by the ML analysis, but it appears that they could be sister to the Pyrgomatidae. What is presently clear is that despite the close morphological and ecological affinity with the Acastinae they are the result of a different colonisation event. Yu et al. (2020a) were the first to include *Membranobalanus* in a molecular phylogenetic study and the genus was recovered as sister to the Pyrgomatidae and *Conopea* clade, but it was similarly not well supported. Their inclusion of *Pyrgosopniga* within *Membranobalanus* is also supported here. It would appear that the lack of calcareous shell plates and the form of the opercular plates are a derived set of characters similar in progression to those seen in coral-inhabiting *Pyrgopsella* (Zullo, 1967) within the pyrgomatid clade of *Trevathana* Anderson, 1992 and *Neotrevathana* Ross, 1999b (Malay & Michonneau, 2014; Simon-Blecher et al., 2007). As such are a good example of convergent morphological evolution that has confoundedattempts at classifying it. A key host group of the *Membranobalanus* clade are the Clionaida, a group of sponges well known for their bioeroding of calcareous substrates. The genus *Cliona* in particular, is known to attack corals, and is host to a number of *Membranobalanus* species (Van Syoc, 1988). Given the close association this sponge group has with corals it is possible that this could explain the close relationship these barnacles have with the Pyrgomatidae.

5.4.3. Implications for classification

The presented phylogenies reinforce the results of many previous phylogenetic studies (Kolbasov et al., 2016; Malay & Michonneau, 2014; Pérez-Losada et al., 2008; Pérez-Losada et al., 2014; Pitombo, 2004; Simon-Blecher et al., 2007; Tsang et al., 2014; Yu et al., 2020a) as well as shedding new light on the relationships of the Balanoidea. The apparent conflict with the established classification shows that a need for revision of the balanoids is clear, but this chapter with its reliance on molecular data does not provide a clear alternative to the current arrangement. Key nodes between major clades are unresolved in the trees presented and many genera are not represented and many of those that are, were not recovered as monophyletic. Broader sampling of both species and genetic data combined with morphological data is required prior to making significant changes. This section will highlight some of the key areas where the present classification was not consistent with the presented phylogenies.

The Balanoidea as defined by Chan et al. (2021) was recovered as monophyletic, except for *Notobalanus vestitus* (Darwin, 1854), which was found to clade within the Coronuloidea. This placement shows a closer relationship to *Austrobalanus imperator* (Darwin, 1854), which had been recognised by Darwin (1854), and Pilsbry (1916) united them within *Balanus* (*Austrobalanus*) Pilsbry, 1916. However, Newman & Ross (1976) placed *N. vestitus* in *Notobalanus* Newman & Ross, 1976 when they transferred Austrobalanus to the Tetraclitidae (Gruvel, 1903). Buckeridge (1983, p. 121) points out similarities between *Notobalanus* (and other archaeobalanids) and members of the Coronuloidea. As members of the former Archaeobalanidae are dispersed across the phylogenetic trees presented here a potential hypothesis is that these groups represent relictual fauna (with ancestral morphotypes) and this would explain why these phylogenetically disparate groups could be classified together. As opposed to the shared morphological characters being the result of convergent evolution. To test this, future studies would need to include re-evaluating extinct fossil genera such as *Palaeobalanus* to better calibrate the sequence and timing of divergences in phylogenetic analyses.

The decision of Chan et al.'s (2021) to synonymise Archaeobalanidae with Balanidae is upheld, as neither family is recovered here as monophyletic in concordance with other phylogenetic studies (Pérez-Losada et al., 2008; Pérez-Losada et al., 2014; Yu et al., 2020a). Neither the families Pyrgomatidae or the Balanidae were supported as reciprocally monophyletic either, which is in agreement with the phylogeny presented in Yu et al. (2020a). Even the Archaeobalaninae was not supported here. This suggests the Balanoidea should either be reduced to containing a single family, Balanidae, or split further into additional families.

The focus in this chapter was to elucidate the relationships between the symbiotic groups within the Balanidae with particular attention to sponge and soft coral symbionts: Acastinae, Bryozobiinae, *Membranobalanus*, *Conopea* and the remainder of this section will be devoted to these groups.

5.4.3.1. Clade A *Membranobalanus*

Pyrgospongia was originally placed within the Pyrgomatidae owing to the loss of the calcareous wall plates and similarities in the opercular plates, which appears to be a case of convergent evolution with *Pyrgopsella* found in scleractinians and are therefore homoplasious. Therefore, this genus should not be considered a member of the Pyrgomatidae in the present sense.

The morphology of the species identified as *Archiacasta* within this clade are consistent with the diagnosis of *Membranobalanus*. The two *Archiacasta* are almost indistinguishable from each other morphologically, and either could be ascribed to Broch's (1947) description of *A. tenuivalvata*, which was described based on empty shells. The short rostrum described by Broch is a variable character in the present specimens and is probably influenced by the positioning within and growth of the host. As such, the two species can simply be transferred to *Membranobalanus.*

Two morphological groups have been identified within *Membranobalanus* based on the armament of cirrus IV and details of the scutum (Hosie et al., 2019; Van Syoc, 1988). In the present phylogeny these groups do not form separate lineages, with *M. koreanus* nested within the clade with members of the unarmed species. Obtaining sequences of the type species, *M. declivis* (Darwin, 1854), and other 'American' species would be necessary in determining if any further nomenclatural action is required.

5.4.3.2. Clade B Acastinae

The Acastinae was shown to be polyphyletic with one clade, containing *A. cyathus* and *A.* cf. *cyathus*, sister to a clade containing members of the Concaviinae, Balaninae and Semibalaninae. These species warrant being placed in a new genus, but this genus would currently be considered incertae sedis within the Balanidae. *Acasta cyathus* has been reported from the Atlantic (Darwin, 1854), western Indian (Ren, 1989) and Pacific Oceans (Jones et al., 2000) and representation from across this geographic range, along with the morphologically allied *A. newmani*, will be needed to elucidate where to place and this group. A close re-examination is also required to diagnose this genus based on synapomorphies to differentiate it from the Acastinae.

The remaining Acastinae are found in three well-supported clades that indicate significant change to the generic makeup of the subfamily. Whether the five current genera are reduced to three or if further subdivision within these clades is warranted requires more molecular data and the inclusion of morphological data from additional species. This clade also includes a subclade of *Armatobalanus* spp. and *Multatria filigranus.* These species indicate that potentially intermediate forms, from a host association perspective, are still extant and that at least some species of the Bryozobiinae should be considered to belong to the Acastinae. An alternative interpretation is that these intruding genera indicate that the Acastinae should be split into two or three groups. The relationship between Clades

D and E is not well resolved and should further division be required it is unclear if these would necessarily still be contained within a single clade.

5.4.3.3. Clade C *Acasta, Archiacasta* and *Neoacasta*

The placement of the *Acasta spongites* complex as sister to a large clade containing the type species *Neoacasta glans* and *Archiacasta membranacea* suggests that these genera would need to be synonymised within *Acasta*. The basis in this clade is highly variable and ranges from flat to deeply cupped, fully membranous through to fully calcified, and with complicated perforations, showing that the characters of the basis are generally not of value above species level. All species in this clade lack the strong hooked teeth on cirrus IV, but many species have smaller erect spines. This group also lacks the membranous windows between the wall plates.

5.4.3.4. Clade D *Euacasta*

This clade is relatively neat compared to the others as all members are easily identified as belonging to the *Euacasta* (i.e. having an exceptionally narrow carinolatus). It is unclear if the type species, *E. dofleini* (Krüger, 1911), has been sampled in this study, owing to difficulty with definitively identifying this species from the varying accounts in the literature (Krüger, 1911; Ren, 1984; Rosell, 1972). This should be a priority species to revise based on historic and contemporary specimens. Based on the morphological similarity of some of the species within this clade to *E. dofleini*, it is expected that this clade would ultimately retain *Euacasta* as the genus for now. All species assigned to this clade have strong hooked teeth and some also bear erect spines on cirrus IV, but further species presently assigned to *Euacasta* have been described without these teeth. Ideally, species lacking teeth such as *E. tabachniki* (Kolbasov, 1990) need to be sequenced to test the constancy of these characters within this clade.

5.4.3.5. Clade E *Pectinoacasta*

This clade contains the remaining Acastinae species including representatives of the Alcyonacean-inhabiting *Acasta*, the *Pectinoacasta* (including the type species *P. pectinipes*) and four species that are identifiable as being members of *Euacasta.* Should this clade be considered as a single genus then the members would all be referred to *Pectinoacasta.* However, defining and diagnosing this group would prove problematic owing to the morphological characters seen within this group. Certainly, the characters of carinolatus width, basis shape and calcification, sculpture of the tergum and cirral armament used to diagnose these genera are intermingled within this clade. *Armatobalanus palaoensis* (Hiro, 1937a) is an interesting case in that it should have been originally placed within *Acasta* as even in the original description Hiro describes this species as being embedded within the thin encrusting sponge and not attached to the underlying bivalve. The placement of the alcyonacean-inhabiting species in this clade supports the results of Kolbasov et al. (2016) and Van Syoc (2014).

5.4.3.6. *Conopea*

Members of *Conopea* were recovered within the broader Pyrgomatidae along with *Armatobalanus allium* as seen in other studies (Yu et al., 2020a) as well as sister to the Megabalaninae (Pérez-Losada et al., 2014). The present study did not, and neither did the previous studies, include the type species *C. galeata* (Linneaus, 1771), without which it is difficult to determine which group would retain the genus name. The morphological phylogeny of Kolbasov et al. (2016) does not provide a clear indication of further subdivision within *Conopea* on morphological grounds. The implication is that the definition of the Pyrgomatidae needs to be broadened to include these species. Interestingly, the association of *Conopea* with the Megabalaninae was suggested by Darwin (1854) who doubtfully placed *Megabalanus stultus* (Darwin, 1854) within his Section B along with the members of what are now *Conopea.* He remarked that *M. stultus* and *M. ajax* (both symbionts with the hydrozoan *Millepora*) formed intermediates between the two groups. A potential morphological link is that *C. calceola* has parietal and basal tubes that could be used as a basis for inclusion within the similarly tubiferous Megabalaninae.

5.5. Conclusions

The analyses described herein indicate that the evolution of symbiosis within the Balanoidea has occurred independently in several lineages but has only resulted in significant adaptive radiations twice. The other colonisation event seem to have had relatively limited success so far, or perhaps the species are no longer extant. The main Acastinae clade represents the greatest of these adaptive radiations. The colonisation of sponges occurred relatively early within the radiation of balanoid barnacles and predates the emergence of other subfamilies such as the Megabalaninae.

The generic arrangement within the Acastinae is not reflected in the phylogeny and it would seem that only three genera may be warranted. While some species could be simply transferred to different genera e.g. *Archiacasta tenuivalvata* to *Membranobalanus*, others will require significant re-evaluation of related groups e.g. the *A. cyathus* complex*.*

Although the phylogenies demonstrated some interesting relationships within the Balanoidea, the statistical supports within the phylogenetic analyses are not strong enough to simply conclude that the trees represent an accurate representation of the evolutionary history of these barnacles. Broader sampling of species and genera alongside additional molecular data in the form of more loci or more advanced methods such as single nucleotide polymorphisms, ultra-conserved elements and mito- or full genomes alongside morphological data are required to provide a more robust phylogeny.

5.6. References

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5.7. Chapter 5 supplementary information

Table S5.1. Evolutionary models selected for maximum likelihood analysis by ModelFinder, as implemented with IQTree webserver.

Model	**Bayesian score**	**Partition**
TVM+F+I+G4	42889.586	12S
TN+F+I+G4	20563.989	H3
TIMe+I+G4	12366.748	COI 1st & 2nd codons
TIM3+F+G4	48364.115	COI 3rd codon
TIM2+F+I+G4	35328.474	RPII
GTR+F+I+G4	28344.422	28S

S5.2 Command block used for Bayesian inference analysis implemented in MrBayes 3.6.

```
Begin MrBayes;
charset 12S = 1-518;
Charset H3 = 519-845;
Charset COI1 = 847-1500\3 848-1500\3;
Charset COI3 = 846-1500\3;
Charset RPII = 1501-2424;
Charset 28S = 2425-3569;
partition by_gene = 6: 12s, H3, COI1, COI3, RPII, 28s;
set partition=by_gene;
lset Nst=mixed rates=invgamma ngammacat=4;
prset brlenspr=unconstrained:gammadir(1.0,0.1,1.0,1.0) shapepr=exponential(10.0);
mcmc ngen=11000000 burninfrac=0.25 samplefreq=200 printfreq=1000 nchains=4 temp=0.2
savebrlens=yes starttree=random;
set seed=22702;
sumt burnin=500 contype=Allcompat;
sump burnin=500;
End;
```

Chapter 6. General discussion

This thesis describes the application of molecular sequence data to explore and answer questions on the taxonomy, host dynamics and evolution of barnacles symbiotic with sponges. Such methods provide a source of data that is character rich and independent from the effects of an organism's life history that may influence the morphology, ecology and biogeography. In this final discussion I bring together the main themes and findings of the individual research chapters to address the significance and limitations of the research as a whole. This discussion will be followed by an exploration of future directions that will further the work begun here and answer some of the new questions that have arisen in the process. Several main findings are summarized below.

6.1. Evolutionary origins

Through this study the evolutionary history of sponge-inhabiting barnacles may be traced back to three independent sponge colonisation events. The evolution of the commensal lifestyle occurred once for the main Acastinae Kolbasov, 1993 clade, once for the *Membranobalanus* Hoek, 1913 and *Pyrgospongia* Achituv & Blecher, 2006 clade and lastly with the clade of the *Acasta cyathus* Darwin, 1854 complex. Within the Acastinae clade three clear lineages emerged and subsequently radiated and represent the most successful of these colonisation events, both in terms of the number of extant species and the range of host species colonised across the group.

According to the molecular dating analyses presented in Chapter 5 (Figure 5.3), the first two transitions occurred near the Cretaceous-Paleogene boundary and the extinction event that led to the loss of an estimated 75% of species globally (Jablonski, 1994). The impacts on the marine environment during this event heavily affected plankton feeding communities (Robertson et al., 2013) and correspondingly reduced the diversity and abundance of barnacles in the fossil record (Brezina et al., 2017; Chan et al., 2021; Foster & Buckeridge, 1987; Gale & Sørensen, 2015; Newman et al., 1969). The estimated age indicates an early origin relative to the broader radiation of the Balanoidea, which began in the late Cretaceous. The radiation of the Acastinae subsequently occurs from the Eocene and is likely still ongoing. These predictions predate the appearance of related groups in the fossil record, which for the broader Balanoidea appear in the Eocene (Buckeridge, 1983; Chan et al., 2021) and the earliest fossils attributed to the Acastinae occur in the Oligocene and are most diverse in the Miocene (Carriol, 2008).

Kolbasov (1993) proposed that sponge symbiosis began with ancestral Acastinae settling onto sponges as well as other substrates, before becoming embedded and dependent on sponges. An alternative proposal by Van Syoc and Newman (2010) for the Bryozobiinae requires that barnacles are overgrown by encrusting sponges while still cemented to the underlying substrate. Larval settlement of *Euacasta dofleini* (Krüger, 1911), as documented by Yu et al. (2020b) showed the cyprid settling onto the surface of the sponge host and not burrowing into it. The inclusion in Chapter 5 of *Multatria* Van Syoc & Newman, 2010 and a sponge associated *Armatobalanus* Hoek, 1913 within the Acastinae clade suggests that the latter pathway is likely and that directly settling onto the sponge was a step subsequent to the initial evolution of a sponge association. Once the association with sponge transitioned from facultative to obligate then direct settlement may have evolved three times within the Acastinae clade. Inclusion of additional Bryozobiinae into phylogenetic analyses will provide better understanding of this aspect of sponge-barnacle evolution.

6.2. Host driven species richness

Prior to this study the Australian barnacle fauna was known to be represented by approximately 300 species and about half of these belong to the sessile Balanomorpha (ABRS, 2021; Jones, 2012). The original proposal for this PhD estimated that potentially there were an additional 40 species more than the roughly 20 known species symbiotic with sponges, with an expectation that at least five would be new to science and need to be described. Using DNA barcodes to provide an initial assessment of sponge-inhabiting barnacles (presented in Chapter 2) revealed that there were potentially over 100 species of sponge-specialists, of which more than 50 are considered undescribed. This is a remarkable increase in species and raises the question as to how this has arisen.

The key driver for sponge barnacle species richness appears to be in the restricted range of hosts any barnacle species can colonise. While restricted host use in sponge barnacles has been documented previously (Van Syoc et al., 2015), the genetic analyses used in this research were able to demonstrate that clades of closely related barnacles are found in closely related hosts (Chapter 4). Thus, host use is not random, and is instead phylogenetically conserved. This restriction can be explained in part by assortative mating that has resulted from barnacles only being able to mate with adjacent barnacles on the same host individual as they are not broadcast spawners.

Generally speaking, the more heterogenous an environment is the more species will be found inhabiting it (McIntosh, 1985). The conclusion here is that Australia's diverse sponge fauna is highly heterogenous and presents a remarkable range of individual niches from which the observed barnacle adaptive radiation has been facilitated. While this may explain how the present diversity is maintained, what is still a mystery is what drives barnacles to colonise new hosts.

6.3. Future directions

Since the beginning of this thesis a total of 17 sponge and soft coral inhabiting species of the Acastinae and *Membranobalanus* have been described from Taiwan, Thailand, Philippines, and Australia. This marks the beginning of a period of rapid species discovery that has been facilitated by the application of molecular data to help determine species-specific diagnostic characters by controlling for the confounding effects of intra-specific variation and conserved morphological characters (Hosie et al., 2019; Hosie et al., 2021; Van Syoc et al., 2014; Yu et al., 2017a; Yu et al., 2020a; Yu et al., 2016; Yu et al., 2017b; Yu et al., 2020c). This thesis presents data that will fuel ongoing species descriptions for many years to come. However, the task to describe and re-describe all species delimited in the present study will require additional research to ensure a rigorous approach that maximises utility without further confusion with the historical data.

While there is temptation to simply work on the new discoveries, there is a strong need to undertake a significant amount of taxonomic housekeeping. Numerous species have not been reported on since their original description, and some of the more commonly reported species are likely the result of misidentification (see Chapter 3 for discussion on *A. fenestrata* Darwin, 1854). Attempts to seek out type specimens alongside contemporary topotypic material continue to be needed in the molecular age to confidently assign both haplotypes and morphotypes to species names. Also, the importance of accurate host identification cannot be understated. Without these processes the risk of establishing species destined for synonymy is greatly elevated.

All questions addressed in this thesis would benefit from the inclusion of barnacles from a combination of a broader geographic and host range. It is anticipated that further sampling from eastern and southern Australia will discover additional species. Despite many specimens being housed in collections across Australia, these regions are under-represented in the molecular analyses because sequencing failed for many of these owing to preservation history or age, leading to degraded DNA that was not able to be amplified using standard means. The Western Australian specimens, for the most part, were collected and preserved with this project in mind.

While some species were able to be sourced and sequenced from outside Australia e.g. *Acasta spongites* (Poli, 1791) from the Mediterranean and *Archiacasta membranacea* (Barnard, 1924) from South Africa, the study would have benefited from specimens from adjacent regions such as south east Asia, which was considered to be the centre of biodiversity by Kolbasov (1993). A broader geographic scope would be able to provide greater context for the evolution of the Australian fauna.

For the analyses on host usage in Chapter 4 the limited geographic scope was a strength, as it minimised the potential issues of isolation by distance, which could confound the analyses. This was particularly important when determining host specificity as genetic isolation in sympatry is easily explained when barnacles are inhabiting separate host species. While it is clear that there are groups of species within Australia with clear host-driven lineages, there are also sudden jumps to unrelated hosts. These are in the form of jumps between different families and orders, as well as different phyla. What drives these jumps is still unknown, perhaps there are grades of host use that simply have not yet been sampled, which could be resolved with including specimens outside Australia. For the relatively generalist species that are able to inhabit distantly related sponge species there will be other factors that determine host selection, such as spiculation of host tissues (Yu et al., 2020b). Another avenue to explore is the role of sponge biochemistry in explaining the phylogenetic patterns shown in this thesis, as classes of secondary metabolites show a phylogenetic signal (Galitz et al., 2021).

One aspect that was not explored in this thesis was the functional morphology of some of the shell characters of the barnacles. The role of the large membranous windows between shell plates seen in some species such as *A. fenestrata* and *A. caveata* Hosie, Fromont, Munyard and Jones, 2021, would make for a worthwhile study, especially to determine if these represent a strategy to reduce the cost of shell construction or if the membranes serve some purpose for transfer of metabolites as suggested by Kolbasov (1993). In the current study they appear to have evolved independently numerous times within Clade E.

The results of Chapter 5 did not support the current classification of the predominantly sponge-inhabiting Acastinae, *Membranobalanus* or *Bryozobiinae* nor did it provide clear answers to how they or the broader Balanoidea should be classified. Primarily, support values were not strong enough to form the base for a new classification. Future efforts should work to redress this shortcoming. This would likely be achieved through better genetic coverage, either by the use of additional loci or through advanced next-generation techniques that have now come to dominate phylogenetics in the time since this project began. Although Sanger sequencing is still common practice in barnacle studies (e.g. Chan et al., 2018; Høeg et al., 2019; Yu et al., 2020b) sequencing technology has outpaced the methods used in this thesis. Ever larger and complex datasets are being economically produced and analysed, for crustacean biodiversity and phylogenetic research (de Mazancourt et al., 2019; Gan et al., 2020; Yang et al., 2021; Yuan et al., 2020).

The present classification within the Balanoidea is largely based on morphological data, and much of it has not been tested using phylogenetic methods. The phylogenetic analyses to date, indicate that convergent evolution has led to numerous homoplasious, or perhaps symplesiomorphic, characters that have confounded interpretations by previous authors (Pérez-Losada et al., 2014; Pitombo, 2004; Simon-Blecher et al., 2007; Tsang et al., 2015). Examples of this are the degree of calcification of the basis, shape of the labrum, and fusion of wall or opercular plates. However, morphological data should not be simply discounted, and future phylogenies should incorporate a careful re-examination of all data sources. Inclusion of morphological analyses would also provide support and context to the branching patterns of the phylogenetic trees. The amount of paraphyly demonstrated by family, subfamily and genus level groupings suggests that species coverage, particularly of type species, should also be increased, as having one or a few representatives of some genera may not be sufficient. Further Bryozobiinae genera such as *Bryozobia* Ross & Newman, 1996 and *Poratria* Van Syoc & Newman, 2010 and further representation from *Armatobalanus* are important to understand if they should be included within Acastinae, or in part at least, belong to a distinct evolutionary lineage. For *Membranobalanus* and *Conopea* the inclusion of additional pyrgomatid subfamilies such as the Ceratoconchiinae and Megatrematinae would provide more certainty for their position sister and nested within the Pyrgomatidae, respectively.

The overarching aim in this study was to understand the diversity of sponge-inhabiting barnacles in Australia using genetic sequence data to identify species, explore host usage and reconstruct evolutionary history. This attempt at identifying the diversity of barnacle species in Australia led to the conclusion that, even though around 100 species were identified, there are likely many more to be discovered as more samples are examined. This expectation is largely driven by the unexpected level of host specificity exhibited by the studied specimens. The restricted host use also explains, in part, the small clades of barnacles inhabiting related species of sponges, indicating that the barnacles have adapted to inhabiting sponges with phylogenetically shared traits and that different groups of sponges present different barriers to settling barnacles. The evolutionary trends in this thesis would not have been as accessible without the application of molecular phylogenetics.

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Appendix I. Specimens examined, host identifications and locality details. Sorted by identification and primary species hypothesis (PSH).

Unidentified hosts indicated as unknown in the host family column. NMITS = National Institute of Water and Atmospheric Research, Wellington, QM = Queensland Museum, SAMA = South Australian Museum, SMBL = Seto Marin Biological Laboratory, WAM = Western Australian Museum, , ZMUC = Zoological Museum University of Copenhagen..

Specimen Accession	Family	Identification	PSH	Host accession	Host Order	Host family	Host identification	Locality	Coordinates	Depth
SAMAC8689	Balanidae	*Acasta*	26	SAMA S1067	Haplosclerida	Phloeodictyidae	*Siphonodictyon*	Ward Islands, SA	-33.7381, 134.2803	6.6
WAMC55326	Balanidae	*Acasta*	37	WAMZ83224	Haplosclerida	Chalinidae	*Haliclona* KMB3	Clerke Reef, WA	-17.317, 119.3838	12
WAMC55328	Balanidae	*Acasta*	37	WAMZ83224	Haplosclerida	Chalinidae	*Haliclona* KMB3	Clerke Reef, WA	-17.317, 119.3838	12
WAMC55329	Balanidae	*Acasta*	37	WAMZ83224	Haplosclerida	Chalinidae	*Haliclona* KMB3	Clerke Reef, WA	-17.317, 119.3838	12
WAMC55390	Balanidae	*Acasta*	37	WAMZ83224	Haplosclerida	Chalinidae	*Haliclona* KMB3	Clerke Reef, WA	-17.317, 119.3838	12
WAMC55391	Balanidae	*Acasta*	37	WAMZ83224	Haplosclerida	Chalinidae	*Haliclona* KMB3	Clerke Reef, WA	-17.317, 119.3838	12
WAMC61428	Balanidae	*Acasta*	39		Unknown sponge			Ah Chong Island, WA	-20.5193, 115.5677	16.5
WAMC61429	Balanidae	*Acasta*	39		Unknown sponge			Ah Chong Island, WA	-20.5193, 115.5677	16.5
WAMC61430	Balanidae	*Acasta*	39		Unknown sponge			Ah Chong Island, WA	-20.5193, 115.5677	16.5
WAMC55346	Balanidae	*Acasta*	39	WAMZ65150	Haplosclerida	Chondropsidae	*Chondropsis* sp.1	Onslow, WA	-21.5263, 115.0922	12
WAMC71740	Balanidae	*Acasta*	39	WAMZ86870	Haplosclerida	Chondropsidae	*Chondropsis* sp.1	Dampier Archipelago, WA	-20.618, 116.464	16
WAMC71767	Balanidae	*Acasta*	39	WAMZ86867	Haplosclerida	Halichondriidae	*Chondropsis* sp.1	Dampier Archipelago, WA	-20.618, 116.464	16
WAMC61363	Balanidae	*Acasta*	39	WAMZ84194	Poecilosclerida	Desmacididae	*Desmacidon*?	Ah Chong Island, WA	-20.5193, 115.5677	16.5
WAMC61364	Balanidae	*Acasta*	39	WAMZ84194	Poecilosclerida	Desmacididae	*Desmacidon*?	Ah Chong Island, WA	-20.5193, 115.5677	16.5
WAMC61365	Balanidae	*Acasta*	39	WAMZ84194	Poecilosclerida	Desmacididae	*Desmacidon*?	Ah Chong Island, WA	-20.5193, 115.5677	16.5
WAMC58859	Balanidae	*Acasta*	44	WAMZ84299	Unknown sponge			South Murion Island, WA	-21.6659, 114.3312	17
WAMC66661	Balanidae	*Acasta*	44	WAMZ97084	Scopalinida	Scopalinidae	*Styliisa flabelliformis*	South Muiron Island, WA	-21.6835, 114.311	18
WAMC67755	Balanidae	*Acasta*	44	WAMZ97077	Scopalinida	Scopalinidae	*Stylissa flabelliformis*	South Muiron Island, WA	-21.6835, 114.311	18
WAMC55243	Balanidae	*Acasta*	44		Tetractinellida	Geodiidae	*Melophlus sarasinorum*	Ashmore Reef, WA	-12.2372, 123.16	15
WAMC67735	Balanidae	*Acasta*	56	WAMZ97116	Poecilosclerida	Crambeidae	*Monanchora*	Exmouth Gulf, WA	-21.8202, 114.2101	25
WAMC67736	Balanidae	*Acasta*	56	WAMZ97116	Poecilosclerida	Crambeidae	*Monanchora*	Exmouth Gulf, WA	-21.8202, 114.2101	25
WAMC67769	Balanidae	*Acasta*	56	WAMZ97120	Poecilosclerida	Crambeidae	*Monanchora*	Exmouth Gulf, WA	-21.8202, 114.2101	25
WAMC67770	Balanidae	*Acasta*	56	WAMZ97120	Poecilosclerida	Crambeidae	*Monanchora*	Exmouth Gulf, WA	-21.8202, 114.2101	25
WAMC71875	Balanidae	*Acasta*	56		Poecilosclerida	Microcionidae	*Clathria* (*Thalyssias*)	Rottnest Island, WA	-32.0148, 115.5588	12
WAMC71876	Balanidae	*Acasta*	56		Poecilosclerida	Microcionidae	*Clathria* (*Thalyssias*)	Rottnest Island, WA	-32.0148, 115.5588	12
WAMC71877	Balanidae	*Acasta*	56		Poecilosclerida	Microcionidae	*Clathria* (*Thalyssias*)	Rottnest Island, WA	-32.0148, 115.5588	12
WAMC61342	Balanidae	*Acasta*	64		Unknown sponge			Trimouille Island, WA	-20.372, 115.564	11
WAMC61343	Balanidae	*Acasta*	64		Unknown sponge			Trimouille Island, WA	-20.372, 115.564	11
WAMC61344	Balanidae	*Acasta*	64		Unknown sponge			Trimouille Island, WA	-20.372, 115.564	11
WAMC61345	Balanidae	*Acasta*	64		Unknown sponge			Trimouille Island, WA	-20.372, 115.564	11
WAMC61346	Balanidae	*Acasta*	64		Unknown sponge			Trimouille Island, WA	-20.372, 115.564	11
WAMC58808	Balanidae	*Acasta*	64	WAMZ84229	Haplosclerida	Callyspongiidae	*Arenosclera*	Montebello Islands, WA	-20.384, 115.539	11
WAMC58809	Balanidae	*Acasta*	64	WAMZ84229	Haplosclerida	Callyspongiidae	*Arenosclera*	Montebello Islands, WA	-20.384, 115.539	11
WAMC58810	Balanidae	*Acasta*	64	WAMZ84229	Haplosclerida	Callyspongiidae	*Arenosclera*	Montebello Islands, WA	-20.384, 115.539	11
WAMC58811	Balanidae	*Acasta*	64	WAMZ84229	Haplosclerida	Callyspongiidae	*Arenosclera*	Montebello Islands, WA	-20.384, 115.539	11
WAMC67777	Balanidae	*Acasta*	64	WAMZ97017	Haplosclerida	Callyspongiidae	*Callyspongia*	Exmouth Gulf, WA	-21.871, 114.159	6
WAMC46001	Balanidae	*Acasta*	64	WAMZ28870	Haplosclerida	Chalinidae	*Haliclona* NG4	Ningaloo Reef, WA	-22.6626, 113.6396	10
WAMC55367	Balanidae	*Acasta*	64	WAMZ82348	Haplosclerida	Chalinidae	*Haliclona* sp.7	Hayman Rock, WA	-21.6705, 114.6675	15
WAMC55368	Balanidae	*Acasta*	64	WAMZ82348	Haplosclerida	Chalinidae	*Haliclona* sp.7	Hayman Rock, WA	-21.6705, 114.6675	15
WAMC58346	Balanidae	*Acasta*	64	WAMZ84197	Haplosclerida	Chalinidae	*Haliclona BAR39*	Ah Chong Island, WA	-20.5193, 115.5677	16.5
WAMC71805	Balanidae	*Acasta*	64		Haplosclerida	Chalinidae	*Haliclona BAR39*	Dampier Archipelago, WA	-20.618, 116.464	16
WAMC58789	Balanidae	*Acasta*	73	WAMZ84258	Haplosclerida	Chalinidae	*Haliclona* (*Reniera*)	Bluebell Island, WA	-20.4034, 115.5247	8
WAMC58790	Balanidae	*Acasta*	73	WAMZ84258	Haplosclerida	Chalinidae	*Haliclona* (*Reniera*)	Bluebell Island, WA	-20.4034, 115.5247	8
WAMC58791	Balanidae	*Acasta*	73	WAMZ84258	Haplosclerida	Chalinidae	*Haliclona* (*Reniera*)	Bluebell Island, WA	-20.4034, 115.5247	8
WAMC71836	Balanidae	*Acasta*	73	WAMZ84258	Haplosclerida	Chalinidae	*Haliclona* (*Reniera*)	Bluebell Island, WA	-20.4034, 115.5247	8
WAMC61358	Balanidae	*Acasta*	74		Unknown sponge			South Murion Island, WA	-21.6659, 114.3312	17
WAMC61403	Balanidae	*Acasta*	74		Unknown sponge			Montebello Islands, WA	-20.388, 115.4923	22

Specimen Accession	Family	Identification	PSH	Host accession	Host Order	Host family	Host identification	Locality	Coordinates	Depth
WAMC71820	Balanidae	*Acasta*	74	WAMZ86860	Haplosclerida	Callyspongiidae	*Callyspongia*	Dampier Archipelago, WA	-20.3511, 116.8353	22.9
WAMC71917	Balanidae	*Acasta*	75		Unknown sponge			Amathole Region, South Africa	-32.83, 28.4593	87
WAMC71897	Balanidae	*Acasta*	75	WAMZ86929	Tetractinellida	Pachastrellidae	*Pachastrella* sp.2	Amathole Region, South Africa	-32.8166, 28.45	87
WAMC55186	Balanidae	*Acasta*	91	WAMZ82035	Poecilosclerida	Microcionidae	*Clathria vulpina*	Sultan Reef, WA	-21.4, 115.0897	19.3
WAMC55187	Balanidae	*Acasta*	91	WAMZ82035	Poecilosclerida	Microcionidae	*Clathria vulpina*	Sultan Reef, WA	-21.4, 115.0897	19.3
WAMC71854	Balanidae	*Acasta*	91	WAMZ86862	Poecilosclerida	Microcionidae	*Clathria* (*Thalyssias*) cf. *abietina*	Dampier Archipelago, WA	-20.5852, 116.5944	17
WAMC71862	Balanidae	*Acasta*	91	WAMZ86862	Poecilosclerida	Microcionidae	*Clathria* (*Thalyssias*) cf. *abietina*	Dampier Archipelago, WA	-20.5852, 116.5944	17
WAMC55369	Balanidae	*Acasta*	94		Haplosclerida	Chondropsidae	*Chondropsis*	Hayman Rock, WA	-21.6706, 114.6676	15.1
WAMC55370	Balanidae	*Acasta*	94		Haplosclerida	Chondropsidae	*Chondropsis*	Hayman Rock, WA	-21.6706, 114.6676	15.1
WAMC71741	Balanidae	*Acasta*	94	WAMZ86870	Haplosclerida	Chondropsidae	*Chondropsis*	Dampier Archipelago, WA	-20.618, 116.464	16
WAMC54239	Balanidae	*Acasta*	103	WAMZ69883	Polymastiida	Polymastiidae	*Polymastia* KMB1	Ashmore Reef, WA	-12.2623, 122.9848	1
WAMC58812	Balanidae	*Acasta aspera*	13	WAMZ84171	Poecilosclerida	Coelosphaeridae	*Lissodendoryx* (*Acanthodoryx*) KMB1	Ah Chong Island, WA	-20.4992, 115.5899	14.5
WAMC58813	Balanidae	*Acasta aspera*	13	WAMZ84171	Poecilosclerida	Coelosphaeridae	*Lissodendoryx* (*Acanthodoryx*) KMB1	Ah Chong Island, WA	-20.4992, 115.5899	14.5
WAMC58815	Balanidae	*Acasta aspera*	13	WAMZ84171	Poecilosclerida	Coelosphaeridae	*Lissodendoryx* (*Acanthodoryx*) KMB1	Ah Chong Island, WA	-20.4992, 115.5899	14.5
WAMC71837	Balanidae	*Acasta aspera*	13	WAMZ84171	Poecilosclerida	Coelosphaeridae	*Lissodendoryx* (*Acanthodoryx*) KMB1	Ah Chong Island, WA	-20.4992, 115.5899	14.5
WAMC71838	Balanidae	*Acasta aspera*	13	WAMZ84171	Poecilosclerida	Coelosphaeridae	*Lissodendoryx* (*Acanthodoryx*) KMB1	Ah Chong Island, WA	-20.4992, 115.5899	14.5
WAMC55057	Balanidae	*Acasta aspera*	13	WAMZ39845	Poecilosclerida	Crellidae	*Crella* (*Yvesia*) *spinulata*	Rottnest Island, WA	-31.9738, 115.537	10
WAMC58741	Balanidae	*Acasta aspera*	13	WAMZ28859	Poecilosclerida	Crellidae	*Crella* (*Yvesia*) *spinulata*	Ningaloo Reef, WA	-22.6758, 113.6877	0
WAMC58742	Balanidae	*Acasta aspera*	13	WAMZ28859	Poecilosclerida	Crellidae	*Crella* (*Yvesia*) *spinulata*	Ningaloo Reef, WA	-22.6758, 113.6877	0
WAMC58743	Balanidae	*Acasta aspera*	13	WAMZ28859	Poecilosclerida	Crellidae	*Crella* (*Yvesia*) *spinulata*	Ningaloo Reef, WA	-22.6758, 113.6877	0
WAMC58835	Balanidae	*Acasta aspera*	13	WAMZ84165	Poecilosclerida	Hymedesmiidae	*Hamigera* PB1	Ah Chong Island, WA	-20.4992, 115.5899	14.5
WAMC58837	Balanidae	*Acasta aspera*	13	WAMZ84165	Poecilosclerida	Hymedesmiidae	*Hamigera* PB1	Ah Chong Island, WA	-20.4992, 115.5899	14.5
WAMC58838	Balanidae	*Acasta aspera*	13	WAMZ84165	Poecilosclerida	Hymedesmiidae	*Hamigera* PB1	Ah Chong Island, WA	-20.4992, 115.5899	14.5
WAMC67716	Balanidae	*Acasta caveata*	77	WAMZ97140	Haplosclerida	Niphatidae	*Gelliodes* KMB1	Exmouth Gulf, WA	-21.821, 114.209	22
WAMC67717	Balanidae	*Acasta caveata*	77	WAMZ97140	Haplosclerida	Niphatidae	*Gelliodes* KMB1	Exmouth Gulf, WA	-21.821, 114.209	22
WAMC55066	Balanidae	*Acasta* cf. *aspera*	69	WAMZ39848	Haplosclerida	Phloeodictyidae	*Oceanapia* cf. sp.7	Rottnest Island, WA	-31.9738, 115.537	10
WAMC55067	Balanidae	*Acasta* cf. *aspera*	69	WAMZ39849	Haplosclerida	Phloeodictyidae	*Oceanapia* cf. sp.7	Rottnest Island, WA	-31.9738, 115.537	10
QMG333433	Balanidae	*Acasta* cf. *conica*		QMG333433	Poecilosclerida	Microcionidae	*Clathria*	Great Barrier Reef, QLD	-13.067, 143.8029	13.5
WAMC61359	Balanidae	*Acasta* cf. *conica*	92		Unknown sponge			Bluebell Island, WA	-20.4034, 115.5247	8
WAMC61360	Balanidae	*Acasta* cf. *conica*	92		Unknown sponge			Bluebell Island, WA	-20.4034, 115.5247	8
WAMC61361	Balanidae	*Acasta* cf. *conica*	92		Unknown sponge			Bluebell Island, WA	-20.4034, 115.5247	8
WAMC61373	Balanidae	*Acasta* cf. *conica*	92		Unknown sponge			Trimouille Island, WA	-20.372, 115.564	11
WAMC61374	Balanidae	*Acasta* cf. *conica*	92		Unknown sponge			Trimouille Island, WA	-20.372, 115.564	11
WAMC61375	Balanidae	*Acasta* cf. *conica*	92		Unknown sponge			Trimouille Island, WA	-20.372, 115.564	11
WAMC48002	Balanidae	*Acasta* cf. *conica*	92	WAMZ68734	Poecilosclerida	Microcionidae	*Clathria* (*Thalyssias*) cf. *reinwardti*	Cassini Island, WA	-13.9154, 125.7743	13
WAMC55270	Balanidae	*Acasta* cf. *conica*	92	WAMZ68734	Poecilosclerida	Microcionidae	*Clathria* (*Thalyssias*) cf. *reinwardti*	Cassini Island, WA	-13.9154, 125.7743	13
WAMC55280	Balanidae	*Acasta* cf. *conica*	92	WAMZ29238	Poecilosclerida	Microcionidae	*Clathria* (*Thalyssias*) *reinwardti*	Cassini Island, WA	-13.9257, 125.637	13
WAMC58829	Balanidae	*Acasta* cf. *conica*	92	WAMZ84230	Poecilosclerida	Microcionidae	*Clathria* (*Thalyssias*) cf. *reinwardti*	Montebello Islands, WA	-20.384, 115.539	11
WAMC58830	Balanidae	*Acasta* cf. *conica*	92	WAMZ84226	Poecilosclerida	Microcionidae	*Clathria* (*Thalyssias*) *reinwardti*	Montebello Islands, WA	-20.388, 115.4923	22
WAMC58831	Balanidae	*Acasta* cf. *conica*	92	WAMZ84226	Poecilosclerida	Microcionidae	*Clathria* (*Thalyssias*) *reinwardti*	Montebello Islands, WA	-20.388, 115.4923	22
WAMC58832	Balanidae	*Acasta* cf. *conica*	92	WAMZ84226	Poecilosclerida	Microcionidae	*Clathria* (*Thalyssias*) *reinwardti*	Montebello Islands, WA	-20.388, 115.4923	22
WAMC58833	Balanidae	*Acasta* cf. *conica*	92	WAMZ84226	Poecilosclerida	Microcionidae	*Clathria* (*Thalyssias*) *reinwardti*	Montebello Islands, WA	-20.388, 115.4923	22
WAMC58834	Balanidae	*Acasta* cf. *conica*	92	WAMZ84226	Poecilosclerida	Microcionidae	*Clathria* (*Thalyssias*) *reinwardti*	Montebello Islands, WA	-20.388, 115.4923	22
WAMC67757	Balanidae	*Acasta* cf. *conica*	92	WAMZ97027	Poecilosclerida	Microcionidae	*Clathria* (*Thalyssias*) *reinwardti*	Muiron Islands, WA	-21.694, 114.329	7
WAMC67758	Balanidae	*Acasta* cf. *conica*	92	WAMZ97027	Poecilosclerida	Microcionidae	*Clathria* (*Thalyssias*) *reinwardti*	Muiron Islands, WA	-21.694, 114.329	7
WAMC67785	Balanidae	*Acasta* cf. *conica*	92	WAMZ97031	Poecilosclerida	Microcionidae	*Clathria* (*Thalyssias*) *reinwardti*	Muiron Islands, WA	-21.694, 114.329	7
WAMC71828	Balanidae	*Acasta* cf. *conica*	92	WAMZ97026	Poecilosclerida	Microcionidae	*Clathria* (*Thalyssias*) *reinwardti*	Muiron Islands, WA	-21.694, 114.329	7
WAMC71829	Balanidae	*Acasta* cf. *conica*	92	WAMZ97026	Poecilosclerida	Microcionidae	*Clathria* (*Thalyssias*) *reinwardti*	Muiron Islands, WA	-21.694, 114.329	7
WAMC71830	Balanidae	*Acasta* cf. *conica*	92	WAMZ97026	Poecilosclerida	Microcionidae	*Clathria* (*Thalyssias*) *reinwardti*	Muiron Islands, WA	-21.694, 114.329	7
WAMC58804	Balanidae	*Acasta* cf. *conica*	93	WAMZ84164	Poecilosclerida	Microcionidae	*Clathria* (*Thalyssias*) *reinwardti*	Ah Chong Island, WA	-20.4992, 115.5899	14.5
WAMC58805	Balanidae	*Acasta* cf. *conica*	93	WAMZ84164	Poecilosclerida	Microcionidae	*Clathria* (*Thalyssias*) *reinwardti*	Ah Chong Island, WA	-20.4992, 115.5899	14.5
WAMC58806	Balanidae	*Acasta* cf. *conica*	93	WAMZ84164	Poecilosclerida	Microcionidae	*Clathria* (*Thalyssias*) *reinwardti*	Ah Chong Island, WA	-20.4992, 115.5899	14.5
WAMC58807	Balanidae	*Acasta* cf. *conica*	93	WAMZ84164	Poecilosclerida	Microcionidae	*Clathria* (*Thalyssias*) *reinwardti*	Ah Chong Island, WA	-20.4992, 115.5899	14.5

Specimen Accession	Family	Identification	PSH	Host accession	Host Order	Host family	Host identification	Locality	Coordinates	Depth
WAMC58816	Balanidae	*Acasta* cf. conica	93	WAMZ84227	Poecilosclerida	Microcionidae	*Clathria* (*Thalyssias*) *reinwardti*	Montebello Islands, WA	-20.388, 115.4923	22
WAMC58817	Balanidae	*Acasta* cf. *conica*	93	WAMZ84227	Poecilosclerida	Microcionidae	*Clathria* (*Thalyssias*) *reinwardti*	Montebello Islands, WA	-20.388, 115.4923	22
WAMC58818	Balanidae	*Acasta* cf. *conica*	93	WAMZ84227	Poecilosclerida	Microcionidae	*Clathria* (*Thalyssias*) *reinwardti*	Montebello Islands, WA	-20.388, 115.4923	22
WAMC58825	Balanidae	*Acasta* cf. *conica*	93	WAMZ84230	Poecilosclerida	Microcionidae	*Clathria* (*Thalyssias*) cf. *reinwardti*	Montebello Islands, WA	-20.384, 115.539	11
WAMC58826	Balanidae	*Acasta* cf. *conica*	93	WAMZ84230	Poecilosclerida	Microcionidae	*Clathria* (*Thalyssias*) cf. *reinwardti*	Montebello Islands, WA	-20.384, 115.539	11
WAMC58827	Balanidae	*Acasta* cf. *conica*	93	WAMZ84230	Poecilosclerida	Microcionidae	*Clathria* (*Thalyssias*) cf. *reinwardti*	Montebello Islands, WA	-20.384, 115.539	11
WAMC58828	Balanidae	*Acasta* cf. *conica*	93	WAMZ84230	Poecilosclerida	Microcionidae	*Clathria* (*Thalyssias*) cf. *reinwardti*	Montebello Islands, WA	-20.384, 115.539	11
WAMC71822	Balanidae	*Acasta* cf. *conica*	93	WAMZ86863	Poecilosclerida	Microcionidae	*Clathria* (*Thalyssias*) *reinwardti*	Dampier Archipelago, WA	-20.5853, 116.5944	17
WAMC48913	Balanidae	*Acasta* cf. *crucibasis*	30		Haplosclerida	Phloeodictyidae	*Siphonodictyon* SS9	Cape Leveque, WA	-15.0944, 121.7864	79
WAMC55338	Balanidae	*Acasta* cf. *crucibasis*	70	WAMZ65260	Axinellida	Axinellidae	*Reniochalina stalagmitis*	Onslow, WA	-21.5961, 115.0606	12.2
WAMC55339	Balanidae	*Acasta* cf. *crucibasis*	70	WAMZ65260	Axinellida	Axinellidae	*Reniochalina stalagmitis*	Onslow, WA	-21.5961, 115.0606	12.2
WAMC58766	Balanidae	*Acasta* cf. *cyathus*			Alcyonacea	Alcyoniidae	*Sinularia*	Montebello Islands, WA	-20.3555, 115.5508	26
WAMC58767	Balanidae	*Acasta* cf. *cyathus*			Alcyonacea	Alcyoniidae	*Sinularia*	Montebello Islands, WA	-20.3555, 115.5508	26
WAMC58768	Balanidae	*Acasta* cf. *cyathus*			Alcyonacea	Alcyoniidae	*Sinularia*	Montebello Islands, WA	-20.3555, 115.5508	26
WAMC58770	Balanidae	*Acasta* cf. *cyathus*			Alcyonacea	Alcyoniidae	*Sinularia*	Montebello Islands, WA	-20.3555, 115.5508	26
WAMC67718	Balanidae	*Acasta* cf. *cyathus*		WAMZ97034	Alcyonacea	Alcyoniidae	*Lobophytum sarcophytoides*	Muiron Islands, WA	-21.694, 114.329	7
WAMC71850	Balanidae	*Acasta* cf. *cyathus*			Alcyonacea	Alcyoniidae	*Sinularia*?	Montebello Islands, WA	-20.3555, 115.5508	26
WAMC61497	Balanidae	*Acasta* cf. *flexuosa* D10	21	WAMZ95204	Dictyoceratida	Dysideidae	*Lamellodysidea* KB1	East Holothuria Reef, WA	-13.583, 126.019	1
WAMC61498	Balanidae	*Acasta* cf. *flexuosa* D10	21	WAMZ95204	Dictyoceratida	Dysideidae	*Lamellodysidea* KB1	East Holothuria Reef, WA	-13.583, 126.019	1
WAMC61499	Balanidae	*Acasta* cf. *flexuosa* D10	21	WAMZ95204	Dictyoceratida	Dysideidae	*Lamellodysidea* KB1	East Holothuria Reef, WA	-13.583, 126.019	1
WAMC67636	Balanidae	*Acasta* cf. *flexuosa* D18	52	WAMZ86069	Dictyoceratida	Dysideidae	*Dysidea* P1	Lowendal Island, WA	-20.599, 115.738	33.4
WAMC67638	Balanidae	*Acasta* cf. *flexuosa* D18	52	WAMZ86069	Dictyoceratida	Dysideidae	*Dysidea* P1	Lowendal Island, WA	-20.599, 115.738	33.4
WAMC67639	Balanidae	*Acasta* cf. *flexuosa* D18	52	WAMZ86069	Dictyoceratida	Dysideidae	*Dysidea* P1	Lowendal Island, WA	-20.599, 115.738	33.4
WAMC55358	Balanidae	*Acasta* cf. *flexuosa* D4	19	WAMZ82370	Dictyoceratida	Dysideidae	*Dysidea* sp.3	Abutilon Island, WA	-20.707, 115.748	25
WAMC61421	Balanidae	*Acasta* cf. *flexuosa* D4	19	WAMZ84220	Dictyoceratida	Dysideidae	*Dysidea* MM2	Montebello Islands, WA	-20.388, 115.492	22
WAMC61422	Balanidae	*Acasta* cf. *flexuosa* D4	19	WAMZ84220	Dictyoceratida	Dysideidae	*Dysidea* MM2	Montebello Islands, WA	-20.388, 115.492	22
WAMC61423	Balanidae	*Acasta* cf. *flexuosa* D4	19	WAMZ84220	Dictyoceratida	Dysideidae	*Dysidea* MM2	Montebello Islands, WA	-20.388, 115.492	22
WAMC67697	Balanidae	*Acasta* cf. *flexuosa* D8		WAMZ9939	Dictyoceratida	Dysideidae	*Dysidea* sp.4	Dampier Archipelago, WA	-20.618, 116.445	16
WAMC67698	Balanidae	*Acasta* cf. *flexuosa* D8		WAMZ9939	Dictyoceratida	Dysideidae	*Dysidea* sp.4	Dampier Archipelago, WA	-20.618, 116.445	16
WAMC58844	Balanidae	*Acasta* cf. *flexuosa* D8	66	WAMZ84242	Dictyoceratida	Dysideidae	*Dysidea* MM1	Trimouille Island, WA	-20.384, 115.539	11
WAMC58846	Balanidae	*Acasta* cf. *flexuosa* D8	66	WAMZ84242	Dictyoceratida	Dysideidae	*Dysidea* MM1	Trimouille Island, WA	-20.384, 115.539	11
SAMAC12790	Balanidae	*Acasta* cf. *spongites*	81		Dictyoceratida			Whyalla, SA	-32.7403, 137.8361	15
WAMC55403	Balanidae	*Acasta* cf. *spongites* D5	82	WAMZ84420	Dictyoceratida	Dysideidae	*Dysidea* cf.*granulosa*	Maret Islands, WA	-14.431, 124.875	12
WAMC55404	Balanidae	*Acasta* cf. *spongites* D5	82	WAMZ84420	Dictyoceratida	Dysideidae	*Dysidea* cf.*granulosa*	Maret Islands, WA	-14.431, 124.875	12
WAMC67811	Balanidae	*Acasta* cf. *spongites* D5	82	WAMZ86913	Dictyoceratida	Thorectidae	*Luffariella* SS11?	Rob Roy Reef, WA	-14.43, 124.861	12
WAMC67812	Balanidae	*Acasta* cf. *spongites* D5	82	WAMZ86913	Dictyoceratida	Thorectidae	*Luffariella* SS11?	Rob Roy Reef, WA	-14.43, 124.861	12
WAMC67813	Balanidae	*Acasta* cf. *spongites* D5	82	WAMZ86913	Dictyoceratida	Thorectidae	*Luffariella* SS11?	Rob Roy Reef, WA	-14.43, 124.861	12
WAMC55393	Balanidae	*Acasta* cf. *sulcata*	1		Unknown sponge			Condillac Island, WA	-14.1105, 125.5595	13
WAMC55394	Balanidae	*Acasta* cf. *sulcata*	1		Unknown sponge			Condillac Island, WA	-14.1105, 125.5595	13
WAMC55395	Balanidae	*Acasta* cf. *sulcata*	1		Unknown sponge			Condillac Island, WA	-14.1105, 125.5595	13
WAMC55396	Balanidae	*Acasta* cf. *sulcata*	1		Unknown sponge			Condillac Island, WA	-14.1105, 125.5595	13
WAMC58559	Balanidae	*Acasta* cf. *sulcata*	1		Unknown sponge			Dampier Archipelago, WA	-20.4231, 116.8622	12
WAMC66714	Balanidae	*Acasta* cf. *sulcata*	1	WAMZ97114	Axinellida	Axinellidae	*Axinella*	Exmouth Gulf, WA	-21.8202, 114.2101	25
WAMC55271	Balanidae	*Acasta* cf. *sulcata*	1	WAMZ68734	Poecilosclerida	Microcionidae	*Clathria* (*Thalyssias*) cf.*reinwardti*	Cassini Island, WA	-13.9154, 125.7743	13
WAMC55389	Balanidae	*Acasta* cf. *vipensis*			Alcyonacea			Lesueur Island, WA	-13.8312, 127.2646	29.5
WAMC58777	Balanidae	*Acasta* cf. *vipensis*		WAMZ67604	Alcyonacea	Subergorgiidae	*Subergorgia*?	Montebello Islands, WA	-20.388, 115.4923	22
WAMC61367	Balanidae	*Acasta cyathus*			Unknown sponge			Ah Chong Island, WA	-20.5193, 115.5677	16.5
WAMC55298	Balanidae	*Acasta cyathus*	3		Unknown sponge			Mermaid Reef, WA	-17.0266, 119.6189	25
WAMC55299	Balanidae	*Acasta cyathus*	3		Unknown sponge			Mermaid Reef, WA	-17.0266, 119.6189	25
WAMC61366	Balanidae	*Acasta cyathus*	3		Unknown sponge			Ah Chong Island, WA	-20.5193, 115.5677	16.5
WAMC46029	Balanidae	*Acasta cyathus*	3	WAMZ28855	Haplosclerida	Petrosiidae	*Petrosia* (*petrosia*) SS2	Ningaloo Reef, WA	-22.6626, 113.6396	10
WAMC46073	Balanidae	*Acasta cyathus*	3	WAMZ28856	Haplosclerida	Petrosiidae	*Petrosia* (*petrosia*) SS2	Ningaloo Reef, WA	-22.6626, 113.6396	10
WAMC46101	Balanidae	*Acasta cyathus*	3	WAMZ28861	Haplosclerida	Petrosiidae	*Xestospongia* NG3	Ningaloo Reef, WA	-22.6626, 113.6396	10

Specimen Accession	Family	Identification	PSH	Host accession	Host Order	Host family	Host identification	Locality	Coordinates	Depth
WAMC55255	Balanidae	*Acasta cyathus*	3	WAMZ69885	Haplosclerida	Petrosiidae	*Petrosia* (*petrosia*) sp.1	Hibernia Reef, WA	-11.9882, 123.3359	12
WAMC58878	Balanidae	*Acasta cyathus*	3	WAMZ28856	Haplosclerida	Petrosiidae	*Petrosia* SS2	Ningaloo Reef, WA	-22.8028, 113.6939	30
WAMC66644	Balanidae	*Acasta cyathus*	3	WAMZ97046	Haplosclerida	Petrosiidae	*Petrosia*	South Muiron Island, WA	-21.6944, 114.3319	8
WAMC74374	Balanidae	Acasta cyathus	3		Haplosclerida	Petrosiidae	*Petrosia*	Scarborough Reef, WA	-31.8768, 115.7067	15
WAMC58786	Balanidae	Acasta cyathus	3	WAMZ84301	Suberitida	Halichondriidae	*Halichondria*	South Murion Island, WA	-21.6659, 114.3312	17
WAMC67723	Balanidae	Acasta cyathus	3	WAMZ97080	Suberitida	Halichondriidae	*Halichondria*	South Muiron Island, WA	-21.6835, 114.311	18
WAMC54159	Balanidae	*Acasta* D34		WAMZ69688	Dictyoceratida	Spongiidae	*Spongia* (*Australospongia*) cf. sp.1	Ashmore Reef, WA	-12.275, 122.981	13.5
WAMC46096	Balanidae	*Acasta fenestrata*	80	WAMZ28854	Haplosclerida	Petrosiidae	*Neopetrosia chaliniformis*	Ningaloo Reef, WA	-22.6626, 113.6396	10
WAMC46669	Balanidae	*Acasta fenestrata*	80	WAMZ29257	Haplosclerida	Petrosiidae	*Neopetrosia chaliniformis*	Long Reef, WA	-13.832, 125.8119	2
WAMC55251	Balanidae	*Acasta fenestrata*	80	WAMZ69889	Haplosclerida	Petrosiidae	*Neopetrosia chaliniformis*	Ashmore Reef, WA	-12.2773, 123.1361	1
WAMC55319	Balanidae	*Acasta fenestrata*	80	WAMZ84014	Haplosclerida	Petrosiidae	*Neopetrosia chaliniformis*	Mermaid Reef, WA	-17.0724, 119.6271	12
WAMC55320	Balanidae	*Acasta fenestrata*	80	WAMZ84014	Haplosclerida	Petrosiidae	*Neopetrosia chaliniformis*	Mermaid Reef, WA	-17.0724, 119.6271	12
WAMC55321	Balanidae	*Acasta fenestrata*	80	WAMZ84014	Haplosclerida	Petrosiidae	*Neopetrosia chaliniformis*	Mermaid Reef, WA	-17.0724, 119.6271	12
WAMC55322	Balanidae	*Acasta fenestrata*	80	WAMZ84014	Haplosclerida	Petrosiidae	*Neopetrosia chaliniformis*	Mermaid Reef, WA	-17.0724, 119.6271	12
WAMC55323	Balanidae	*Acasta fenestrata*	80	WAMZ83364	Haplosclerida	Petrosiidae	*Neopetrosia chaliniformis*	Clerke Reef, WA	-17.3143, 119.375	5
WAMC55324	Balanidae	*Acasta fenestrata*	80	WAMZ83364	Haplosclerida	Petrosiidae	*Neopetrosia chaliniformis*	Clerke Reef, WA	-17.3143, 119.375	5
WAMC55325	Balanidae	*Acasta fenestrata*	80	WAMZ83364	Haplosclerida	Petrosiidae	*Neopetrosia chaliniformis*	Clerke Reef, WA	-17.3143, 119.375	5
WAMC58748	Balanidae	*Acasta fenestrata*	80	WAMZ54173	Haplosclerida	Petrosiidae	*Neopetrosia chaliniformis*	Champagney Island, WA	-15.331, 124.217	0
WAMC58749	Balanidae	*Acasta fenestrata*	80	WAMZ54173	Haplosclerida	Petrosiidae	*Neopetrosia chaliniformis*	Champagney Island, WA	-15.331, 124.217	0
WAMC67829	Balanidae	*Acasta fenestrata*	80	WAMZ86889	Haplosclerida	Petrosiidae	*Neopetrosia chaliniformis*	Dampier Archipelago, WA	-20.5903, 116.6056	9.7
WAMC71738	Balanidae	*Acasta fenestrata*	80	WAMZ86889	Haplosclerida	Petrosiidae	*Neopetrosia chaliniformis*	Dampier Archipelago, WA	-20.5903, 116.6056	9.7
WAMC71739	Balanidae	*Acasta fenestrata*	80	WAMZ86889	Haplosclerida	Petrosiidae	*Neopetrosia chaliniformis*	Dampier Archipelago, WA	-20.5903, 116.6056	9.7
WAMC72909	Balanidae	*Acasta fenestrata*	80		Haplosclerida	Petrosiidae	*Neopetrosia chaliniformis*	Ningaloo Reef, WA	-22.6626, 113.6396	10
WAMC72914	Balanidae	*Acasta fenestrata*	80		Haplosclerida	Petrosiidae	*Neopetrosia chaliniformis*	Ningaloo Reef, WA	-22.6626, 113.6396	10
WAMC74419	Balanidae	*Acasta fenestrata*	80		Haplosclerida	Petrosiidae	*Neopetrosia chaliniformis*	Hook Island, QLD	-20.1044, 148.9025	2
WAMC47383	Balanidae	*Acasta sandwichi*	76	WAMZ29261	Haplosclerida	Petrosiidae	*Xestospongia testudinaria*	Cassini Island, WA	-13.8186, 125.7797	12
WAMC53344	Balanidae	*Acasta sandwichi*	76		Haplosclerida	Petrosiidae	*Xestospongia testudinaria*	Lesueur Island, WA	-13.8312, 127.2646	29.5
WAMC58753	Balanidae	*Acasta spinitergum*			Alcyonacea	Gorgoniidae	*Rumphella*	Ah Chong Island, WA	-20.5193, 115.5677	16.5
WAMC58754	Balanidae	*Acasta spinitergum*			Alcyonacea	Gorgoniidae	*Rumphella*	Ah Chong Island, WA	-20.5193, 115.5677	16.5
WAMC58755	Balanidae	*Acasta spinitergum*			Alcyonacea	Gorgoniidae	*Rumphella*	Ah Chong Island, WA	-20.5193, 115.5677	16.5
WAMC58756	Balanidae	*Acasta spinitergum*			Alcyonacea	Gorgoniidae	*Rumphella*	Ah Chong Island, WA	-20.5193, 115.5677	16.5
WAMC58763	Balanidae	*Acasta spinitergum*			Alcyonacea	Gorgoniidae	*Rumphella*	Montebello Islands, WA	-20.3755, 115.5734	22
WAMC58764	Balanidae	*Acasta spinitergum*			Alcyonacea	Gorgoniidae	*Rumphella*	Montebello Islands, WA	-20.3755, 115.5734	22
WAMC58765	Balanidae	*Acasta spinitergum*			Alcyonacea	Gorgoniidae	*Rumphella*	Montebello Islands, WA	-20.3755, 115.5734	22
WAMC58773	Balanidae	*Acasta spinitergum*			Alcyonacea	Gorgoniidae	*Rumphella*	Montebello Islands, WA	-20.388, 115.4923	22
WAMC58774	Balanidae	*Acasta spinitergum*			Alcyonacea	Gorgoniidae	*Rumphella*	Montebello Islands, WA	-20.388, 115.4923	22
WAMC58775	Balanidae	*Acasta spinitergum*			Alcyonacea	Gorgoniidae	*Rumphella*	Montebello Islands, WA	-20.388, 115.4923	22
WAMC58776	Balanidae	*Acasta spinitergum*			Alcyonacea	Gorgoniidae	*Rumphella*	Montebello Islands, WA	-20.388, 115.4923	22
WAMC67649	Balanidae	*Acasta spongites* D20	115	WAMZ86916	Dictyoceratida	Irciniidae	*Ircinia variabilis*	Marseille, France	43.314, 5.32	10
WAMC67711	Balanidae	*Acasta spongites* D20	115	WAMZ86916	Dictyoceratida	Irciniidae	*Ircinia variabilis*	Marseille, France	43.314, 5.32	10
WAMC67712	Balanidae	*Acasta spongites* D20	115	WAMZ86916	Dictyoceratida	Irciniidae	*Ircinia variabilis*	Marseille, France	43.314, 5.32	10
SAMAC8686	Balanidae	*Acasta sulcata*	106	SAMA S823	Poecilosclerida	Microcionidae	*Clathria*	Great Australian Bight, SA	-31.6794, 131.2439	55
WAMC67827	Balanidae	*Acasta sulcata*	106		Poecilosclerida	Microcionidae	*Antho* (*Plocamia*)	Dampier Archipelago, WA	-20.468, 116.828	9
WAMC67730	Balanidae	*Amphibalanus cirratus*						Exmouth Gulf, WA	-22.3123, 114.1271	0
WAMC58760	Balanidae	*Amphibalanus poecilotheca*		WAMZ67545				Montebello Islands, WA	-20.3755, 115.5734	22
WAMC58761	Balanidae	*Amphibalanus poecilotheca*		WAMZ67545				Montebello Islands, WA	-20.3755, 115.5734	22
WAMC58762	Balanidae	*Amphibalanus poecilotheca*		WAMZ67545				Montebello Islands, WA	-20.3755, 115.5734	22
WAMC58757	Balanidae	*Amphibalanus poecilotheca*			Hydrozoa	HYDROZOA		Montebello Islands, WA	-20.388, 115.4923	22
WAMC58758	Balanidae	*Amphibalanus poecilotheca*			Hydrozoa	HYDROZOA		Montebello Islands, WA	-20.388, 115.4923	22
WAMC58759	Balanidae	*Amphibalanus poecilotheca*			Hydrozoa	HYDROZOA		Montebello Islands, WA	-20.388, 115.4923	22
WAMC52760	Balanidae	*Amphibalanus* sp.1						King George River, WA	-13.9716, -127	0
WAMC52761	Balanidae	*Amphibalanus* sp.1						King George River, WA	-13.9716, -127	0
WAMC48917	Balanidae	*Archiacasta*	31		Haplosclerida	Petrosiidae	*Petrosia SS5*	Cape Leveque, WA	-15.0944, 121.7864	79

Specimen Accession	Family	Identification	PSH	Host accession	Host Order	Host family	Host identification	Locality	Coordinates	Depth
WAMC55385	Balanidae	*Archiacasta* cf. *membranacea*	95	WAMZ82337	Suberitida	Halichondriidae	*Ciocalypta tyleri*	Bowers Ledge, WA	-21.5509, 114.8003	14.3
WAMC58728	Balanidae	*Archiacasta* cf. *membranacea*	95	WAMZ86887	Suberitida	Halichondriidae	*Ciocalypta tyleri*	Dampier Archipelago, WA	-20.502, 116.633	12
WAMC61353	Balanidae	*Archiacasta* cf. *membranacea*	95	WAMZ84163	Suberitida	Halichondriidae	*Topsentia halichondroides*	Montebello Islands, WA	-20.384, 115.539	11
WAMC67825	Balanidae	*Archiacasta* cf. *membranacea*	95	WAMZ86876	Suberitida	Halichondriidae	*Ciocalypta*	Dampier Archipelago, WA	-20.5022, 117.0606	12
WAMC66631	Balanidae	*Archiacasta* D16	86	WAMZ97036	Dictyoceratida	Spongiidae	*Spongia* (*Heterofibria*) cf.NG1	Muiron Islands, WA	-21.694, 114.329	7
WAMC67745	Balanidae	*Archiacasta* D16	86	WAMZ97020	Dictyoceratida	Spongiidae	*Spongia* (*Heterofibria*) cf.NG1	Exmouth Gulf, WA	-21.871, 114.159	6
WAMC67746	Balanidae	*Archiacasta* D16	86	WAMZ97020	Dictyoceratida	Spongiidae	*Spongia* (*Heterofibria*) cf.NG1	Exmouth Gulf, WA	-21.871, 114.159	6
WAMC67747	Balanidae	*Archiacasta* D16	86	WAMZ97020	Dictyoceratida	Spongiidae	*Spongia* (*Heterofibria*) cf.NG1	Exmouth Gulf, WA	-21.871, 114.159	6
WAMC67788	Balanidae	*Archiacasta* D16	86	WAMZ97020	Dictyoceratida	Spongiidae	*Spongia* (*Heterofibria*) cf.NG1	Exmouth Gulf, WA	-21.871, 114.159	6
WAMC61529	Balanidae	*Archiacasta* D16	86	WAMZ69508	Dictyoceratida	Thorectidae	*Dactylospongia elegans*	Ashmore Reef, WA	-12.231, 123	10.8
WAMC61531	Balanidae	*Archiacasta* D16	86	WAMZ69706	Dictyoceratida	Thorectidae	*Dactylospongia elegans*	Ashmore Reef, WA	-12.244, 122.926	14.8
WAMC67686	Balanidae	*Archiacasta* D36	17	WAMZ87471	Dictyoceratida	Irciniidae	*Sarcotragus* cf.sp.2	Camden Sound, WA	-15.376, 124.14	39.2
WAMC67678	Balanidae	*Archiacasta* D37	53	WAMZ9753	Dictyoceratida	Irciniidae	*Sarcotragus* sp.2	Dampier Archipelago, WA	-20.618, 116.564	29
WAMC61489	Balanidae	*Archiacasta* D40		WAMZ12466	Dictyoceratida	Spongiidae	*Leiosella* sp.1	North West Cape, WA	-21.44, 114.138	250
WAMC61490	Balanidae	*Archiacasta* D40		WAMZ12466	Dictyoceratida	Spongiidae	*Leiosella* sp.1	North West Cape, WA	-21.44, 114.138	250
WAMC61491	Balanidae	*Archiacasta* D40		WAMZ12466	Dictyoceratida	Spongiidae	*Leiosella* sp.1	North West Cape, WA	-21.44, 114.138	250
WAMC67705	Balanidae	*Archiacasta* D40		WAMZ88416	Dictyoceratida	Spongiidae	*Spongia* (*Heterofibria*) RA1	Recherche Archipelago, WA	-34.001, 122.83	15
WAMC58850	Balanidae	*Archiacasta hainanensis* D9	20	WAMZ84237	Dictyoceratida	Thorectidae	*Hyrtios erectus*	Trimouille Island, WA	-20.384, 115.539	11
WAMC61496	Balanidae	*Archiacasta hainanensis* D9	20	WAMZ95250	Dictyoceratida	Thorectidae	*Hyrtios* KMB1	Eclipse Islands, WA	-13.658, 126.192	64.7
WAMC61522	Balanidae	*Archiacasta hainanensis* D9	20	WAMZ94203	Dictyoceratida	Thorectidae	*Hyrtios* SS2	Maret Islands, WA	-14.424, 125.041	55.6
WAMC61523	Balanidae	*Archiacasta hainanensis* D9	20	WAMZ94203	Dictyoceratida	Thorectidae	*Hyrtios* SS2	Maret Islands, WA	-14.424, 125.041	55.6
WAMC71922	Balanidae	*Archiacasta membranacea*	61		Unknown sponge			Amathole Region, South Africa	-32.758, 28.4589	62
WAMC71923	Balanidae	*Archiacasta membranacea*	61		Unknown sponge			Amathole Region, South Africa	-32.758, 28.4589	62
WAMC71925	Balanidae	*Archiacasta membranacea*	61		Unknown sponge			Amathole Region, South Africa	-32.8345, 28.4682	76
WAMC71906	Balanidae	*Archiacasta membranacea*	61		Tetractinellida			Amathole Region, South Africa	-32.758, 28.4589	62
WAMC71909	Balanidae	*Archiacasta membranacea*	61		Tetractinellida			Amathole Region, South Africa	-32.7541, 28.4553	54
WAMC71902	Balanidae	*Archiacasta membranacea*	61	WAMZ86933	Tetractinellida	Pachastrellidae	*Pachastrella*	Amathole Region, South Africa	-32.6666, 28.45	55
WAMC71903	Balanidae	*Archiacasta membranacea*	61		Tetractinellida	Pachastrellidae		Amathole Region, South Africa	-32.7597, 28.411	45
WAMC71904	Balanidae	*Archiacasta membranacea*	61	WAMZ86935	Tetractinellida	Pachastrellidae	*Pachastrella* sp.1	Amathole Region, South Africa	-32.75, 28.4	45
WAMC71914	Balanidae	*Archiacasta membranacea*	61	WAMZ86945	Tetractinellida	Pachastrellidae	*Pachastrella* sp.1	Amathole Region, South Africa	-33.2, 27.85	76
WAMC71920	Balanidae	*Archiacasta membranacea*	61	WAMZ86935	Tetractinellida	Pachastrellidae	*Pachastrella* sp.1	Amathole Region, South Africa	-32.75, 28.4	45
WAMC71926	Balanidae	*Archiacasta membranacea*	61	WAMZ86936	Tetractinellida	Pachastrellidae	*Pachastrella* sp.1	Amathole Region, South Africa	-32.75, 28.4	45
WAMC54383	Balanidae	*Archiacasta tenuivalvata*		WAMZ69887	Haplosclerida	Petrosiidae	*Petrosia* (*Strongylata*) cf.*strongylata*	Hibernia Reef, WA	-11.9761, 123.3897	17
WAMC48735	Balanidae	*Archiacasta tenuivalvata*	10		Unknown sponge			Conway Island, WA	-15.8716, 123.6635	11
WAMC61381	Balanidae	*Archiacasta tenuivalvata*	10		Unknown sponge			Montebello Islands, WA	-20.3755, 115.5734	22
WAMC61382	Balanidae	*Archiacasta tenuivalvata*	10		Unknown sponge			Montebello Islands, WA	-20.3755, 115.5734	22
WAMC61383	Balanidae	*Archiacasta tenuivalvata*	10		Unknown sponge			Montebello Islands, WA	-20.3755, 115.5734	22
WAMC61384	Balanidae	*Archiacasta tenuivalvata*	10		Unknown sponge			Montebello Islands, WA	-20.3755, 115.5734	22
WAMC61385	Balanidae	*Archiacasta tenuivalvata*	10		Unknown sponge			Montebello Islands, WA	-20.3755, 115.5734	22
WAMC55408	Balanidae	*Archiacasta tenuivalvata*	10	WAMZ54698	Biemnida	Biemnidae	*Neofibularia* KMB1	Echuca Shoal, WA	-13.9006, 123.8934	18
WAMC48914	Balanidae	*Archiacasta tenuivalvata*	10		Haplosclerida	Petrosiidae	*Petrosia* SS5	Cape Leveque, WA	-15.0944, 121.7864	79
WAMC61399	Balanidae	*Archiacasta tenuivalvata*	10	WAMZ84193	Haplosclerida	Petrosiidae	*Petrosia*	Ah Chong Island, WA	-20.5193, 115.5677	16.5
WAMC61400	Balanidae	*Archiacasta tenuivalvata*	10	WAMZ84193	Haplosclerida	Petrosiidae	*Petrosia*	Ah Chong Island, WA	-20.5193, 115.5677	16.5
WAMC61401	Balanidae	*Archiacasta tenuivalvata*	10	WAMZ84193	Haplosclerida	Petrosiidae	*Petrosia*	Ah Chong Island, WA	-20.5193, 115.5677	16.5
WAMC67773	Balanidae	*Archiacasta tenuivalvata*	10	WAMZ97044	Haplosclerida	Petrosiidae	*Petrosia*	South Muiron Island, WA	-21.6944, 114.3319	8
WAMC67713	Balanidae	*Armatobalanus arcuatus*			Scleractinia	Dendrophylliidae	*Turbinaria*	Muiron Islands, WA	-21.694, 114.329	7
WAMC71806	Balanidae	Armatobalanus cf. *quadrivittatus*			Unknown sponge			Dampier Archipelago, WA	-20.4231, 116.8622	12
WAMC71807	Balanidae	Armatobalanus cf. *quadrivittatus*			Unknown sponge			Dampier Archipelago, WA	-20.4231, 116.8622	12
WAMC55247	Balanidae	*Armatobalanus palaoensis*			Poecilosclerida	Crambeidae	*Monanchora*	Ashmore Reef, WA	-12.2935, 123.1237	12
WAMC54220	Balanidae	*Armatobalanus palaoensis*	63		Poecilosclerida	Crambeidae	*Monanchora*	Ashmore Reef, WA	-12.1945, 123.0502	7
WAMC55240	Balanidae	*Armatobalanus palaoensis*	63		Poecilosclerida	Crambeidae	*Monanchora*	Ashmore Reef, WA	-12.1945, 123.0502	7
WAMC55241	Balanidae	*Armatobalanus palaoensis*	63		Poecilosclerida	Crambeidae	*Monanchora*	Ashmore Reef, WA	-12.1945, 123.0502	7
WAMC55242	Balanidae	*Armatobalanus palaoensis*	63		Poecilosclerida	Crambeidae	*Monanchora*	Ashmore Reef, WA	-12.1945, 123.0502	7

Specimen Accession	Family	Identification	PSH	Host accession	Host Order	Host family	Host identification	Locality	Coordinates	Depth
WAMC55246	Balanidae	*Armatobalanus palaoensis*	63		Poecilosclerida	Crambeidae	*Monanchora*	Ashmore Reef, WA	-12.2935, 123.1237	12
WAMC67828	Balanidae	*Armatobalanus palaoensis*	63		Poecilosclerida	Microcionidae	*Echinochalina*	Dampier Archipelago, WA	-20.618, 116.464	16
WAMC58330	Balanidae	*Armatobalanus quadrivittatus*	102		Unknown sponge			Montebello Islands, WA	-20.384, 115.539	11
WAMC54216	Balanidae	*Conopea basicuneata*			Alcyonacea			Ashmore Reef, WA	-12.1945, 123.0502	7
WAMC55257	Balanidae	*Conopea basicuneata*			Alcyonacea			Ashmore Reef, WA	-12.1885, 123.1289	12
WAMC67786	Balanidae	*Conopea* cf. *calceola*		WAMZ97082	Alcyonacea	Alcyoniidae		South Muiron Island, WA	-21.6835, 114.311	18
WAMC55310	Balanidae	*Conopea* cf. *calceola*			Alcyonacea	Plexauridae	*Echinogorgia* sp.10	Pilbara Shelf, WA	-20.702, 116.2906	15.7
WAMC55413	Balanidae	*Conopea* cf. *calceola*		WAMZ54816	Alcyonacea	Plexauridae	*Euplexaura*	Albert Reef, WA	-15.6044, 123.3179	16
WAMC58778	Balanidae	*Conopea* cf. *calceola*		WAMZ67604	Alcyonacea	Subergorgiidae	*Subergorgia*?	Montebello Islands, WA	-20.388, 115.4923	22
WAMC55258	Balanidae	*Conopea granulata*			Alcyonacea			Ashmore Reef, WA	-12.1885, 123.1289	12
WAMC55259	Balanidae	*Conopea granulata*			Alcyonacea			Ashmore Reef, WA	-12.1885, 123.1289	12
WAMC55256	Balanidae	*Conopea* sp.1			Antipatharia			Ashmore Reef, WA	-12.1885, 123.1289	12
WAMC67756	Balanidae	*Conopea titani*		WAMZ97143	Alcyonacea	Alcyoniidae		Exmouth Gulf, WA	-21.821, 114.209	22
WAMC55386	Balanidae	*Conopea willhearsti*			Alcyonacea			Lesueur Island, WA	-13.8312, 127.2646	29.5
WAMC58772	Balanidae	*Conopea willhearsti*		WAMZ67619	Alcyonacea			Montebello Islands, WA	-20.3555, 115.5508	26
WAMC55314	Balanidae	*Conopea willhearsti*		WAMZ70363	Alcyonacea	Melithaeaidae	*Melithaea sp.5*	Pilbara Shelf, WA	-20.9811, 115.2699	14.3
WAMC55315	Balanidae	*Conopea willhearsti*		WAMZ70363	Alcyonacea	Melithaeaidae	*Melithaea sp.5*	Pilbara Shelf, WA	-20.9811, 115.2699	14.3
WAMC55316	Balanidae	*Conopea willhearsti*		WAMZ70363	Alcyonacea	Melithaeaidae	*Melithaea sp.5*	Pilbara Shelf, WA	-20.9811, 115.2699	14.3
WAMC55317	Balanidae	*Conopea willhearsti*		WAMZ70363	Alcyonacea	Melithaeaidae	*Melithaea sp.5*	Pilbara Shelf, WA	-20.9811, 115.2699	14.3
WAMC55318	Balanidae	*Conopea willhearsti*		WAMZ70345	Alcyonacea	Melithaeaidae	*Melithaea* sp.10	Pilbara Shelf, WA	-21.7707, 114.5264	14
WAMC58839	Balanidae	*Euacasta*		WAMZ84233	Haplosclerida	Callyspongiidae	*Callyspongia* (*Toxochalina*)	Montebello Islands, WA	-20.384, 115.539	11
WAMC58841	Balanidae	*Euacasta*		WAMZ84233	Haplosclerida	Callyspongiidae	*Callyspongia* (*Toxochalina*)	Montebello Islands, WA	-20.384, 115.539	11
WAMC58578	Balanidae	*Euacasta*		WAMZ86883	Poecilosclerida	Microcionidae	*Clathria* (*Thalyssias*) *reinwardti*	Dampier Archipelago, WA	-20.5022, 117.0606	12
WAMC61446	Balanidae	*Euacasta*			Verongiida	Ianthellidae	*Ianthella basta*	Ah Chong Island, WA	-20.4992, 115.5899	14.5
WAMC58856	Balanidae	*Euacasta*	27		Unknown sponge			Montebello Islands, WA	-20.4513, 115.5827	6.5
WAMC58858	Balanidae	*Euacasta*	27		Unknown sponge			Montebello Islands, WA	-20.3555, 115.5508	26
WAMC61386	Balanidae	*Euacasta*	27		Unknown sponge			Montebello Islands, WA	-20.3555, 115.5508	26
WAMC61387	Balanidae	*Euacasta*	27		Unknown sponge			Montebello Islands, WA	-20.3555, 115.5508	26
WAMC55051	Balanidae	*Euacasta*	27	WAMZ39847	Haplosclerida	Callyspongiidae	*Callyspongia* (*Toxochalina*) *MR1*	Rottnest Island, WA	-31.9738, 115.537	10
WAMC55054	Balanidae	*Euacasta*	27	WAMZ39847	Haplosclerida	Callyspongiidae	*Callyspongia* (*Toxochalina*) *MR1*	Rottnest Island, WA	-31.9738, 115.537	10
WAMC55055	Balanidae	*Euacasta*	27	WAMZ39847	Haplosclerida	Callyspongiidae	*Callyspongia* (*Toxochalina*) *MR1*	Rottnest Island, WA	-31.9738, 115.537	10
WAMC58241	Balanidae	*Euacasta*	27	WAMZ84103	Haplosclerida	Callyspongiidae	*Callyspongia* (*Toxochalina*) KMB1	Trimouille Island, WA	-20.372, 115.564	11
WAMC58842	Balanidae	*Euacasta*	27	WAMZ84233	Haplosclerida	Callyspongiidae	*Callyspongia* (*Toxochalina*)	Montebello Islands, WA	-20.384, 115.539	11
WAMC58843	Balanidae	*Euacasta*	27	WAMZ84233	Haplosclerida	Callyspongiidae	*Callyspongia* (*Toxochalina*)	Montebello Islands, WA	-20.384, 115.539	11
WAMC61410	Balanidae	*Euacasta*	27	WAMZ84152	Haplosclerida	Callyspongiidae	*Callyspongia* (*Toxochalina*) KMB1	Montebello Islands, WA	-20.4513, 115.5827	6.5
WAMC61411	Balanidae	*Euacasta*	27	WAMZ84152	Haplosclerida	Callyspongiidae	*Callyspongia* (*Toxochalina*) KMB1	Montebello Islands, WA	-20.4513, 115.5827	6.5
WAMC61412	Balanidae	*Euacasta*	27	WAMZ84152	Haplosclerida	Callyspongiidae	*Callyspongia* (*Toxochalina*) KMB1	Montebello Islands, WA	-20.4513, 115.5827	6.5
WAMC67823	Balanidae	*Euacasta*	27	WAMZ58532	Haplosclerida	Callyspongiidae	*Callyspongia*	Dampier Archipelago, WA	-20.5022, 117.0606	12
WAMC71770	Balanidae	*Euacasta*	27	WAMZ86869	Haplosclerida	Callyspongiidae	*Callyspongia*	Dampier Archipelago, WA	-20.618, 116.464	16
WAMC55058	Balanidae	*Euacasta*	27	WAMZ39846	Haplosclerida	Chalinidae	*Haliclona*	Rottnest Island, WA	-31.9738, 115.537	10
WAMC61424	Balanidae	*Euacasta*	27	WAMZ84195	Haplosclerida	Chalinidae	*Haliclona amboinensis*	Ah Chong Island, WA	-20.5193, 115.5677	16.5
WAMC61425	Balanidae	*Euacasta*	27	WAMZ84195	Haplosclerida	Chalinidae	*Haliclona amboinensis*	Ah Chong Island, WA	-20.5193, 115.5677	16.5
WAMC71878	Balanidae	*Euacasta*	27	WAMZ99868	Haplosclerida	Chalinidae	*Haliclona djeedara*	Rottnest Island, WA	-32.0148, 115.5588	12
WAMC71879	Balanidae	*Euacasta*	27	WAMZ99868	Haplosclerida	Chalinidae	*Haliclona djeedara*	Rottnest Island, WA	-32.0148, 115.5588	12
WAMC71882	Balanidae	*Euacasta*	27		Haplosclerida	Chalinidae	*Geodia/Haliclona*	Rottnest Island, WA	-32.0258, 115.5452	18
WAMC71883	Balanidae	*Euacasta*	27		Haplosclerida	Chalinidae	*Geodia/Haliclona*	Rottnest Island, WA	-32.0258, 115.5452	18
WAMC67726	Balanidae	*Euacasta*	27	WAMZ97096	Haplosclerida	Petrosiidae	*Petrosia*	North Muiron Island, WA	-21.6277, 114.3737	17
WAMC67742	Balanidae	*Euacasta*	27	WAMZ97099	Haplosclerida	Petrosiidae	*Petrosia* (*Strongylophora*)	North Muiron Island, WA	-21.6277, 114.3737	17
WAMC67743	Balanidae	*Euacasta*	27	WAMZ97099	Haplosclerida	Petrosiidae	*Petrosia* (*Strongylophora*)	North Muiron Island, WA	-21.6277, 114.3737	17
WAMC67774	Balanidae	*Euacasta*	27	WAMZ97028	Haplosclerida	Petrosiidae	*Petrosia*	Muiron Islands, WA	-21.694, 114.329	7
WAMC71831	Balanidae	*Euacasta*	27	WAMZ97016	Haplosclerida	Petrosiidae	*Petrosia*	North West Cape, WA	-21.7949, 114.1384	13
WAMC74375	Balanidae	*Euacasta*	27		Haplosclerida	Petrosiidae	*Petrosia*	Scarborough Reef, WA	-31.8768, 115.7067	15
WAMC71761	Balanidae	*Euacasta*	27	WAMZ86904	Poecilosclerida	Tedaniidae	*Tedania* (*Trachytedania*)	Dampier Archipelago, WA	-20.4419, 116.6697	15

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WAMC71762	Balanidae	*Euacasta*	27	WAMZ86904	Poecilosclerida	Tedaniidae	*Tedania* (*Trachytedania*)	Dampier Archipelago, WA	-20.4419, 116.6697	15
WAMC67822	Balanidae	*Euacasta*	27	WAMZ86876	Suberitida	Halichondriidae	*Ciocalypta*	Dampier Archipelago, WA	-20.5022, 117.0606	12
WAMC55061	Balanidae	*Euacasta*	33	WAMZ39844	Bubarida	Dictyonellidae	*Acanthella* MR1	Rottnest Island, WA	-31.9743, 115.5417	25
WAMC55293	Balanidae	*Euacasta*	36	WAMZ81742	Axinellida	Raspailiidae	*Echinodictyum mesenterium*	Pilbara Shelf, WA	-21.4922, 115.0997	15.5
WAMC55294	Balanidae	*Euacasta*	36	WAMZ81742	Axinellida	Raspailiidae	*Echinodictyum mesenterium*	Pilbara Shelf, WA	-21.4922, 115.0997	15.5
WAMC55334	Balanidae	*Euacasta*	38		Haplosclerida	Niphatidae	*Amphimedon*	Taunton Reef, WA	-21.31, 115.2594	17.3
WAMC55335	Balanidae	*Euacasta*	38		Haplosclerida	Niphatidae	*Amphimedon*	Taunton Reef, WA	-21.31, 115.2594	17.3
WAMC55359	Balanidae	*Euacasta*	38	WAMZ82198	Haplosclerida	Niphatidae	*Amphimedon* cf.*paraviridis*	Taunton Reef, WA	-21.31, 115.2594	17.3
WAMC55360	Balanidae	*Euacasta*	38	WAMZ82198	Haplosclerida	Niphatidae	*Amphimedon* cf.*paraviridis*	Taunton Reef, WA	-21.31, 115.2594	17.3
WAMC55361	Balanidae	*Euacasta*	38	WAMZ82198	Haplosclerida	Niphatidae	*Amphimedon* cf.*paraviridis*	Taunton Reef, WA	-21.31, 115.2594	17.3
WAMC55362	Balanidae	*Euacasta*	38	WAMZ82198	Haplosclerida	Niphatidae	*Amphimedon* cf.*paraviridis*	Taunton Reef, WA	-21.31, 115.2594	17.3
WAMC55363	Balanidae	*Euacasta*	38	WAMZ82198	Haplosclerida	Niphatidae	*Amphimedon* cf.*paraviridis*	Taunton Reef, WA	-21.31, 115.2594	17.3
WAMC55364	Balanidae	*Euacasta*	38	WAMZ82198	Haplosclerida	Niphatidae	*Amphimedon* cf.*paraviridis*	Taunton Reef, WA	-21.31, 115.2594	17.3
WAMC67762	Balanidae	*Euacasta*	38	WAMZ97023	Haplosclerida	Niphatidae	*Amphimedon* cf. *paraviridis*	Exmouth Gulf, WA	-21.871, 114.159	6
WAMC67763	Balanidae	*Euacasta*	38	WAMZ97023	Haplosclerida	Niphatidae	*Amphimedon* cf. *paraviridis*	Exmouth Gulf, WA	-21.871, 114.159	6
WAMC58519	Balanidae	*Euacasta*	42		Unknown sponge			Dampier Archipelago, WA	-20.5022, 117.0606	12
WAMC71780	Balanidae	*Euacasta*	42		Unknown sponge			Dampier Archipelago, WA	-20.458, 117.0575	14.5
WAMC61479	Balanidae	*Euacasta*	42	WAMZ68731	Suberitida	Halichondriidae	*Ciocalypta tyleri*			
WAMC61480	Balanidae	*Euacasta*	42	WAMZ68731	Suberitida	Halichondriidae	*Ciocalypta tyleri*			
WAMC61370	Balanidae	*Euacasta*	45		Verongiida			Ah Chong Island, WA	-20.5193, 115.5677	16.5
WAMC61371	Balanidae	*Euacasta*	45		Verongiida			Ah Chong Island, WA	-20.5193, 115.5677	16.5
WAMC61372	Balanidae	*Euacasta*	45		Verongiida			Ah Chong Island, WA	-20.5193, 115.5677	16.5
WAMC61406	Balanidae	*Euacasta*	45		Verongiida			Montebello Islands, WA	-20.4513, 115.5827	6.5
WAMC61378	Balanidae	*Euacasta*	46		Polymastiida	Polymastiidae	*Polymastia*	Montebello Islands, WA	-20.3555, 115.5508	26
WAMC61407	Balanidae	*Euacasta*	47		Verongiida			Montebello Islands, WA	-20.4513, 115.5827	6.5
WAMC67759	Balanidae	*Euacasta*	47	WAMZ97015	Verongiida			North West Cape, WA	-21.7949, 114.1384	13
WAMC67760	Balanidae	*Euacasta*	47	WAMZ97015	Verongiida			North West Cape, WA	-21.7949, 114.1384	13
WAMC67761	Balanidae	*Euacasta*	47	WAMZ97015	Verongiida			North West Cape, WA	-21.7949, 114.1384	13
WAMC71744	Balanidae	*Euacasta*	47	WAMZ86905	Verongiida			Dampier Archipelago, WA	-20.5025, 116.6808	10
WAMC71745	Balanidae	*Euacasta*	47	WAMZ86905	Verongiida			Dampier Archipelago, WA	-20.5025, 116.6808	10
WAMC61426	Balanidae	*Euacasta*	48		Axinellida	Axinellidae	*Axinella*	South Murion Island, WA	-21.6659, 114.3312	17
WAMC61427	Balanidae	*Euacasta*	48		Axinellida	Axinellidae	*Axinella*	South Murion Island, WA	-21.6659, 114.3312	17
WAMC71858	Balanidae	*Euacasta*	59	WAMZ95501	Dendroceratida	Dictyodendrillidae	*Dictyodendrilla* KMB2	Lynher Bank, WA	-15.7918, 121.9649	77.4
WAMC71859	Balanidae	*Euacasta*	59	WAMZ95501	Dendroceratida	Dictyodendrillidae	*Dictyodendrilla* KMB2	Lynher Bank, WA	-15.7918, 121.9649	77.4
WAMC55048	Balanidae	*Euacasta*	89	WAMZ39841	Axinellida	Axinellidae	*Axinella* cf.NG3	Rottnest Island, WA	-31.9743, 115.5417	25
WAMC71826	Balanidae	*Euacasta*	89	WAMZ97117	Axinellida	Axinellidae	*Axinella*	Exmouth Gulf, WA	-21.8202, 114.2101	25
WAMC55188	Balanidae	*Euacasta*	89		Unknown sponge			Abutilon Island, WA	-20.7395, 115.5993	12
WAMC55401	Balanidae	*Euacasta*	89		Unknown sponge			Mavis Reef, WA	-15.4764, 123.5682	12
WAMC55402	Balanidae	*Euacasta*	89		Unknown sponge			Mavis Reef, WA	-15.4764, 123.5682	12
WAMC58242	Balanidae	*Euacasta*	89		Unknown sponge			Trimouille Island, WA	-20.372, 115.564	11
WAMC58600	Balanidae	*Euacasta*	89		Unknown sponge			Dampier Archipelago, WA	-20.4581, 117.0575	14.5
WAMC58682	Balanidae	*Euacasta*	89		Unknown sponge			Dampier Archipelago, WA	-20.4581, 117.0575	14.5
WAMC61355	Balanidae	*Euacasta*	89		Unknown sponge			Trimouille Island, WA	-20.372, 115.564	11
WAMC61356	Balanidae	*Euacasta*	89		Unknown sponge			Trimouille Island, WA	-20.372, 115.564	11
WAMC61357	Balanidae	*Euacasta*	89		Unknown sponge			Trimouille Island, WA	-20.372, 115.564	11
WAMC61419	Balanidae	*Euacasta*	89		Unknown sponge			Montebello Islands, WA	-20.388, 115.4923	22
WAMC61420	Balanidae	*Euacasta*	89		Unknown sponge			Montebello Islands, WA	-20.388, 115.4923	22
WAMC71839	Balanidae	*Euacasta*	89		Unknown sponge			Trimouille Island, WA	-20.372, 115.564	11
WAMC55383	Balanidae	*Euacasta*	89	WAMZ82245	Axinellida	Axinellidae	*Reniochalina* sp.2	Regnard Island, WA	-20.7695, 116.182	18.7
WAMC55384	Balanidae	*Euacasta*	89	WAMZ82245	Axinellida	Axinellidae	*Reniochalina* sp.2	Regnard Island, WA	-20.7695, 116.182	18.7
WAMC71742	Balanidae	*Euacasta*	89	WAMZ86903	Axinellida	Axinellidae	*Reniochalina stalagmitis*	Dampier Archipelago, WA	-20.4581, 117.0575	14.5
WAMC71743	Balanidae	*Euacasta*	89	WAMZ86903	Axinellida	Axinellidae	*Reniochalina stalagmitis*	Dampier Archipelago, WA	-20.4581, 117.0575	14.5
WAMC71768	Balanidae	*Euacasta*	89	WAMZ86844	Axinellida	Axinellidae	*Reniochalina stalagmitis*	Dampier Archipelago, WA	-20.5006, 116.5022	14

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WAMC71783	Balanidae	*Euacasta*	89	WAMZ86879	Axinellida	Axinellidae	*Axinella* NG3	Dampier Archipelago, WA	-20.5022, 117.0606	12
WAMC71794	Balanidae	*Euacasta*	89	WAMZ86861	Axinellida	Axinellidae	*Reniochalina* sp.2	Dampier Archipelago, WA	-20.5853, 116.5944	17
WAMC71795	Balanidae	*Euacasta*	89	WAMZ86861	Axinellida	Axinellidae	*Reniochalina* sp.2	Dampier Archipelago, WA	-20.5853, 116.5944	17
WAMC71804	Balanidae	*Euacasta*	89	WAMZ86877	Axinellida	Axinellidae	*Reniochalina stalagmitis*	Dampier Archipelago, WA	-20.5022, 117.0606	12
WAMC71827	Balanidae	*Euacasta*	89	WAMZ97117	Axinellida	Axinellidae	*Axinella*	Exmouth Gulf, WA	-21.8202, 114.2101	25
WAMC71872	Balanidae	*Euacasta*	89		Axinellida	Axinellidae	*Axinella* NG3	Rottnest Island, WA	-32.0148, 115.5588	12
WAMC71873	Balanidae	*Euacasta*	89		Axinellida	Axinellidae	*Axinella* NG3	Rottnest Island, WA	-32.0148, 115.5588	12
WAMC55261	Balanidae	*Euacasta*	89	WAMZ68736	Axinellida	Raspailiidae	*Ceratopsion montebelloensis*	Port Hedland, WA		
WAMC55296	Balanidae	*Euacasta*	89	WAMZ82128	Axinellida	Raspailiidae	*Trikentrion flabelliforme*	Pilbara Shelf, WA	-21.0802, 115.18	21.4
WAMC55297	Balanidae	*Euacasta*	89	WAMZ82128	Axinellida	Raspailiidae	*Trikentrion flabelliforme*	Pilbara Shelf, WA	-21.0802, 115.18	21.4
WAMC55341	Balanidae	*Euacasta*	89	WAMZ65146	Axinellida	Raspailiidae	*Ectyoplaisia frondosa*	Onslow, WA	-21.5263, 115.0922	12
WAMC55342	Balanidae	*Euacasta*	89	WAMZ53880	Axinellida	Raspailiidae	*Ectyoplaisia tabula*	Onslow, WA	-21.5372, 115.0525	13
WAMC55349	Balanidae	*Euacasta*	89	WAMZ53948	Axinellida	Raspailiidae	*Trikentrion flabelliforme*	Onslow, WA	-21.5444, 115.0331	14
WAMC55350	Balanidae	*Euacasta*	89	WAMZ53857	Axinellida	Raspailiidae	*Trikentrion flabelliforme*	Onslow, WA	-21.5372, 115.0525	13.6
WAMC55351	Balanidae	*Euacasta*	89	WAMZ53857	Axinellida	Raspailiidae	*Trikentrion flabelliforme*	Onslow, WA	-21.5372, 115.0525	13.6
WAMC67733	Balanidae	*Euacasta*	89	WAMZ97118	Axinellida	Raspailiidae	*Trikentrion flabellliforme*	Exmouth Gulf, WA	-21.8202, 114.2101	25
WAMC67734	Balanidae	*Euacasta*	89	WAMZ97118	Axinellida	Raspailiidae	*Trikentrion flabellliforme*	Exmouth Gulf, WA	-21.8202, 114.2101	25
WAMC67771	Balanidae	*Euacasta*	89	WAMZ97111	Axinellida	Raspailiidae	*Trikentrion flabellliforme*	Exmouth Gulf, WA	-21.8202, 114.2101	25
WAMC67824	Balanidae	*Euacasta*	89	WAMZ86901	Axinellida	Raspailiidae	*Thrinacophora*?	Dampier Archipelago, WA	-20.468, 116.828	9
WAMC71782	Balanidae	*Euacasta*	89	WAMZ86878	Axinellida	Stellegeridae	*Higginsia*	Dampier Archipelago, WA	-20.5022, 117.0606	12
WAMC67826	Balanidae	*Euacasta*	89	WAMZ86880	Haplosclerida	Petrosiidae	*Xestospongia* cf.sp.3	Dampier Archipelago, WA	-20.5022, 117.0606	12
WAMC71766	Balanidae	*Euacasta*	89	WAMZ86902	Haplosclerida	Petrosiidae	*Xestospongia* sp.3	Dampier Archipelago, WA	-20.4581, 117.0575	14.5
WAMC71779	Balanidae	*Euacasta*	89	WAMZ86880	Haplosclerida	Petrosiidae	*Xestospongia* cf. sp.3	Dampier Archipelago, WA	-20.5022, 117.0606	12
WAMC74376	Balanidae	*Euacasta*	89		Haplosclerida	Petrosiidae	*Petrosia*	Scarborough Reef, WA	-31.8768, 115.7067	15
WAMC74377	Balanidae	*Euacasta*	89		Haplosclerida	Petrosiidae	*Petrosia*	Scarborough Reef, WA	-31.8768, 115.7067	15
WAMC66761	Balanidae	*Euacasta*	89	WAMZ97131	Poecilosclerida			Exmouth Gulf, WA	-21.821, 114.209	22
WAMC71789	Balanidae	*Euacasta*	89	WAMZ86865	Poecilosclerida	Iotrochotidae	*Iotrochota*	Dampier Archipelago, WA	-20.5853, 116.5944	17
WAMC71790	Balanidae	*Euacasta*	89	WAMZ86865	Poecilosclerida	Iotrochotidae	*Iotrochota*	Dampier Archipelago, WA	-20.5853, 116.5944	17
WAMC71769	Balanidae	*Euacasta*	89	WAMZ86883	Poecilosclerida	Microcionidae	*Clathria* (*Thalyssias*) *reinwardti*	Dampier Archipelago, WA	-20.5022, 117.0606	12
WAMC71843	Balanidae	*Euacasta*	89	WAMZ86862	Poecilosclerida	Microcionidae	*Clathria* (*Thalyssias*) *abietina*	Dampier Archipelago, WA	-20.5853, 116.5944	17
WAMC61539	Balanidae	*Euacasta*	89		Scopalinida	Scopalinidae	*Styliisa flabelliformis*	Ningaloo Reef, WA	-22.2146, 113.8235	49.8
WAMC61540	Balanidae	*Euacasta*	89		Scopalinida	Scopalinidae	*Styliisa flabelliformis*	Ningaloo Reef, WA	-22.2146, 113.8235	49.8
WAMC67737	Balanidae	*Euacasta*	89	WAMZ94892	Scopalinida	Scopalinidae	*Svenzea* sp.1	Eclipse Archipelago, WA	-13.8305, 126.1386	60
WAMC67738	Balanidae	*Euacasta*	89	WAMZ94892	Scopalinida	Scopalinidae	*Svenzea* sp.1	Eclipse Archipelago, WA	-13.8305, 126.1386	60
WAMC67739	Balanidae	*Euacasta*	89	WAMZ94892	Scopalinida	Scopalinidae	*Svenzea* sp.1	Eclipse Archipelago, WA	-13.8305, 126.1386	60
WAMC71796	Balanidae	*Euacasta*	89	WAMZ86899	Scopalinida	Scopalinidae	*Stylissa flabelliformis*	Dampier Archipelago, WA	-20.468, 116.828	9
WAMC61477	Balanidae	*Euacasta*	89	WAMZ84362	Suberitida	Halichondriidae	*Ciocalypta* PB3	Montebello Islands, WA		
WAMC71791	Balanidae	*Euacasta*	89	WAMZ86881	Suberitida	Halichondriidae	*Halichondria*?	Dampier Archipelago, WA	-20.5022, 117.0606	12
WAMC74371	Balanidae	*Euacasta*	89	WAMZ39841	Suberitida	Suberitidae	*Caulospongia biflabellata*	Scarborough Reef, WA	-31.8768, 115.7067	15
WAMC74372	Balanidae	*Euacasta*	89	WAMZ39841	Suberitida	Suberitidae	*Caulospongia biflabellata*	Scarborough Reef, WA	-31.8768, 115.7067	15
WAMC74373	Balanidae	*Euacasta*	89	WAMZ39841	Suberitida	Suberitidae	*Caulospongia biflabellata*	Scarborough Reef, WA	-31.8768, 115.7067	15
WAMC55353	Balanidae	*Euacasta*	89	WAMZ65314	Tethyida	Hemiasterellidae	*Axos flabelliformis*	Onslow, WA	-21.6069, 114.9331	12
WAMC55354	Balanidae	*Euacasta*	89	WAMZ65314	Tethyida	Hemiasterellidae	*Axos flabelliformis*	Onslow, WA	-21.6069, 114.9331	12
WAMC55355	Balanidae	*Euacasta*	89	WAMZ65314	Tethyida	Hemiasterellidae	*Axos flabelliformis*	Onslow, WA	-21.6069, 114.9331	12
WAMC55356	Balanidae	*Euacasta*	89	WAMZ65314	Tethyida	Hemiasterellidae	*Axos flabelliformis*	Onslow, WA	-21.6069, 114.9331	12
WAMC55357	Balanidae	*Euacasta*	89	WAMZ65314	Tethyida	Hemiasterellidae	*Axos flabelliformis*	Onslow, WA	-21.6069, 114.9331	12
WAMC61457	Balanidae	*Euacasta*	89	WAMZ28707	Tethyida	Hemiasterellidae	*Hemiasterella* SS2	Ningaloo Reef, WA		.
WAMC71821	Balanidae	*Euacasta*	89	WAMZ86875	Tethyida	Hemiasterellidae	*Axos flabelliformis*	Dampier Archipelago, WA	-20.5022, 117.0606	12
WAMC55382	Balanidae	*Euacasta*	89	WAMZ82314	Tetractinellida	Ancorinidae	*Jaspis* cf.SS2	Bare Rock, WA	-20.4747, 116.3072	38
WAMC53978	Balanidae	*Euacasta*	90		Unknown sponge			Ashmore Reef, WA	-12.1839, 123.1006	12
WAMC61348	Balanidae	*Euacasta*	90		Unknown sponge			Ah Chong Island, WA	-20.4992, 115.5899	14.5
WAMC61349	Balanidae	*Euacasta*	90		Unknown sponge			Ah Chong Island, WA	-20.4992, 115.5899	14.5
WAMC61350	Balanidae	*Euacasta*	90		Unknown sponge			Ah Chong Island, WA	-20.4992, 115.5899	14.5

Specimen Accession	Family	Identification	PSH	Host accession	Host Order	Host family	Host identification	Locality	Coordinates	Depth
WAMC61397	Balanidae	*Euacasta*	90		Unknown sponge			Montebello Islands, WA	-20.4513, 115.5827	6.5
WAMC61398	Balanidae	*Euacasta*	90		Unknown sponge			Montebello Islands, WA	-20.4513, 115.5827	6.5
WAMC61404	Balanidae	*Euacasta*	90		Unknown sponge			Montebello Islands, WA	-20.3555, 115.5508	26
WAMC61405	Balanidae	*Euacasta*	90		Unknown sponge			Montebello Islands, WA	-20.3555, 115.5508	26
WAMC61417	Balanidae	*Euacasta*	90		Unknown sponge			Trimouille Island, WA	-20.372, 115.564	11
WAMC61418	Balanidae	*Euacasta*	90		Unknown sponge			Trimouille Island, WA	-20.372, 115.564	11
WAMC58820	Balanidae	*Euacasta*	90	WAMZ84166	Tethyida	Hemiasterellidae	*Hemiasterella* cf.CERF1	Ah Chong Island, WA	-20.4992, 115.5899	14.5
WAMC58823	Balanidae	*Euacasta*	90	WAMZ84166	Tethyida	Hemiasterellidae	*Hemiasterella* cf.CERF1	Ah Chong Island, WA	-20.4992, 115.5899	14.5
WAMC66622	Balanidae	*Euacasta*	90	WAMZ97029	Tethyida	Hemiasterellidae	*Hemiasterella* CERF1	Muiron Islands, WA	-21.694, 114.329	7
WAMC66652	Balanidae	*Euacasta*	90	WAMZ97079	Tethyida	Hemiasterellidae	*Hemiasterella* CERF1	South Muiron Island, WA	-21.6835, 114.311	18
WAMC67740	Balanidae	*Euacasta*	90	WAMZ97101	Tethyida	Hemiasterellidae	*Hemiasterella* CERF1	North Muiron Island, WA	-21.6277, 114.3737	17
WAMC67741	Balanidae	*Euacasta*	90	WAMZ97101	Tethyida	Hemiasterellidae	*Hemiasterella* CERF1	North Muiron Island, WA	-21.6277, 114.3737	17
WAMC67753	Balanidae	*Euacasta*	90	WAMZ97041	Tethyida	Hemiasterellidae	*Hemiasterella* CERF1	South Muiron Island, WA	-21.6944, 114.3319	8
WAMC67754	Balanidae	*Euacasta*	90	WAMZ97041	Tethyida	Hemiasterellidae	*Hemiasterella* CERF1	South Muiron Island, WA	-21.6944, 114.3319	8
WAMC67728	Balanidae	*Euacasta*	97	WAMZ97112	Verongiida	Ianthellidae	*Ianthella flabelliformis*	Exmouth Gulf, WA	-21.8202, 114.2101	25
WAMC67751	Balanidae	*Euacasta*	97	WAMZ97119	Verongiida	Ianthellidae	*Ianthella flabelliformis*	Exmouth Gulf, WA	-21.8202, 114.2101	25
WAMC67752	Balanidae	*Euacasta*	97	WAMZ97119	Verongiida	Ianthellidae	*Ianthella flabelliformis*	Exmouth Gulf, WA	-21.8202, 114.2101	25
WAMC67766	Balanidae	*Euacasta*	97	WAMZ97139	Verongiida	Ianthellidae	*Ianthella flabelliformis*	Exmouth Gulf, WA	-21.821, 114.209	22
WAMC67767	Balanidae	*Euacasta*	97	WAMZ97139	Verongiida	Ianthellidae	*Ianthella flabelliformis*	Exmouth Gulf, WA	-21.821, 114.209	22
WAMC67768	Balanidae	*Euacasta*	97	WAMZ97139	Verongiida	Ianthellidae	*Ianthella flabelliformis*	Exmouth Gulf, WA	-21.821, 114.209	22
WAMC71773	Balanidae	*Euacasta*	97	WAMZ86886	Verongiida	Ianthellidae	*Ianthella flabelliformis*	Dampier Archipelago, WA	-20.502, 116.633	12
WAMC71774	Balanidae	*Euacasta*	97	WAMZ86886	Verongiida	Ianthellidae	*Ianthella flabelliformis*	Dampier Archipelago, WA	-20.502, 116.633	12
WAMC67764	Balanidae	*Euacasta*	98	WAMZ97113	Verongiida	Ianthellidae	*Ianthella basta*	Exmouth Gulf, WA	-21.8202, 114.2101	25
WAMC67765	Balanidae	*Euacasta*	98	WAMZ97113	Verongiida	Ianthellidae	*Ianthella basta*	Exmouth Gulf, WA	-21.8202, 114.2101	25
WAMC71840	Balanidae	*Euacasta*	98		Verongiida	Ianthellidae	*Ianthella basta*	Montebello Islands, WA	-20.3755, 115.5734	22
WAMC71841	Balanidae	*Euacasta*	98		Verongiida	Ianthellidae	*Ianthella basta*	Ah Chong Island, WA	-20.4992, 115.5899	14.5
WAMC71784	Balanidae	*Euacasta*	99		Verongiida	Ianthellidae	*Ianthella reticulata*	Dampier Archipelago, WA	-20.5903, 116.6056	9.7
WAMC71785	Balanidae	*Euacasta*	99		Verongiida	Ianthellidae	*Ianthella reticulata*	Dampier Archipelago, WA	-20.5903, 116.6056	9.7
WAMC72912	Balanidae	*Euacasta*	100		Verongiida	Pseudoceratiniidae	*Pseudoceratina*	Ningaloo Reef, WA	-22.6626, 113.6396	10
WAMC61369	Balanidae	*Euacasta*	101		Verongiida			Ah Chong Island, WA	-20.5193, 115.5677	16.5
WAMC58744	Balanidae	Euacasta acutaflava	43	WAMZ29216	Axinellida	Axinellidae	*Cymbastela stipatata*	Dampier Archipelago, WA	-15.8982, 124.1817	0
WAMC58745	Balanidae	Euacasta acutaflava	43	WAMZ29216	Axinellida	Axinellidae	*Cymbastela stipatata*	Dampier Archipelago, WA	-15.8982, 124.1817	0
WAMC58746	Balanidae	Euacasta acutaflava	43	WAMZ29216	Axinellida	Axinellidae	*Cymbastela stipatata*	Dampier Archipelago, WA	-15.8982, 124.1817	0
WAMC61434	Balanidae	Euacasta acutaflava	43	WAMZ84101	Axinellida	Axinellidae	*Cymbastela* cf.*stipatata*	Trimouille Island, WA	-20.372, 115.564	11
WAMC61435	Balanidae	Euacasta acutaflava	43	WAMZ84101	Axinellida	Axinellidae	*Cymbastela* cf.*stipatata*	Trimouille Island, WA	-20.372, 115.564	11
WAMC58252	Balanidae	*Euacasta* cf. *aculeata*	88		Unknown sponge			Trimouille Island, WA	-20.372, 115.564	11
WAMC58727	Balanidae	*Euacasta* cf. *aculeata*	88		Unknown sponge			Dampier Archipelago, WA	-20.502, 116.633	12
WAMC46111	Balanidae	*Euacasta* cf. *aculeata*	88	WAMZ28873	Tetractinellida	Ancorinidae	*Cinachyrella* NG1	Ningaloo Reef, WA	-22.6626, 113.6396	10
WAMC58384	Balanidae	*Euacasta* cf. *aculeata*	88		Tetractinellida	Ancorinidae	*Rhabdastrella*	Montebello Islands, WA	-20.388, 115.4923	22
WAMC61436	Balanidae	*Euacasta* cf. *aculeata*	88		Tetractinellida	Ancorinidae	*Rhabdastrella*	Ah Chong Island, WA	-20.4992, 115.5899	14.5
WAMC61437	Balanidae	*Euacasta* cf. *aculeata*	88		Tetractinellida	Ancorinidae	*Rhabdastrella*	Ah Chong Island, WA	-20.4992, 115.5899	14.5
WAMC61438	Balanidae	*Euacasta* cf. *aculeata*	88		Tetractinellida	Ancorinidae	*Rhabdastrella*	Ah Chong Island, WA	-20.4992, 115.5899	14.5
WAMC71799	Balanidae	*Euacasta* cf. *aculeata*	88	WAMZ86897	Tetractinellida	Tetillidae	*Cinachyrella tenuiviolacea*	Dampier Archipelago, WA	-20.468, 116.828	9
WAMC61362	Balanidae	*Euacasta* cf. *porata*	28		Unknown sponge			Montebello Islands, WA	-20.4513, 115.5827	6.5
WAMC46102	Balanidae	*Euacasta* cf. *porata*	28	WAMZ28859	Tetractinellida	Ancorinidae	*Rhabdastrella globostellata*	Ningaloo Reef, WA	-22.6626, 113.6396	10
WAMC53901	Balanidae	*Euacasta* cf. *porata*	28		Tetractinellida	Ancorinidae	*Rhabdastrella globostellata*	Ashmore Reef, WA	-12.2306, 123	12
WAMC55277	Balanidae	*Euacasta* cf. *porata*	28	WAMZ29286	Tetractinellida	Ancorinidae	*Rhabdastrella globostellata*	Cassini Island, WA	-13.9321, 125.6182	12
WAMC55278	Balanidae	*Euacasta* cf. *porata*	28	WAMZ29286	Tetractinellida	Ancorinidae	*Rhabdastrella globostellata*	Cassini Island, WA	-13.9321, 125.6182	12
WAMC61389	Balanidae	*Euacasta* cf. *porata*	28	WAMZ84261	Tetractinellida	Ancorinidae	*Rhabdastrella globostellata*	Bluebell Island, WA	-20.4034, 115.5247	8
WAMC61390	Balanidae	*Euacasta* cf. *porata*	28	WAMZ84261	Tetractinellida	Ancorinidae	*Rhabdastrella globostellata*	Bluebell Island, WA	-20.4034, 115.5247	8
WAMC61413	Balanidae	*Euacasta* cf. *porata*	28	WAMZ84245	Tetractinellida	Ancorinidae	*Rhabdastrella globostellata*	Montebello Islands, WA	-20.384, 115.539	11
WAMC71797	Balanidae	*Euacasta* cf. *porata*	28	WAMZ86898	Tetractinellida	Ancorinidae	*Rhabdastrella globostellata*	Dampier Archipelago, WA	-20.468, 116.828	9
WAMC71798	Balanidae	*Euacasta* cf. *porata*	28	WAMZ86898	Tetractinellida	Ancorinidae	*Rhabdastrella globostellata*	Dampier Archipelago, WA	-20.468, 116.828	9

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WAMC71817	Balanidae	*Euacasta* cf. *porata*	28	WAMZ86885	Tetractinellida	Ancorinidae	*Rhabdastrella globostellata*	Dampier Archipelago, WA	-20.5006, 116.5022	14
WAMC71818	Balanidae	*Euacasta* cf. *porata*	28	WAMZ86885	Tetractinellida	Ancorinidae	*Rhabdastrella globostellata*	Dampier Archipelago, WA	-20.5006, 116.5022	14
WAMC71819	Balanidae	*Euacasta* cf. *porata*	28	WAMZ86885	Tetractinellida	Ancorinidae	*Rhabdastrella globostellata*	Dampier Archipelago, WA	-20.5006, 116.5022	14
WAMC72908	Balanidae	*Euacasta* cf. *porata*	28		Tetractinellida	Ancorinidae	*Rhabdastrella globostellata*	Ningaloo Reef, WA	-22.6626, 113.6396	10
WAMC71752	Balanidae	*Euacasta* cf. *sporillus*	65	WAMZ94237	Clionaida	Clionaidae	*Spheciospongia* sp.2	Maret Islands, WA	-14.4631, 124.8803	34
WAMC71753	Balanidae	*Euacasta* cf. *sporillus*	65	WAMZ94237	Clionaida	Clionaidae	*Spheciospongia* sp.2	Maret Islands, WA	-14.4631, 124.8803	34
WAMC67810	Balanidae	*Euacasta* cf. *sporillus*	65	WAMZ94237	Clionaida	Spirastrellidae	*Spheciospongia* sp.2	Maret Islands, WA	-14.4631, 124.8803	34
WAMC67722	Balanidae	*Euacasta* cf. *sporillus*	65	WAMZ97080	Suberitida	Halichondriidae	*Halichondria*	South Muiron Island, WA	-21.6835, 114.311	18
WAMC67727	Balanidae	*Euacasta* cf. *sporillus*	65	WAMZ97035	Suberitida	Halichondriidae	*Halichondria*?	Muiron Islands, WA	-21.694, 114.329	7
WAMC67744	Balanidae	*Euacasta* cf. *sporillus*	65	WAMZ97037	Suberitida	Halichondriidae	*Halichondria*	Muiron Islands, WA	-21.694, 114.329	7
WAMC71934	Balanidae	*Euacasta* cf. *sporillus*	65	WAMZ97174	Suberitida	Halichondriidae	*Halichondria* B1	Bonaparte Archipelago, WA	-14.5056, 124.9786	15
WAMC71869	Balanidae	*Euacasta* cf. *sporillus*	65		Tetractinellida	Ancorinidae	*Rhabdastrella*	Rottnest Island, WA	-32.0258, 115.5452	18
WAMC71871	Balanidae	*Euacasta* cf. *sporillus*	65		Tetractinellida	Ancorinidae	*Rhabdastrella*	Rottnest Island, WA	-32.0258, 115.5452	18
WAMC61527	Balanidae	*Euacasta* D15	22	WAMZ45346	Dictyoceratida	Thorectidae	*Hyrtios* sp.1	Ningaloo Reef, WA	-22.76, 113.643	16.4
WAMC67696	Balanidae	*Euacasta* D26		WAMZ88464	Dictyoceratida	Thorectidae	*Thorectandra* NG1	Ningaloo Reef, WA	-22.112, 113.795	154
WAMC58855	Balanidae	*Euacasta* D6	18		Unknown sponge			Montebello Islands, WA	-20.4513, 115.5827	6.5
WAMC72907	Balanidae	*Euacasta* D6	18		Unknown sponge			Unknown		
WAMC71815	Balanidae	*Euacasta* D6	18	WAMZ86874	Clionaida	Clionaidae	*Spheciospongia*	Dampier Archipelago, WA	-20.5367, 116.5442	0
WAMC71816	Balanidae	*Euacasta* D6	18	WAMZ86874	Clionaida	Clionaidae	*Spheciospongia*	Dampier Archipelago, WA	-20.5367, 116.5442	0
WAMC55406	Balanidae	*Euacasta* D6	18	WAMZ84420	Dictyoceratida	Dysideidae	*Dysidea* cf. *granulosa*	Maret Islands, WA	-14.431, 124.875	12
WAMC55407	Balanidae	*Euacasta* D6	18	WAMZ84420	Dictyoceratida	Dysideidae	*Dysidea* cf. *granulosa*	Maret Islands, WA	-14.431, 124.875	12
WAMC61351	Balanidae	*Euacasta* D6	18	WAMZ84240	Haplosclerida	Callyspongiidae	*Callyspongia* (*Toxochalina*)	Montebello Islands, WA	-20.388, 115.4923	22
WAMC61352	Balanidae	*Euacasta* D6	18	WAMZ84240	Haplosclerida	Callyspongiidae	*Callyspongia* (*Toxochalina*)	Montebello Islands, WA	-20.388, 115.4923	22
WAMC58803	Balanidae	*Euacasta* D6	18	WAMZ84295	Poecilosclerida	Mycalidae	*Aegropila* PB1	South Murion Island, WA	-21.6659, 114.3312	17
WAMC71760	Balanidae	*Euacasta* D6	18	WAMZ86904	Poecilosclerida	Tedaniidae	*Tedania* (*Trachytedania*)	Dampier Archipelago, WA	-20.4419, 116.6697	15
WAMC71933	Balanidae	*Euacasta* D6	18	WAMZ97185	Suberitida	Halichondriidae	*Halichondria* NW1	Bonaparte Archipelago, WA	-14.2666, 125.297	0
WAMC71936	Balanidae	*Euacasta* D6	18	WAMZ97229	Suberitida	Halichondriidae	*Hymeniacidon* KMB1	Bonaparte Archipelago, WA	-14.2823, 125.2219	0
WAMC61475	Balanidae	*Euacasta excoriatrix*	49	WAMZ54014	Suberitida	Halichondriidae	*Halichondria* NW1	Champagney Island, WA	-15.3324, 124.236	0
WAMC71800	Balanidae	*Euacasta excoriatrix*	49	WAMZ86895	Suberitida	Halichondriidae	*Halichondria* BAR1	Dampier Archipelago, WA	-20.468, 116.828	9
WAMC71801	Balanidae	*Euacasta excoriatrix*	49	WAMZ86895	Suberitida	Halichondriidae	*Halichondria* BAR1	Dampier Archipelago, WA	-20.468, 116.828	9
WAMC55337	Balanidae	*Euacasta porata*	35		Axinellida	Axinellidae	*Phycopsis*	Muiron Islands, WA	-21.6307, 114.2394	48.8
WAMC55348	Balanidae	*Euacasta porata*	35	WAMZ82210	Axinellida	Axinellidae	*Phycopsis* P1	Muiron Islands, WA	-21.6307, 114.2394	48.8
WAMC55059	Balanidae	*Euacasta porata*	35	WAMZ39844	Bubarida	Dictyonellidae	*Acanthella MR1*	Rottnest Island, WA	-31.9743, 115.5417	25
WAMC66687	Balanidae	*Euacasta porata*	35	WAMZ97097	Bubarida	Dictyonellidae	*Acanthella pulcherrima*	North Muiron Island, WA	-21.6277, 114.3737	17
WAMC55064	Balanidae	*Euacasta porata*	35	WAMZ39843	Clionaida	Spirastrellidae	*Diplastrella* ML1	Rottnest Island, WA	-31.9743, 115.5417	25
WAMC58788	Balanidae	*Euacasta porata*	35	WAMZ84301	Suberitida	Halichondriidae	*Halichondria*	South Murion Island, WA	-21.6659, 114.3312	17
WAMC58291	Balanidae	*Euacasta sporillus*	8		Suberitida	Halichondriidae	*Hymeniacidon*	Montebello Islands, WA	-20.3555, 115.5508	26
WAMC61392	Balanidae	*Euacasta sporillus*	8	WAMZ84219	Suberitida	Halichondriidae	*Hymeniacidon*	Ah Chong Island, WA	-20.5193, 115.5677	16.5
WAMC61393	Balanidae	*Euacasta sporillus*	8	WAMZ84219	Suberitida	Halichondriidae	*Hymeniacidon*	Ah Chong Island, WA	-20.5193, 115.5677	16.5
WAMC61415	Balanidae	*Euacasta sporillus*	8		Suberitida	Halichondriidae	*Hymeniacidon*	Montebello Islands, WA	-20.3555, 115.5508	26
WAMC61416	Balanidae	*Euacasta sporillus*	8		Suberitida	Halichondriidae	*Hymeniacidon*	Montebello Islands, WA	-20.3555, 115.5508	26
WAMC71763	Balanidae	*Euacasta sporillus*	8	WAMZ86946	Suberitida	Halichondriidae	*Hymeniacidon*	Dampier Archipelago, WA	-20.618, 116.464	16
WAMC71764	Balanidae	*Euacasta sporillus*	8	WAMZ86946	Suberitida	Halichondriidae	*Hymeniacidon*	Dampier Archipelago, WA	-20.618, 116.464	16
WAMC71765	Balanidae	*Euacasta sporillus*	8	WAMZ86946	Suberitida	Halichondriidae	*Hymeniacidon*	Dampier Archipelago, WA	-20.618, 116.464	16
WAMC71802	Balanidae	*Euacasta sporillus*	8	WAMZ86906	Suberitida	Halichondriidae	*Hymeniacidon*	Dampier Archipelago, WA	-20.5025, 116.6808	10
WAMC71803	Balanidae	*Euacasta sporillus*	8	WAMZ86906	Suberitida	Halichondriidae	*Hymeniacidon*	Dampier Archipelago, WA	-20.5025, 116.6808	10
WAMC67782	Balanidae	*Fistulobalanus*						Exmouth Gulf, WA	-22.3123, 114.1271	0
WAMC67783	Balanidae	*Fistulobalanus*						Exmouth Gulf, WA	-22.3123, 114.1271	0
WAMC54824	Balanidae	*Fistulobalanus kondakovi*						Hull Fouling, WA		2
WAMC74107	Balanidae	*Fistulobalanus* sp.						Dampier Archipelago, WA	-20.6105, 116.5306	0
WAMC74108	Balanidae	*Fistulobalanus* sp.						Dampier Archipelago, WA	-20.6105, 116.5306	0
WAMC54197	Balanidae	*Megabalanus ajax*			Anthoathecata	Milleporidae	*Millepora*	Ashmore Reef, WA	-12.2437, 122.2437	12
WAMC52752	Balanidae	*Megabalanus occator*						Onslow, WA	-21.85, 114.65	0

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WAMC52753	Balanidae	*Megabalanus occator*						Onslow, WA	-21.85, 114.65	0
WAMC52754	Balanidae	*Megabalanus occator*						Onslow, WA	-21.85, 114.65	0
WAMC52757	Balanidae	*Megabalanus* sp.1						Onslow, WA	-21.85, 114.65	0
WAMC55244	Balanidae	*Membranobalanus*			Polymastiida	Polymastiidae	*Polymastia*	Ashmore Reef, WA	-12.2623, 122.9848	1
WAMC55245	Balanidae	*Membranobalanus*			Polymastiida	Polymastiidae	*Polymastia*	Ashmore Reef, WA	-12.2623, 122.9848	1
WAMC55158	Balanidae	*Membranobalanus*	34	WAMZ69890	Haplosclerida	Petrosiidae	*Petrosia* (*Strongylata*) cf.*strongylata*	Ashmore Reef, WA	-12.1885, 123.1289	22
WAMC71775	Balanidae	*Membranobalanus*	57	WAMZ86894	Clionaida	Clionaidae	*Clionaidae orientalis*	Dampier Archipelago, WA	-20.468, 116.828	9
WAMC71777	Balanidae	*Membranobalanus*	57	WAMZ86894	Clionaida	Clionaidae	*Clionaidae orientalis*	Dampier Archipelago, WA	-20.468, 116.828	9
WAMC71778	Balanidae	*Membranobalanus*	57	WAMZ86894	Clionaida	Clionaidae	*Clionaidae orientalis*	Dampier Archipelago, WA	-20.468, 116.828	9
WAMC71787	Balanidae	*Membranobalanus*	57		Clionaida	Clionaidae	*Cliona*	Dampier Archipelago, WA	-20.5025, 116.6808	10
WAMC71886	Balanidae	*Membranobalanus*	57	WAMZ86917	Tetractinellida	Pachastrellidae	*Pachastrella* sp.1	Amathole Region, South Africa	-32.8333, 28.4666	76
WAMC71866	Balanidae	*Membranobalanus*	60		Clionaida	Clionaidae	*Cliona* cf.*orientalis*	Rottnest Island, WA	-32.0258, 115.5452	18
WAMC71867	Balanidae	*Membranobalanus*	60		Clionaida	Clionaidae	*Cliona* cf.*orientalis*	Rottnest Island, WA	-32.0258, 115.5452	18
WAMC71868	Balanidae	*Membranobalanus*	60		Clionaida	Clionaidae	*Cliona* cf.*orientalis*	Rottnest Island, WA	-32.0258, 115.5452	18
WAMC55378	Balanidae	*Membranobalanus*	71	WAMZ81751	Clionaida	Clionaidae	*Spheciospongia* PB1	Rosily Shoals, WA	-21.3301, 115.0207	18.2
WAMC55379	Balanidae	*Membranobalanus*	71	WAMZ81751	Clionaida	Clionaidae	*Spheciospongia* PB1	Rosily Shoals, WA	-21.3301, 115.0207	18.2
WAMC55380	Balanidae	*Membranobalanus*	71	WAMZ81751	Clionaida	Clionaidae	*Spheciospongia* PB1	Rosily Shoals, WA	-21.3301, 115.0207	18.2
WAMC55381	Balanidae	*Membranobalanus*	71	WAMZ81751	Clionaida	Clionaidae	*Spheciospongia* PB1	Rosily Shoals, WA	-21.3301, 115.0207	18.2
WAMC71847	Balanidae	*Membranobalanus brachialis*	9		Clionaida			Dampier Archipelago, WA	-20.618, 116.464	16
WAMC71848	Balanidae	*Membranobalanus brachialis*	9		Clionaida			Dampier Archipelago, WA	-20.618, 116.464	16
WAMC71861	Balanidae	*Membranobalanus brachialis*	9		Clionaida			Dampier Archipelago, WA	-20.618, 116.464	16
WAMC71930	Balanidae	*Membranobalanus brachialis*	9		Clionaida	Spirastrellidae	*Spheciospongia*	Dampier Archipelago, WA	-20.618, 116.464	16
WAMC58783	Balanidae	*Membranobalanus koreanus*	72	WAMZ84302	Clionaida	Clionaidae	*Cliona*	South Murion Island, WA	-21.6659, 114.3312	17
WAMC58785	Balanidae	*Membranobalanus koreanus*	72	WAMZ84302	Clionaida	Clionaidae	*Cliona*	South Murion Island, WA	-21.6659, 114.3312	17
WAMC71832	Balanidae	*Membranobalanus koreanus*	72	WAMZ84302	Clionaida	Clionaidae	*Cliona*	Muiron Islands, WA	-21.6659, 114.3312	17
WAMC71833	Balanidae	*Membranobalanus koreanus*	72	WAMZ84302	Clionaida	Clionaidae	*Cliona*	Muiron Islands, WA	-21.6659, 114.3312	17
WAMC56664	Balanidae	*Membranobalanus longirostrum*	41		Clionaida	Clionaidae	*Clionaidae*	Imperieuse Reef, WA	-17.5935, 118.9772	12
WAMC71853	Balanidae	*Membranobalanus porphyrophilus*	58	WAMZ86959	Clionaida	Clionaidae	*Spheciospongia purpurea*	Rottnest Island, WA	-32.0148, 115.5588	12
WAMC71881	Balanidae	*Membranobalanus porphyrophilus*	58	WAMZ86959	Clionaida	Clionaidae	*Spheciospongia purpurea*	Rottnest Island, WA	-32.0148, 115.5588	12
WAMC48563	Balanidae	*Multatria filigranus*	67		Pocilscerlida	Crambeidae	*Monanchora*	Kimberley, WA	-14.9741, 124.3975	16
WAMC71865	Balanidae	*Multatria filigranus*	67		Poecilosclerida	Crambeidae	*Monanchora*	Rottnest Island, WA	-32.0258, 115.5452	18
WAMC71915	Balanidae	*Multatria filigranus*	67		Poecilosclerida	Crambeidae	*Monanchora* cf. sp.3	Rottnest Island, WA	-32.0258, 115.5452	18
WAMC67680	Balanidae	*Neoacasta* cf. coriobasis D22		WAMZ53961	Dictyoceratida	Irciniidae	*Sarcotragus* PB2	Onslow, WA	-21.513, 115.001	14.7
WAMC67682	Balanidae	*Neoacasta* cf. *coriobasis* D22		WAMZ53961	Dictyoceratida	Irciniidae	*Sarcotragus* PB2	Onslow, WA	-21.513, 115.001	14.7
WAMC67657	Balanidae	*Neoacasta* cf. *coriobasis* D22		WAMZ9748	Dictyoceratida	Irciniidae	*Psammocinia* sp.6	Cape Legendre, WA	-20.327, 116.898	38
WAMC67658	Balanidae	*Neoacasta* cf. *coriobasis* D22		WAMZ9748	Dictyoceratida	Irciniidae	*Psammocinia* sp.6	Cape Legendre, WA	-20.327, 116.898	38
WAMC67673	Balanidae	*Neoacasta* cf. *coriobasis* D22	24	WAMZ81896	Dictyoceratida	Irciniidae	*Sarcotragus* PB1	Barrow Island, WA	-21.119, 115.541	13
WAMC67675	Balanidae	*Neoacasta* cf. *coriobasis* D22	24	WAMZ81896	Dictyoceratida	Irciniidae	*Sarcotragus* PB1	Barrow Island, WA	-21.119, 115.541	13
WAMC67679	Balanidae	*Neoacasta* cf. *coriobasis* D22	24	WAMZ53961	Dictyoceratida	Irciniidae	*Sarcotragus* PB2	Onslow, WA	-21.513, 115.001	14.7
WAMC67692	Balanidae	*Neoacasta* cf. *coriobasis* D22	24	WAMZ88477	Dictyoceratida	Irciniidae	*Sarcotragus* SS8	Camden Sound, WA	-15.613, 124.073	35.3
WAMC67693	Balanidae	*Neoacasta* cf. *coriobasis* D22	24	WAMZ88477	Dictyoceratida	Irciniidae	*Sarcotragus* SS8	Camden Sound, WA	-15.613, 124.073	35.3
WAMC67694	Balanidae	*Neoacasta* cf. *coriobasis* D22	24	WAMZ88477	Dictyoceratida	Irciniidae	*Sarcotragus* SS8	Camden Sound, WA	-15.613, 124.073	35.3
WAMC71751	Balanidae	*Neoacasta* cf. *coriobasis* D22	24	WAMZ86866	Dictyoceratida	Irciniidae	*Sarcotragus* DA1	Dampier Archipelago, WA	-20.6, 116.462	16
WAMC67691	Balanidae	*Neoacasta* cf. *coriobasis* D24	55	WAMZ36194	Dictyoceratida	Irciniidae	*Sarcotragus* SS14	Cape Leveque, WA	-15.081, 121.78	97
WAMC67695	Balanidae	*Neoacasta* cf. *coriobasis* D25	108	WAMZ36189	Dictyoceratida	Irciniidae	*Sarcotragus* SS11	Cape Leveque, WA	-15.094, 121.786	78
WAMC72925	Balanidae	*Neoacasta* cf. *coriobasis* D29	108	WAMZ95514	Dictyoceratida	Irciniidae	*Sarcotragus* KMB5	Lynher Bank, WA	-15.792, 121.965	76.9
WAMC43665	Balanidae	*Neoacasta* cf. *laevigata*		WAMZ29266	Dictyoceratida	Thorectidae	*Polyfibrospongia flabellifera*	Montgomery Reef, WA	-15.8765, 124.3299	0
WAMC58344	Balanidae	*Neoacasta* cf. *laevigata*	16	WAMZ84196	Dictyoceratida	Thorectidae	*Polyfibrospongia flabellifera*	Ah Chong Island, WA	-20.5193, 115.5677	16.5
WAMC71935	Balanidae	*Neoacasta* cf. *laevigata*	16	WAMZ97193	Dictyoceratida	Thorectidae	*Lamellodysidea herbacea*	Bonaparte Archipelago, WA	-14.2528, 125.3068	0
WAMC74449	Balanidae	*Neoacasta* cf. *laevigata*	16	WAMZ88894	Dictyoceratida	Thorectidae	*Polyfibrospongia kulit*	Exmouth Gulf, WA	-21.8386, 114.0478	1
WAMC58877	Balanidae	*Neoacasta* cf. *laevigata* D1		WAMZ54274	Dictyoceratida	Thorectidae	*Phyllospongia foliascens*	Champagney Island, WA	-15.331, 124.217	0
WAMC58885	Balanidae	*Neoacasta* cf. *laevigata* D1		WAMZ29270	Dictyoceratida	Thorectidae	*Phyllospongia papyracea*	Montgomery Reef, WA	-16.014, 124.173	0
WAMC58912	Balanidae	*Neoacasta* cf. *laevigata* D1		WAMZ29269	Dictyoceratida	Thorectidae	*Phyllospongia papyracea*	Long Reef, WA	-13.915, 125.774	5

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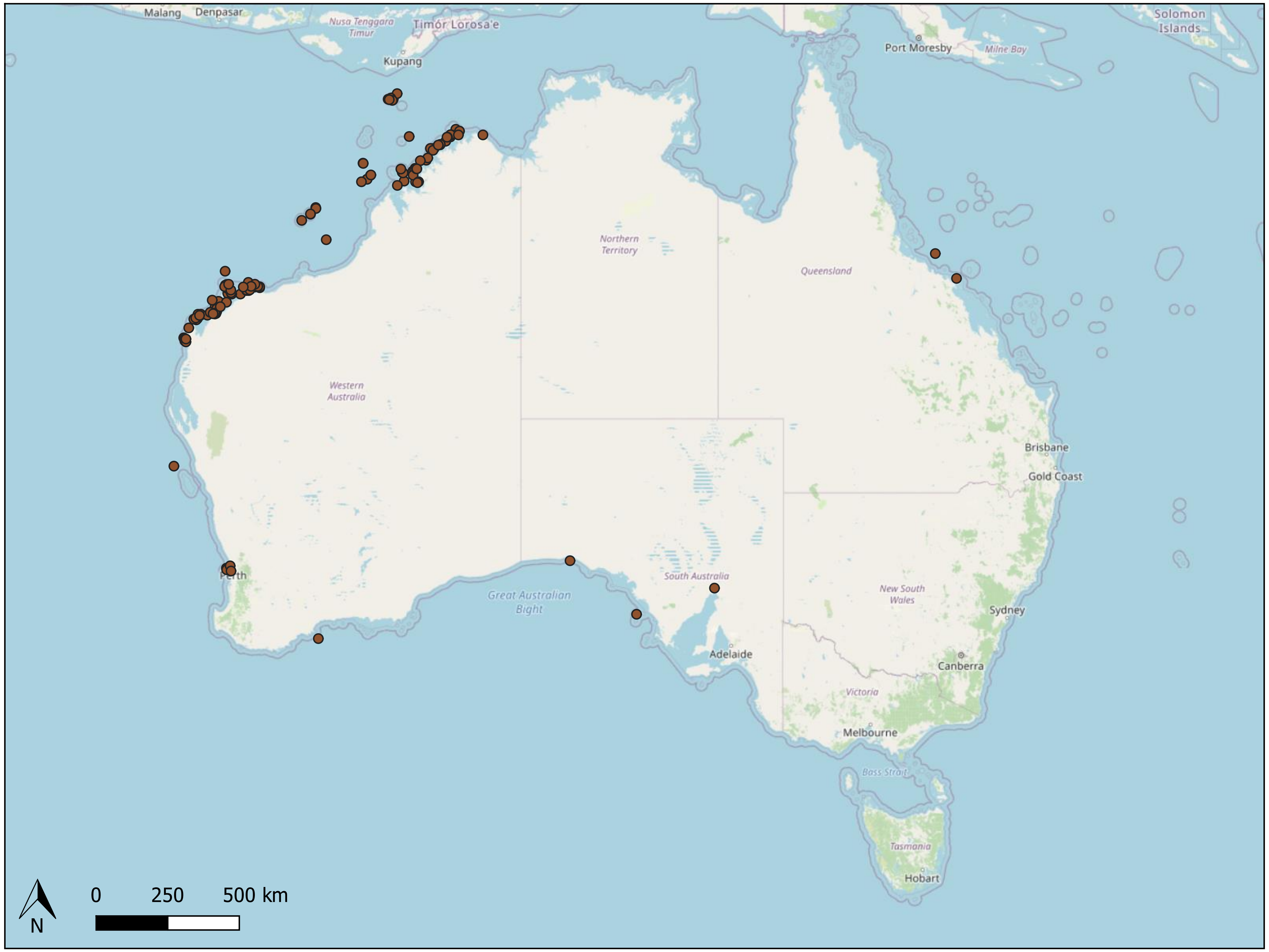
WAMC50622	Balanidae	*Neoacasta* cf. *laevigata* D1	83	WAMZ54694	Dictyoceratida	Thorectidae	*Phyllospongia papyracea*	Hedey Island, WA	-14.954, 124.673	0
WAMC55429	Balanidae	*Neoacasta* cf. *laevigata* D1	83	WAMZ29268	Dictyoceratida	Thorectidae	*Phyllospongia papyracea*	Montgomery Reef, WA	-15.897, 124.324	0
WAMC55431	Balanidae	*Neoacasta* cf. *laevigata* D1	83	WAMZ29269	Dictyoceratida	Thorectidae	*Phyllospongia papyracea*	Long Reef, WA	-13.915, 125.774	5
WAMC55432	Balanidae	*Neoacasta* cf. *laevigata* D1	83	WAMZ29269	Dictyoceratida	Thorectidae	*Phyllospongia papyracea*	Long Reef, WA	-13.915, 125.774	5
WAMC58881	Balanidae	*Neoacasta* cf. *laevigata* D1	83	WAMZ84421	Dictyoceratida	Thorectidae	*Phyllospongia foliascens*	Woodward Island, WA	-14.848, 124.74	0
WAMC58893	Balanidae	*Neoacasta* cf. *laevigata* D1	83	WAMZ29267	Dictyoceratida	Thorectidae	*Phyllospongia papyracea*	Montgomery Reef, WA	-15.944, 124.267	0
WAMC58894	Balanidae	*Neoacasta* cf. *laevigata* D1	83	WAMZ29267	Dictyoceratida	Thorectidae	*Phyllospongia papyracea*	Montgomery Reef, WA	-15.944, 124.267	0
WAMC58895	Balanidae	*Neoacasta* cf. *laevigata* D1	83	WAMZ29267	Dictyoceratida	Thorectidae	*Phyllospongia papyracea*	Montgomery Reef, WA	-15.944, 124.267	0
WAMC58909	Balanidae	*Neoacasta* cf. *laevigata* D1	83	WAMZ29269	Dictyoceratida	Thorectidae	*Phyllospongia papyracea*	Long Reef, WA	-13.915, 125.774	5
WAMC58910	Balanidae	*Neoacasta* cf. *laevigata* D1	83	WAMZ29269	Dictyoceratida	Thorectidae	*Phyllospongia papyracea*	Long Reef, WA	-13.915, 125.774	5
WAMC58911	Balanidae	*Neoacasta* cf. *laevigata* D1	83	WAMZ29269	Dictyoceratida	Thorectidae	*Phyllospongia papyracea*	Long Reef, WA	-13.915, 125.774	5
WAMC61493	Balanidae	*Neoacasta* cf. *laevigata* D1	83	WAMZ95207	Dictyoceratida	Thorectidae	*Lendenfeldia plicata*	Eclipse Islands, WA	-13.583, 126.019	1
WAMC61494	Balanidae	*Neoacasta* cf. *laevigata* D1	83	WAMZ95207	Dictyoceratida	Thorectidae	*Lendenfeldia plicata*	Eclipse Islands, WA	-13.583, 126.019	1
WAMC54067	Balanidae	*Neoacasta* cf. *laevigata* D2	111	WAMZ69882	Dictyoceratida	Thorectidae	*Phyllospongia foliascens*	Ashmore Reef, WA	-12.277, 123.136	1
WAMC54301	Balanidae	*Neoacasta* cf. *laevigata* D2	111	WAMZ69884	Dictyoceratida	Thorectidae	*Phyllospongia foliascens*	Ashmore Reef, WA	-12.21, 123.144	1
WAMC55249	Balanidae	*Neoacasta* cf. *laevigata* D2	111	WAMZ69882	Dictyoceratida	Thorectidae	*Phyllospongia foliascens*	Ashmore Reef, WA	-12.277, 123.136	1
WAMC55250	Balanidae	*Neoacasta* cf. *laevigata* D2	111	WAMZ69882	Dictyoceratida	Thorectidae	*Phyllospongia foliascens*	Ashmore Reef, WA	-12.277, 123.136	1
WAMC55265	Balanidae	*Neoacasta* cf. *laevigata* D2	111	WAMZ69884	Dictyoceratida	Thorectidae	*Phyllospongia foliascens*	Ashmore Reef, WA	-12.21, 123.144	1
WAMC55266	Balanidae	*Neoacasta* cf. *laevigata* D2	111	WAMZ69884	Dictyoceratida	Thorectidae	*Phyllospongia foliascens*	Ashmore Reef, WA	-12.21, 123.144	1
WAMC55267	Balanidae	*Neoacasta* cf. *laevigata* D2	111	WAMZ69884	Dictyoceratida	Thorectidae	*Phyllospongia foliascens*	Ashmore Reef, WA	-12.21, 123.144	1
WAMC55268	Balanidae	*Neoacasta* cf. *laevigata* D2	111	WAMZ69884	Dictyoceratida	Thorectidae	*Phyllospongia foliascens*	Ashmore Reef, WA	-12.21, 123.144	1
WAMC55269	Balanidae	*Neoacasta* cf. *laevigata* D2	111	WAMZ69884	Dictyoceratida	Thorectidae	*Phyllospongia foliascens*	Ashmore Reef, WA	-12.21, 123.144	1
WAMC55284	Balanidae	*Neoacasta* cf. *laevigata* D3		WAMZ29265	Dictyoceratida	Thorectidae	*Polyfibrospongia flabellifera*	Long Reef, WA	-13.915, 125.774	5
WAMC55285	Balanidae	*Neoacasta* cf. *laevigata* D3		WAMZ29265	Dictyoceratida	Thorectidae	*Polyfibrospongia flabellifera*	Long Reef, WA	-13.915, 125.774	5
WAMC55287	Balanidae	*Neoacasta* cf. *laevigata* D3		WAMZ29282	Dictyoceratida	Thorectidae	*Polyfibrospongia kulit*	Montgomery Reef, WA	-15.897, 124.324	0
WAMC55288	Balanidae	*Neoacasta* cf. *laevigata* D3		WAMZ29282	Dictyoceratida	Thorectidae	*Polyfibrospongia kulit*	Montgomery Reef, WA	-15.897, 124.324	0
WAMC55411	Balanidae	*Neoacasta* cf. *laevigata* D3		WAMZ84414	Dictyoceratida	Thorectidae	*Polyfibrospongia kulit*	Champagney Island, WA	-15.331, 124.217	0
WAMC58891	Balanidae	*Neoacasta* cf. *laevigata* D3		WAMZ29289	Dictyoceratida	Thorectidae	*Polyfibrospongia kulit*	Cassini Island, WA	-13.952, 125.624	2
WAMC58892	Balanidae	*Neoacasta* cf. *laevigata* D3		WAMZ29289	Dictyoceratida	Thorectidae	*Polyfibrospongia kulit*	Cassini Island, WA	-13.952, 125.624	2
WAMC61431	Balanidae	*Neoacasta* cf. *laevigata* D3		WAMZ84100	Dictyoceratida	Thorectidae	*Polyfibrospongia flabellifera*	Trimouille Island, WA	-20.372, 115.564	11
WAMC55286	Balanidae	*Neoacasta* cf. *laevigata* D3	16	WAMZ29265	Dictyoceratida	Thorectidae	*Polyfibrospongia flabellifera*	Long Reef, WA	-13.915, 125.774	5
WAMC55410	Balanidae	*Neoacasta* cf. *laevigata* D3	16	WAMZ84414	Dictyoceratida	Thorectidae	*Polyfibrospongia kulit*	Champagney Island, WA	-15.331, 124.217	0
WAMC58797	Balanidae	*Neoacasta* cf. *laevigata* D3	16	WAMZ84232	Dictyoceratida	Thorectidae	*Polyfibrospongia flabellifera*	Montebello Islands, WA	-20.384, 115.539	11
WAMC58798	Balanidae	*Neoacasta* cf. *laevigata* D3	16	WAMZ84232	Dictyoceratida	Thorectidae	*Polyfibrospongia flabellifera*	Montebello Islands, WA	-20.384, 115.539	11
WAMC58799	Balanidae	*Neoacasta* cf. *laevigata* D3	16	WAMZ84232	Dictyoceratida	Thorectidae	*Polyfibrospongia flabellifera*	Montebello Islands, WA	-20.384, 115.539	11
WAMC58800	Balanidae	*Neoacasta* cf. *laevigata* D3	16	WAMZ84232	Dictyoceratida	Thorectidae	*Polyfibrospongia flabellifera*	Montebello Islands, WA	-20.384, 115.539	11
WAMC58801	Balanidae	*Neoacasta* cf. *laevigata* D3	16	WAMZ84232	Dictyoceratida	Thorectidae	*Polyfibrospongia flabellifera*	Montebello Islands, WA	-20.384, 115.539	11
WAMC58886	Balanidae	*Neoacasta* cf. *laevigata* D3	16	WAMZ54335	Dictyoceratida	Thorectidae	*Polyfibrospongia kulit*	Mavis Reef, WA	-15.505, 123.608	12
WAMC58887	Balanidae	*Neoacasta* cf. *laevigata* D3	16	WAMZ54335	Dictyoceratida	Thorectidae	*Polyfibrospongia kulit*	Mavis Reef, WA	-15.505, 123.608	12
WAMC58888	Balanidae	*Neoacasta* cf. *laevigata* D3	16	WAMZ54335	Dictyoceratida	Thorectidae	*Polyfibrospongia kulit*	Mavis Reef, WA	-15.505, 123.608	12
WAMC58889	Balanidae	*Neoacasta* cf. *laevigata* D3	16	WAMZ54371	Dictyoceratida	Thorectidae	*Polyfibrospongia flabellifera*	Mavis Reef, WA	-15.505, 123.608	12
WAMC61433	Balanidae	*Neoacasta* cf. *laevigata* D3	16	WAMZ84100	Dictyoceratida	Thorectidae	*Polyfibrospongia flabellifera*	Montebello Islands, WA	-20.372, 115.564	11
WAMC61500	Balanidae	*Neoacasta* cf. *laevigata* D3	16	WAMZ95269	Dictyoceratida	Thorectidae	*Polyfibrospongia flabellifera*	Long Reef, WA	-13.83, 125.833	1
WAMC61501	Balanidae	*Neoacasta* cf. *laevigata* D3	16	WAMZ95269	Dictyoceratida	Thorectidae	*Polyfibrospongia flabellifera*	Long Reef, WA	-13.83, 125.833	1
WAMC61502	Balanidae	*Neoacasta* cf. *laevigata* D3	16	WAMZ95269	Dictyoceratida	Thorectidae	*Polyfibrospongia flabellifera*	Long Reef, WA	-13.83, 125.833	1
WAMC61517	Balanidae	*Neoacasta* cf. *laevigata* D3	16	WAMZ3237	Dictyoceratida	Thorectidae	*Polyfibrospongia kulit*	Dampier Archipelago, WA	-20.444, 116.973	2.5
WAMC71746	Balanidae	*Neoacasta* cf. *laevigata* D3	16	WAMZ86893	Dictyoceratida	Thorectidae	*Polyfibrospongia flabellifera*	Dampier Archipelago, WA	-20.468, 116.828	9
WAMC71747	Balanidae	*Neoacasta* cf. *laevigata* D3	16	WAMZ86893	Dictyoceratida	Thorectidae	*Polyfibrospongia flabellifera*	Dampier Archipelago, WA	-20.468, 116.828	9
WAMC71748	Balanidae	*Neoacasta* cf. *laevigata* D3	16	WAMZ86893	Dictyoceratida	Thorectidae	*Polyfibrospongia flabellifera*	Dampier Archipelago, WA	-20.468, 116.828	9
WAMC71749	Balanidae	*Neoacasta* cf. *laevigata* D3	16	WAMZ86892	Dictyoceratida	Thorectidae	*Polyfibrospongia flabellifera*	Dampier Archipelago, WA	-20.468, 116.828	9
WAMC71750	Balanidae	*Neoacasta* cf. *laevigata* D3	16	WAMZ86892	Dictyoceratida	Thorectidae	*Polyfibrospongia flabellifera*	Dampier Archipelago, WA	-20.468, 116.828	9
WAMC71756	Balanidae	*Neoacasta* cf. *laevigata* D3	16	WAMZ97190	Dictyoceratida	Thorectidae	*Polyfibrospongia kulit*	East Montelivet Island, WA	-14.267, 125.297	0

Specimen Accession	Family	Identification	PSH	Host accession	Host Order	Host family	Host identification	Locality	Coordinates	Depth
WAMC72913	Balanidae	*Neoacasta* cf. *laevigata* D31	110	WAMZ86304	Dictyoceratida	Thorectidae	*Phyllospongia foliascens*	Fsar Reef, Saudia Arabia	22.243, 39.039	95.6
WAMC67651	Balanidae	*Neoacasta* cf. *planibasis* D13		WAMZ37653	Dictyoceratida	Thorectidae	*Luffariella* cf. SS10	Scott Reef, WA	-14.177, 121.882	12.8
WAMC67652	Balanidae	*Neoacasta* cf. *planibasis* D13		WAMZ37653	Dictyoceratida	Thorectidae	*Luffariella* cf. SS10	Scott Reef, WA	-14.177, 121.882	12.8
WAMC58907	Balanidae	*Neoacasta* cf. *planibasis* D13		WAMZ54277	Dictyoceratida	Thorectidae	*Strepsichordaia lendenfeldi*	Kimberley, WA	-15.336, 123.513	16
WAMC61512	Balanidae	*Neoacasta* cf. *planibasis* D13		WAMZ88188	Dictyoceratida	Thorectidae	*Luffariella* SS11	Onslow, WA	-21.526, 115.092	12.9
WAMC61452	Balanidae	*Neoacasta* cf. *scuticosta*		WAMZ82324	Tethyida	Tethyidae	*Tethya cf.robusta*	Pilbara Shelf, WA	-20.2694, 116.5411	46
WAMC58875	Balanidae	*Neoacasta* cf. *scuticosta*	40	WAMZ87050	Clionaida	Placospongiidae	*Placospongia melobesioides*	Lynher Bank, WA	-15.4313, 124.0592	36
WAMC61460	Balanidae	*Neoacasta* cf. *scuticosta*	40		Clionaida	Placospongiidae	*Placospongia melobesioides*	Lynher Bank, WA	-15.62, 122.1177	46
WAMC61461	Balanidae	*Neoacasta* cf. *scuticosta*	40		Clionaida	Placospongiidae	*Placospongia melobesioides*	Lynher Bank, WA	-15.62, 122.1177	46
WAMC61467	Balanidae	*Neoacasta* cf. *scuticosta*	40		Clionaida	placospongiidae	*Placospongia*	Camden Sound, WA	-15.3114, 124.1629	41.9
WAMC55347	Balanidae	*Neoacasta* cf. *scuticosta*	40	WAMZ82219	Tethyida	Tethyidae	*Tethya cf.robusta*	South East Island, WA	-20.3496, 115.6437	50
WAMC55375	Balanidae	*Neoacasta* cf. *scuticosta*	40	WAMZ82324	Tethyida	Tethyidae	*Tethya cf.robusta*	Quartermaine Island, WA	-20.2693, 116.5412	46
WAMC55376	Balanidae	*Neoacasta* cf. *scuticosta*	40	WAMZ82324	Tethyida	Tethyidae	*Tethya cf.robusta*	Quartermaine Island, WA	-20.2693, 116.5412	46
WAMC55377	Balanidae	*Neoacasta* cf. *scuticosta*	40	WAMZ82324	Tethyida	Tethyidae	*Tethya cf.robusta*	Quartermaine Island, WA	-20.2693, 116.5412	46
WAMC61504	Balanidae	*Neoacasta* D11		WAMZ88457	Dictyoceratida	Spongiidae	*Spongia* CERF1	Gnaraloo, WA	-23.873, 113.434	35.42
WAMC61505	Balanidae	*Neoacasta* D11	50	WAMZ35861	Dictyoceratida	Spongiidae	*Spongia* (*Heterofibria*) SS1	North West Shelf, WA	-19.791, 115.476	92
WAMC61507	Balanidae	*Neoacasta* D12	84	WAMZ35815	Dictyoceratida	Spongiidae	*Hyattella* SS2	Kalbarri, WA	-27.928, 113.138	252
WAMC61508	Balanidae	*Neoacasta* D12	84	WAMZ35815	Dictyoceratida	Spongiidae	*Hyattella* SS2	Kalbarri, WA	-27.928, 113.138	252
WAMC61509	Balanidae	*Neoacasta* D12	84	WAMZ35815	Dictyoceratida	Spongiidae	*Hyattella* SS2	Kalbarri, WA	-27.928, 113.138	252
WAMC75729	Balanidae	*Neoacasta* D12	84		Dictyoceratida	Spongiidae	*Spongia* (*Heterofibria*)	Bremer Canyon, WA	-34.6574, 119.7357	506.524
WAMC58362	Balanidae	*Neoacasta* D13	23		Dictyoceratida			Hermite Island, WA	-20.454, 115.4567	18
WAMC58908	Balanidae	*Neoacasta* D13	23	WAMZ54277	Dictyoceratida	Thorectidae	*Strepsichordaia lendenfeldi*	Kimberley, WA	-15.336, 123.513	16
WAMC61513	Balanidae	*Neoacasta* D13	23	WAMZ65304	Dictyoceratida	Thorectidae	*Luffariella* SS11	Onslow, WA	-21.62, 115.012	10.7
WAMC61534	Balanidae	*Neoacasta* D13	23	WAMZ88441	Dictyoceratida	Thorectidae	*Luffariella* SS11	Ningaloo Reef, WA	-22.628, 113.593	80.3
WAMC61535	Balanidae	*Neoacasta* D13	23	WAMZ88441	Dictyoceratida	Thorectidae	*Luffariella* SS11	Ningaloo Reef, WA	-22.628, 113.593	80.3
WAMC67635	Balanidae	*Neoacasta* D13	23	WAMZ69501	Dictyoceratida	Thorectidae	*Luffariella* SS10	Ashmore Reef, WA	-12.231, 123	10.8
WAMC67643	Balanidae	*Neoacasta* D13	23	WAMZ82700	Dictyoceratida	Thorectidae	*Cacospongia* P1	Quartermaine Island, WA	-20.269, 116.541	44.3
WAMC67644	Balanidae	*Neoacasta* D13	23	WAMZ69599	Dictyoceratida	Thorectidae	*Luffariella* cf. SS10	Ashmore Reef, WA	-12.237, 123.16	13.6
WAMC71809	Balanidae	*Neoacasta* D13	23	WAMZ86888	Dictyoceratida	Thorectidae	*Luffariella* SS11	Dampier Archipelago, WA	-20.502, 116.633	12
WAMC71810	Balanidae	*Neoacasta* D13	23	WAMZ86888	Dictyoceratida	Thorectidae	*Luffariella* SS11	Dampier Archipelago, WA	-20.502, 116.633	12
WAMC71813	Balanidae	*Neoacasta* D13	23	WAMZ86891	Dictyoceratida	Thorectidae	*Strepsichordaia lendenfeldi*	Dampier Archipelago, WA	-20.468, 116.828	9
WAMC71814	Balanidae	*Neoacasta* D13	23	WAMZ86891	Dictyoceratida	Thorectidae	*Strepsichordaia lendenfeldi*	Dampier Archipelago, WA	-20.468, 116.828	9
QM W29526	Balanidae	*Neoacasta* D14		QM G325493	Dictyoceratida	Thorectidae	*Fascaplysinopsis reticulata*	Gulf of Carpentaria, QLD	-15.9354, 139.1692	38
WAMC61516	Balanidae	*Neoacasta* D14		WAMZ65221	Dictyoceratida	Thorectidae	*Cacospongia* PB2	Onslow, WA	-21.584, 115.011	10.4
WAMC61536	Balanidae	*Neoacasta* D14		WAMZ86287	Dictyoceratida	Thorectidae	*Cacospongia* NG1	Muiron Islands, WA	-21.603, 114.296	55.3
WAMC61514	Balanidae	*Neoacasta* D14	112	WAMZ65221	Dictyoceratida	Thorectidae	*Cacospongia* PB2	Onslow, WA	-21.584, 115.011	10.4
WAMC61515	Balanidae	*Neoacasta* D14	112	WAMZ65221	Dictyoceratida	Thorectidae	*Cacospongia* PB2	Onslow, WA	-21.584, 115.011	10.4
WAMC71757	Balanidae	*Neoacasta* D14	112	WAMZ86896	Dictyoceratida	Thorectidae	*Cacospongia* NG1	Dampier Archipelago, WA	-20.468, 116.828	9
WAMC71758	Balanidae	*Neoacasta* D14	112	WAMZ86896	Dictyoceratida	Thorectidae	*Cacospongia* NG1	Dampier Archipelago, WA	-20.468, 116.828	9
WAMC71759	Balanidae	*Neoacasta* D14	112	WAMZ86896	Dictyoceratida	Thorectidae	*Cacospongia* NG1	Dampier Archipelago, WA	-20.468, 116.828	9
WAMC72917	Balanidae	*Neoacasta* D14	112	WAMZ95574	Dictyoceratida	Thorectidae	*Luffariella* PB1	Lynher Bank, WA	-15.792, 121.965	76.9
WAMC61519	Balanidae	*Neoacasta* D14	114	WAMZ35737	Dictyoceratida	Thorectidae	*Hyrtios* SS4	Barrow Island, WA	-21.031, 114.892	93
WAMC61520	Balanidae	*Neoacasta* D14	114	WAMZ35737	Dictyoceratida	Thorectidae	*Hyrtios* SS4	Barrow Island, WA	-21.031, 114.892	93
WAMC61521	Balanidae	*Neoacasta* D14	114	WAMZ35737	Dictyoceratida	Thorectidae	*Hyrtios* SS4	Barrow Island, WA	-21.031, 114.892	93
WAMC71811	Balanidae	*Neoacasta* D14	114	WAMZ86873	Dictyoceratida	Thorectidae	?*Cacospongia* DA1	Dampier Archipelago, WA	-20.618, 116.464	16
WAMC71812	Balanidae	*Neoacasta* D14	114	WAMZ86873	Dictyoceratida	Thorectidae	?*Cacospongia* DA1	Dampier Archipelago, WA	-20.618, 116.464	16
WAMC67632	Balanidae	*Neoacasta* D17		WAMZ87934	Dictyoceratida	Thorectidae	*Hyrtios* SS2	Camden Sound, WA	-15.431, 124.059	35.9
WAMC67640	Balanidae	*Neoacasta* D19	51	WAMZ54294	Dictyoceratida	Spongiidae	*Spongia* (*Australospongia*) KMB1	Fraser Island, WA	-16.055, 123.35	15.6
WAMC67665	Balanidae	*Neoacasta* D21	113	WAMZ81905	Dictyoceratida	Spongiidae	*Hippospongia* P1	Sultan Reef, WA	-21.4, 115.09	18.1
WAMC67666	Balanidae	*Neoacasta* D21	113	WAMZ81905	Dictyoceratida	Spongiidae	*Hippospongia* P1	Sultan Reef, WA	-21.4, 115.09	18.1
WAMC67667	Balanidae	*Neoacasta* D21	113	WAMZ81905	Dictyoceratida	Spongiidae	*Hippospongia* P1	Sultan Reef, WA	-21.4, 115.09	18.1
WAMC67731	Balanidae	*Neoacasta* D21	113	WAMZ97133	Dictyoceratida	Spongiidae	*Hippospongia* P1	Exmouth Gulf, WA	-21.821, 114.209	22

Specimen Accession	Family	Identification	PSH	Host accession	Host Order	Host family	Host identification	Locality	Coordinates	Depth
WAMC67732	Balanidae	*Neoacasta* D21	113	WAMZ97133	Dictyoceratida	Spongiidae	*Hippospongia* P1	Exmouth Gulf, WA	-21.821, 114.209	22
WAMC67683	Balanidae	*Neoacasta* D23	54	WAMZ36016	Dictyoceratida	Irciniidae	*Sarcotragus SS7*	Imperieuse Reef, WA	-18.425, 120.099	103
WAMC67685	Balanidae	*Neoacasta* D23	54	WAMZ36016	Dictyoceratida	Irciniidae	*Sarcotragus SS7*	Imperieuse Reef, WA	-18.425, 120.099	103
WAMC67690	Balanidae	*Neoacasta* D24		WAMZ36194	Dictyoceratida	Irciniidae	*Sarcotragus* SS14	Cape Leveque, WA	-15.081, 121.78	97
WAMC72920	Balanidae	*Neoacasta* D27	85	WAMZ95497	Dictyoceratida	Spongiidae	*Spongia* cf.PB1	Lynher Bank, WA	-15.601, 122.141	76
WAMC72927	Balanidae	*Neoacasta* D27	85	WAMZ95487	Dictyoceratida	Spongiidae	*Spongia* cf.PB1	Lynher Bank, WA	-15.7918, 121.9649	76.9
WAMC72922	Balanidae	*Neoacasta* D28	25	WAMZ90675	Dictyoceratida	Spongiidae	*Hippospongia* SS1	Lynher Bank, WA	-15.898, 121.705	80.4
WAMC72924	Balanidae	*Neoacasta* D29		WAMZ95514	Dictyoceratida	Irciniidae	*Sarcotragus* KMB5	Lynher Bank, WA	-15.898, 121.705	80.4
QM W29522	Balanidae	*Neoacasta* D30	109	QM G25081	Dictyoceratida	Dysideidae	*Candidaspongia flabellata*	Bowden Reef, QLD	-19.0333, 147.9333	24
WAMC58342	Balanidae	*Neoacasta* D30	109		Dictyoceratida	Spongiidae		Ah Chong Island, WA	-20.5193, 115.5677	16.5
SAMAC14356	Balanidae	*Neoacasta* D32		SAMA S839	Dictyoceratida	Thorectidae	*Thorectandra*	Great Australian Bight, SA	-31.7594, 130.6839	53
SAMAC14357	Balanidae	*Neoacasta* D32		SAMA S839	Dictyoceratida	Thorectidae	*Thorectandra*	Great Australian Bight, SA	-31.7594, 130.6839	53
SAMAC14358	Balanidae	*Neoacasta* D33		SAMA S1177	Dictyoceratida	Irciniidae	*Ircinia sp.5*	Spencer Gulf, SA	-33.0333, 137.7667	20
WAMC67688	Balanidae	*Neoacasta* D33		WAMZ21460	Dictyoceratida	Irciniidae	*Sarcotragus* JB1	Jurien Bay, WA	-30.345, 115.038	
WAMC67707	Balanidae	*Neoacasta* D33		WAMZ88435	Dictyoceratida	Irciniidae	*Sarcotragus* JB1	Recherche Archipelago, WA	-34.033, 121.609	15
WAMC67708	Balanidae	*Neoacasta* D33		WAMZ88435	Dictyoceratida	Irciniidae	*Sarcotragus* JB1	Recherche Archipelago, WA	-34.033, 121.609	15
WAMC67709	Balanidae	*Neoacasta* D33		WAMZ88435	Dictyoceratida	Irciniidae	*Sarcotragus* JB1	Recherche Archipelago, WA	-34.033, 121.609	15
WAMC61511	Balanidae	*Neoacasta* D35		WAMZ29082	Dictyoceratida	Spongiidae	*Spongia* (*Australospongia*) sp.1	Shark Bay, WA	-25.754, 113.244	17
WAMC55156	Balanidae	*Neoacasta* D38		WAMZ68651	Dictyoceratida	Irciniidae	*Ircinia* KGR1	Lesueur Island, WA	-13.816, 127.321	72.8
WAMC55157	Balanidae	*Neoacasta* D38		WAMZ68651	Dictyoceratida	Irciniidae	*Ircinia* KGR1	Lesueur Island, WA	-13.816, 127.321	72.8
WAMC67671	Balanidae	*Neoacasta* D39		WAMZ35965	Dictyoceratida	Irciniidae	*Sarcotragus* NG1	North West Shelf, WA	-19.791, 115.476	92
WAMC67676	Balanidae	*Neoacasta* D39		WAMZ35582	Dictyoceratida	Irciniidae	*Sarcotragus* NG1	Barrow Island, WA	-21.031, 114.892	93
QM W29523	Balanidae	*Neoacasta* D41		QM G325466	Dictyoceratida	Spongiidae	*Hyattella intestinalis*	Gulf of Carpentaria, QLD	-16.1443, 139.8419	36
QM W29524	Balanidae	*Neoacasta* D41		QM G325467	Dictyoceratida	Spongiidae	*Hyattella intestinalis*	Gulf of Carpentaria, QLD	-16.1443, 139.8419	36
QM W29525	Balanidae	*Neoacasta* D41		QM G325468	Dictyoceratida	Spongiidae	*Hyattella intestinalis*	Gulf of Carpentaria, QLD	-16.1443, 139.8419	36
WAMC61503	Balanidae	*Neoacasta* D42		WAMZ45290	Dictyoceratida	Spongiidae	*Spongia* (*Heterofibria*) NG1	Ningaloo Reef, WA	-22.626, 113.593	71.9
WAMC55426	Balanidae	*Neoacasta* D7	104	WAMZ68774	Dictyoceratida	Irciniidae	*Ircinia* KMB2	Long Reef, WA	-13.915, 125.774	5
WAMC55427	Balanidae	*Neoacasta* D7	104	WAMZ68774	Dictyoceratida	Irciniidae	*Ircinia* KMB2	Long Reef, WA	-13.915, 125.774	5
WAMC55428	Balanidae	*Neoacasta* D7	104	WAMZ68774	Dictyoceratida	Irciniidae	*Ircinia* KMB2	Long Reef, WA	-13.915, 125.774	5
WAMC71921	Balanidae	*Neoacasta fossata*	87		Unknown sponge			Amathole Region, South Africa	-32.9395, 28.2685	90
WAMC71928	Balanidae	*Neoacasta fossata*	87		Unknown sponge			Amathole Region, South Africa	-32.7531, 28.5177	78
WAMC71929	Balanidae	*Neoacasta fossata*	87		Unknown sponge			Amathole Region, South Africa	-32.7531, 28.5177	78
WAMC71912	Balanidae	*Neoacasta fossata*	87	WAMZ86943	Dictyoceratida	Irciniidae	*Ircinia*	Amathole Region, South Africa	-33.15, 27.7666	36
WAMC71916	Balanidae	*Neoacasta fossata*	87		Dictyoceratida	Irciniidae	*Ircinia*	Amathole Region, South Africa	-33.2856, 27.9099	103
WAMC71919	Balanidae	*Neoacasta fossata*	87		Dictyoceratida	Irciniidae	*Ircinia*	Amathole Region, South Africa	-33.1632, 27.7746	36
WAMC71893	Balanidae	*Neoacasta fossata*	87		Tetractinellida	Pachastrellidae		Amathole Region, South Africa	-32.7531, 28.5177	78
WAMC67630	Balanidae	*Neoacasta glans* D17	105	WAMZ87934	Dictyoceratida	Thorectidae	*Hyrtios* SS2	Camden Sound, WA	-15.431, 124.059	35.9
WAMC67631	Balanidae	*Neoacasta glans* D17	105	WAMZ87934	Dictyoceratida	Thorectidae	*Hyrtios* SS2	Camden Sound, WA	-15.431, 124.059	35.9
NMITS72283	Balanidae	*Notobalanus vestitus*						Wellington, New Zealand	-41.273, 174.7883	
NMITS72288	Balanidae	*Notobalanus vestitus*						Wellington, New Zealand	-41.273, 174.7883	
NMITS72291	Balanidae	*Notobalanus vestitus*						Wellington, New Zealand	-41.273, 174.7883	
NMITS73022	Balanidae	*Notobalanus vestitus*						Wellington, New Zealand	-41.273, 174.7883	
WAMC50791	Balanidae	*Pectinoacasta cancellorum*	68	WAMZ54695	Agelasida	Agelasidae	*Agelas* KMB1	Echuca Shoal, WA	-13.9006, 123.8934	18
WAMC55302	Balanidae	*Pectinoacasta cancellorum*	68		Agelasida	Agelasidae	*Agelas* KMB1	Mermaid Reef, WA	-17.0266, 119.6189	25
WAMC55303	Balanidae	*Pectinoacasta cancellorum*	68		Agelasida	Agelasidae	*Agelas* KMB1	Mermaid Reef, WA	-17.0266, 119.6189	25
WAMC55304	Balanidae	*Pectinoacasta cancellorum*	68		Agelasida	Agelasidae	*Agelas* KMB1	Mermaid Reef, WA	-17.0266, 119.6189	25
WAMC55305	Balanidae	*Pectinoacasta cancellorum*	68		Agelasida	Agelasidae	*Agelas* KMB1	Mermaid Reef, WA	-17.0266, 119.6189	25
WAMC55306	Balanidae	*Pectinoacasta cancellorum*	68		Agelasida	Agelasidae	*Agelas* KMB1	Mermaid Reef, WA	-17.0266, 119.6189	25
WAMC55307	Balanidae	*Pectinoacasta cancellorum*	68		Agelasida	Agelasidae	*Agelas* KMB1	Mermaid Reef, WA	-17.0266, 119.6189	25
WAMC55308	Balanidae	*Pectinoacasta cancellorum*	68		Agelasida	Agelasidae	*Agelas* KMB1	Clerke Reef, WA	-17.317, 119.3838	12
SMBL #149	Balanidae	*Pectinoacasta cancellorum*						Seto, Japan	33.6912, 135.3383	
WAMC58871	Balanidae	*Pectinoacasta pectinipes*	96		Poecilosclerida	Tedaniidae	*Trachytedania* L1	Perth, WA	-32.0772, 115.7511	0
WAMC58872	Balanidae	*Pectinoacasta pectinipes*	96		Poecilosclerida	Tedaniidae	*Trachytedania* L1	Perth, WA	-32.0772, 115.7511	0

Specimen Accession	Family	Identification	PSH	Host accession	Host Order	Host family	Host identification	Locality	Coordinates	Depth
WAMC58873	Balanidae	*Pectinoacasta pectinipes*	96		Poecilosclerida	Tedaniidae	*Trachytedania* L1	Perth, WA	-32.0772, 115.7511	0
WAMC67748	Balanidae	*Pectinoacasta pectinipes*	96	WAMZ97093	Poecilosclerida	Tedaniidae	*Trachytedania* MM1	North Muiron Island, WA	-21.6277, 114.3737	17
WAMC67749	Balanidae	*Pectinoacasta pectinipes*	96	WAMZ97093	Poecilosclerida	Tedaniidae	*Trachytedania* MM1	North Muiron Island, WA	-21.6277, 114.3737	17
WAMC67750	Balanidae	*Pectinoacasta pectinipes*	96	WAMZ97093	Poecilosclerida	Tedaniidae	*Trachytedania* MM1	North Muiron Island, WA	-21.6277, 114.3737	17
WAMC67772	Balanidae	*Pectinoacasta pectinipes*	96	WAMZ97092	Poecilosclerida	Tedaniidae	*Trachytedania* MM1	North Muiron Island, WA	-21.6277, 114.3737	17
WAMC61394	Balanidae	*Pectinoacasta sculpturata*	11		Agelasida	Agelasidae	*Amphinomia sulphurea*	Montebello Islands, WA	-20.3555, 115.5508	26
WAMC61395	Balanidae	*Pectinoacasta sculpturata*	11		Agelasida	Agelasidae	*Amphinomia sulphurea*	Montebello Islands, WA	-20.3555, 115.5508	26
WAMC61396	Balanidae	*Pectinoacasta sculpturata*	11		Agelasida	Agelasidae	*Amphinomia sulphurea*	Montebello Islands, WA	-20.3555, 115.5508	26
ZMUCCRU9003	Balanidae	*Pectinoacasta sculpturata*			Agelasida	Agelasidae	Agelas sp.	Java Island, Indonesia	-5.7833, 106.1167	49
WAMC71844	Balanidae	*Pectinoacasta zevinae*		WAMZ86907	Haplosclerida	Petrosiidae	*Xestospongia* sp. 'lace'	Dampier Archipelago, WA	-20.5025, 116.6808	10
WAMC71845	Balanidae	*Pectinoacasta zevinae*		WAMZ86907	Haplosclerida	Petrosiidae	*Xestospongia* sp. 'lace'	Dampier Archipelago, WA	-20.5025, 116.6808	10
WAMC71846	Balanidae	*Pectinoacasta zevinae*		WAMZ86907	Haplosclerida	Petrosiidae	*Xestospongia* sp. 'lace'	Dampier Archipelago, WA	-20.5025, 116.6808	10
WAMC74099	Balanidae	*Solidobalanus socialis*						Dampier Archipelago, WA	-20.4581, 117.0575	14.5
WAMC74100	Balanidae	*Solidobalanus socialis*						Dampier Archipelago, WA	-20.4581, 117.0575	14.5
WAMC74101	Balanidae	*Solidobalanus socialis*						Dampier Archipelago, WA	-20.4581, 117.0575	14.5
WAMC55372	Balanidae	*Striatobalanus amaryllis*						Onslow, WA	-21.671, 114.668	15
WAMC55374	Balanidae	*Striatobalanus amaryllis*						Onslow, WA	-21.671, 114.668	15
WAMC67720	Chthamalidae	*Euraphia*						Montebello Islands, WA	-20.4114, 115.5257	0
WAMC61380	Pyrgomatidae	*Pyrgospongia* cf. *stellula*	32		Clionaida			Ah Chong Island, WA	-20.4992, 115.5899	14.5
WAMC52691	Pyrgomatidae	*Pyrgospongia* cf. *stellula*	32		Clionaida	Clionaidae	*Spheciospongia vagabunda*?	Minden Reef, WA	-32.0668, 115.727	10
WAMC55365	Pyrgomatidae	*Pyrgospongia* cf. *stellula*	32	WAMZ82226	Clionaida	Clionaidae	*Spheciospongia* K1	Stewart Rocks, WA	-20.7664, 115.7776	22.3
WAMC55366	Pyrgomatidae	*Pyrgospongia* cf. *stellula*	32	WAMZ82226	Clionaida	Clionaidae	*Spheciospongia* K1	Stewart Rocks, WA	-20.7664, 115.7776	22.3
WAMC71855	Pyrgomatidae	*Pyrgospongia* cf. *stellula*	32		Clionaida	Clionaidae	*Spheciospongia*	Dampier Archipelago, WA	-20.618, 116.464	16
WAMC71856	Pyrgomatidae	*Pyrgospongia* cf. *stellula*	32		Clionaida	Clionaidae	*Spheciospongia*	Dampier Archipelago, WA	-20.618, 116.464	16
WAMC71931	Pyrgomatidae	*Pyrgospongia* cf. *stellula*	32		Clionaida	Clionaidae		Dampier Archipelago, WA	-20.618, 116.464	16
WAMC71932	Pyrgomatidae	*Pyrgospongia* cf. *stellula*	62		Clionaida	Clionaidae		Dampier Archipelago, WA	-20.618, 116.464	16
WAMC67714	Tetraclitidae	*Neonrosella vittiata*						Exmouth Gulf, WA	-22.0536, 114.1135	0
WAMC67715	Tetraclitidae	*Tesseropora* sp.1						South Muiron Island, WA	-21.6835, 114.311	18
WAMC55331	Tetraclitidae	*Tesseropora wireni*						Clerke Reef, WA	-17.3059, 119.3806	0
WAMC55332	Tetraclitidae	*Tesseropora wireni*						Imperieuse Reef, WA	-17.5092, 118.9632	0
WAMC56593	Tetraclitidae	*Tesseropora wireni*						Imperieuse Reef, WA	-17.5607, 118.941	7

Appendix II. Map showing distribution of sequenced specimens collected from Australian waters.



Appendix III. GenBank accession numbers of sequences published or downloaded for analyses during this thesis.

Species	Specimen ID	*COI*	*12S*	*H3*	*RPII*	*28S*	References
Balanoidea							
Acasta aspera	SGI20-1	KY581615					Yu et al. 2017
Acasta aspera	SGI20-2	KY581616					Yu et al. 2017
Acasta aspera	SGI2-1	KY581614					Yu et al. 2017
Acasta aspera	WAM C55057	KY581613					Yu et al. 2017
Acasta aspera	WAM C58741	KY581610					Yu et al. 2017
Acasta aspera	WAM C58742	KY581611					Yu et al. 2017
Acasta aspera	WAM C58743	KY581612					Yu et al. 2017
Acasta aspera	WAM C58812	MZ086820					Hosie et al. 2021
Acasta aspera	WAM C58813	MZ086821					Hosie et al. 2021
Acasta aspera	WAM C58815	MZ086822					Hosie et al. 2021
Acasta aspera	WAM C58835	MZ086823					Hosie et al. 2021
Acasta aspera	WAM C58837	MZ086824					Hosie et al. 2021
Acasta aspera	WAM C58838	MZ086825					Hosie et al. 2021
Acasta aspera	WAM C71837	MZ086844					Hosie et al. 2021
Acasta aspera	WAM C71838	MZ086845					Hosie et al. 2021
Acasta caveata	WAM C67716	MZ086833					Hosie et al. 2021
Acasta caveata	WAM C67717	MZ086834					Hosie et al. 2021
Acasta crucibasis	MF796674	MF796674					
Acasta crucibasis	S32-1	MN842021					Yu et al. 2020
Acasta cyathus	SGI265-1	MN842022					Yu et al. 2020
Acasta D10	WAM C61497	MW374013	MW427497	MW364685		MW427359	Hosie et al. 2021
Acasta D10	WAM C61498	MW374014	MW427498	MW364686		MW427360	Hosie et al. 2021

Species	**Specimen ID**	***COI***	***12S***	***H3***	***RPII***	***28S***	**References**
Acasta D10	WAM C61499	MW374015	MW427499	MW364687		MW427361	Hosie et al. 2021
Acasta D18	WAM C67636	MW374040	MW427531	MW364715		MW427380	Hosie et al. 2021
Acasta D18	WAM C67638	MW374041	MW427532	MW364716		MW427381	Hosie et al. 2021
Acasta D18	WAM C67639	MW374042	MW427533	MW364717		MW427382	Hosie et al. 2021
Acasta D30	QM W29522	MW374087		MW364777			Hosie et al. 2021
Acasta D34	WAM C54159		MW427441	MW364646		MW427314	Hosie et al. 2021
Acasta D4	WAM C55358	MW373977	MW427456	MW364653		MW427326	Hosie et al. 2021
Acasta D4	WAM C61421	MW374006					Hosie et al. 2021
Acasta D4	WAM C61422	MW374007					Hosie et al. 2021
Acasta D4	WAM C61423	MW374008	MW427489	MW364681			Hosie et al. 2021
Acasta D5	WAM C55403	MW373979	MW427458	MW364655		MW427328	Hosie et al. 2021
Acasta D5	WAM C55404	MW373980		MW364656		MW427329	Hosie et al. 2021
Acasta D5	WAM C67811	MW374068	MW427577	MW364754		MW427413	Hosie et al. 2021
Acasta D5	WAM C67812	MW374069	MW427578	MW364755		MW427414	Hosie et al. 2021
Acasta D5	WAM C67813	MW374070	MW427579	MW364756		MW427415	Hosie et al. 2021
Acasta D8	WAM C58844	MW373993	MW427468	MW364666		MW427339	Hosie et al. 2021
Acasta D8	WAM C58846	MW373994	MW427469	MW364667		MW427340	Hosie et al. 2021
Acasta D8	WAM C67697		MW427563	MW364745			Hosie et al. 2021
Acasta D8	WAM C67698		MW427564				Hosie et al. 2021
Acasta daedalusa	SGI28-2	MN842023					Yu et al. 2020
Acasta fenestrata	WAM C46669	MZ086796					Hosie et al. 2021
Acasta fenestrata	WAM C55251	MZ086800					Hosie et al. 2021
Acasta fenestrata	WAM C55319	MZ086808					Hosie et al. 2021
Acasta fenestrata	WAM C55320	MZ086809					Hosie et al. 2021
Acasta fenestrata	WAM C55321	MZ086810					Hosie et al. 2021
Acasta fenestrata	WAM C55322	MZ086811					Hosie et al. 2021
Acasta fenestrata	WAM C55323	MZ086812					Hosie et al. 2021

Species	**Specimen ID**	***COI***	***12S***	***H3***	***RPII***	***28S***	**References**
Acasta fenestrata	WAM C55324	MZ086813					Hosie et al. 2021
Acasta fenestrata	WAM C55325	MZ086814					Hosie et al. 2021
Acasta fenestrata	WAM C58748	MZ086818					Hosie et al. 2021
Acasta fenestrata	WAM C58749	MZ086819					Hosie et al. 2021
Acasta fenestrata	WAM C67829	MZ086839					Hosie et al. 2021
Acasta fenestrata	WAM C71738	MZ086840					Hosie et al. 2021
Acasta fenestrata	WAM C71739	MZ086841					Hosie et al. 2021
Acasta fenestrata	WAM C72909	MZ086846					Hosie et al. 2021
Acasta fenestrata	WAM C72914	MZ086847					Hosie et al. 2021
Acasta fenestrata	WAM C74419	MZ086848					Hosie et al. 2021
Acasta huangi	SNE47-4	KY581621					Yu et al. 2017
Acasta radenta	SLQ32-1	MN842024					Yu et al. 2020
Acasta radenta	SNE47-1	KY581619					Yu et al. 2017
Acasta sandwichi	SGI208-1	MN842025					Yu et al. 2020
Acasta sandwichi	SN77-1	MF796675					
Acasta sandwichi	SN77-2	MF796676					
Acasta sandwichi	WAM C47383	MZ086797					Hosie et al. 2021
Acasta sandwichi	WAM C53344	MZ086799					Hosie et al. 2021
Acasta sp. 1 MCY-2020	SJP55-N1	MN842026					Yu et al. 2020
Acasta sp. 2 MCY-2020	SLQ20-2	MN842027					Yu et al. 2020
Acasta sp. 3 MCY-2020	SN81-3	MN842028					Yu et al. 2020
Acasta sp. 4 MCY-2020	SDS4-2	MN842029					Yu et al. 2020
Acasta spongites	STI18-1	MN842030					Yu et al. 2020
Acasta spongites D20	WAM C67649	MW374045	MW427537	MW364721		MW427385	Hosie et al. 2021
Acasta spongites D20	WAM C67711	MW374060	MW427569			MW427405	Hosie et al. 2021
Acasta spongites D20	WAM C67712	MW374061	MW427570	MW364747		MW427406	Hosie et al. 2021
Acasta sulcata	SN48-1	KY581617					Yu et al. 2017

Species	**Specimen ID**	***COI***	***12S***	***H3***	***RPII***	***28S***	**References**
Acasta sulcata	SN48-3	KY581618					Yu et al. 2017
Acasta turriformis	SGI178-1	MF796671					
Acasta turriformis	SGI178-2	MF796672					
Acasta undulaterga	SNE47-3	KY581620					Yu et al. 2017
Acasta undulaterga	SNE47-5	KY581622					Yu et al. 2017
Acasta vipensis	CAS:IZ:187687A	KF587277					Van Syoc et al. 2014
Acasta vipensis	CAS:IZ:187764A	KF587282					Van Syoc et al. 2014
Amphibalanus amphitrite	MSL-Amamp		KF776181	KF776328	KF776380		Chan et al., 2017
Archiacasta D16	WAM C61529	MW374033	MW427522	MW364707			Hosie et al. 2021
Archiacasta D16	WAM C61531	MW374034	MW427523	MW364708		MW427374	Hosie et al. 2021
Archiacasta D16	WAM C67745	MW374064	MW427573	MW364750		MW427409	Hosie et al. 2021
Archiacasta D16	WAM C67746	MW374065	MW427574	MW364751		MW427410	Hosie et al. 2021
Archiacasta D16	WAM C67747	MW374066	MW427575	MW364752		MW427411	Hosie et al. 2021
Archiacasta D16	WAM C67788	MW374067	MW427576	MW364753		MW427412	Hosie et al. 2021
Archiacasta D37	WAM C67678		MW427548	MW364731		MW427393	Hosie et al. 2021
Archiacasta D39	WAM C67671		MW427544	MW364728		MW427390	Hosie et al. 2021
Archiacasta D39	WAM C67676		MW427547				Hosie et al. 2021
Archiacasta D40	WAM C61488		MW427490				Hosie et al. 2021
Archiacasta D40	WAM C61489		MW427491				Hosie et al. 2021
Archiacasta D40	WAM C61490		MW427492				Hosie et al. 2021
Archiacasta D40	WAM C61491		MW427493				Hosie et al. 2021
Archiacasta D40	WAM C67705		MW427565				Hosie et al. 2021
Archiacasta fragilis D36	WAM C67686		MW427554	MW364737			Hosie et al. 2021
Archiacasta hainanensis D9	WAM C58850		MW427470	MW364668			Hosie et al. 2021
Archiacasta hainanensis D9	WAM C61496	MW374012	MW427496	MW364684		MW427358	Hosie et al. 2021
Archiacasta hainanensis D9	WAM C61522	MW374030	MW427519	MW364704		MW427372	Hosie et al. 2021
Archiacasta hainanensis D9	WAM C61523	MW374031	MW427520	MW364705		MW427373	Hosie et al. 2021

Species	**Specimen ID**	***COI***	***12S***	***H3***	***RPII***	***28S***	**References**
Austromegabalanus psittacus	KACb11		AY520668	AY520702		AY520600	Pérez-Losada et al., 2004
Balanus balanus	KACb3		AY520662	AY520696		AY520594	Pérez-Losada et al., 2004
Balanus crenatus	KACb1		AY520658	AY520692		AY520590	Pérez-Losada et al., 2004
Balanus glandula	KACb2		AY520659	AY520693		AY520591	Pérez-Losada et al., 2004
Cantellius acutum	CEL-GI164	MG878744	KF776142		KF776341		Chan et al., 2018; Tsang et al., 2014
Euacasta acutaflava	WAM C58744	MZ086815					Hosie et al. 2021
Euacasta acutaflava	WAM C58745	MZ086816					Hosie et al. 2021
Euacasta acutaflava	WAM C58746	MZ086817					Hosie et al. 2021
Euacasta acutaflava	WAM C61434	MZ086830					Hosie et al. 2021
Euacasta acutaflava	WAM C61435	MZ086831					Hosie et al. 2021
Euacasta D15	WAM C61527	MW374032	MW427521	MW364706			Hosie et al. 2021
Euacasta D26	WAM C67696	MW374059	MW427562	MW364744			Hosie et al. 2021
Euacasta D6	WAM C55406	MW373981	MW427459	MW364657		MW427330	Hosie et al. 2021
Euacasta D6	WAM C55407	MW373982	MW427460	MW364658		MW427331	Hosie et al. 2021
Euacasta dofleini	SGI168-2	MN842036					Yu et al. 2020
Euacasta excoriatrix	WAM C61475	MZ086832					Hosie et al. 2021
Euacasta excoriatrix	WAM C71800	MZ086842					Hosie et al. 2021
Euacasta excoriatrix	WAM C71801	MZ086843					Hosie et al. 2021
Euacasta microforamina	SJJ2-1	MN842037					Yu et al. 2020
Euacasta sporillus	RMNH:CRUS:C.10235	KU986749					
Euacasta sporillus	S14-1	MN842038					Yu et al. 2020
Galkinius altiapiculus	CEL-KT23		KF776158	KF776306	KF776357		Tsang et al., 2014
Galkinius depressus	CEL-TI12-1		KF776159	KF776307	KF776358		Tsang et al., 2014
Hiroa stubbingsi	CEL-RYU139		KF776162	KF776310	KF776361		Tsang et al., 2014
Megabalanus californicus	KACb9		AY520666	AY520700		AY520598	Pérez-Losada et al., 2004

Species	**Specimen ID**	***COI***	***12S***	***H3***	***RPII***	***28S***	**References**
Megabalanus tintinnabulum	KACb8		AY520665	AY520699		AY520597	Pérez-Losada et al., 2004
Membranobalanus porphyrophilus	WAM C71853	MK789771					Hosie et al. 2019
Membranobalanus porphyrophilus	WAM C71881	MK789772					Hosie et al. 2019
Menesiniella aquila	KACb7		AY520664	AY520698		AY520596	Pérez-Losada et al., 2004
Neoacasta D1	WAM C50622	MW373966	MW427439	MW364644		MW427312	Hosie et al. 2021
Neoacasta D1	WAM C55429	MW373985	MW427466	MW364664		MW427337	Hosie et al. 2021
Neoacasta D1	WAM C55431	MW373986					Hosie et al. 2021
Neoacasta D1	WAM C55432	MW373987	MW427467	MW364665		MW427338	Hosie et al. 2021
Neoacasta D1	WAM C58877		MW427471	MW364669		MW427341	Hosie et al. 2021
Neoacasta D1	WAM C58881	MW373995	MW427472			MW427342	Hosie et al. 2021
Neoacasta D1	WAM C58885		MW427473			MW427343	Hosie et al. 2021
Neoacasta D1	WAM C58893	MW374000	MW427480	MW364674		MW427348	Hosie et al. 2021
Neoacasta D1	WAM C58894	MW374001	MW427481	MW364675		MW427349	Hosie et al. 2021
Neoacasta D1	WAM C58895	MW374002	MW427482	MW364676		MW427350	Hosie et al. 2021
Neoacasta D1	WAM C58909	MW374003	MW427485	MW364678		MW427353	Hosie et al. 2021
Neoacasta D1	WAM C58910	MW374004	MW427486	MW364679		MW427354	Hosie et al. 2021
Neoacasta D1	WAM C58911	MW374005	MW427487	MW364680		MW427355	Hosie et al. 2021
Neoacasta D1	WAM C58912		MW427488				Hosie et al. 2021
Neoacasta D1	WAM C61493	MW374010	MW427494	MW364682		MW427356	Hosie et al. 2021
Neoacasta D1	WAM C61494	MW374011	MW427495	MW364683		MW427357	Hosie et al. 2021
Neoacasta D11	WAM C61504		MW427504	MW364691			Hosie et al. 2021
Neoacasta D11	WAM C61505	MW374019	MW427505	MW364692		MW427364	Hosie et al. 2021
Neoacasta D12	WAM C61507	MW374020	MW427506	MW364693			Hosie et al. 2021
Neoacasta D12	WAM C61508	MW374021	MW427507	MW364694			Hosie et al. 2021
Neoacasta D12	WAM C61509	MW374022	MW427508	MW364695		MW427365	Hosie et al. 2021

Species	**Specimen ID**	***COI***	***12S***	***H3***	***RPII***	***28S***	**References**
Neoacasta D13	WAM C58907		MW427483			MW427351	Hosie et al. 2021
Neoacasta D13	WAM C58908		MW427484	MW364677		MW427352	Hosie et al. 2021
Neoacasta D13	WAM C61512		MW427510	MW364696		MW427366	Hosie et al. 2021
Neoacasta D13	WAM C61513	MW374023	MW427511	MW364697		MW427367	Hosie et al. 2021
Neoacasta D13	WAM C61534	MW374035	MW427524				Hosie et al. 2021
Neoacasta D13	WAM C61535	MW374036	MW427525	MW364709			Hosie et al. 2021
Neoacasta D13	WAM C67635	MW374039	MW427530	MW364714		MW427379	Hosie et al. 2021
Neoacasta D13	WAM C67643	MW374044	MW427535	MW364719		MW427383	Hosie et al. 2021
Neoacasta D13	WAM C67644		MW427536	MW364720		MW427384	Hosie et al. 2021
Neoacasta D13	WAM C67651		MW427538	MW364722			Hosie et al. 2021
Neoacasta D13	WAM C67652		MW427539	MW364723		MW427386	Hosie et al. 2021
Neoacasta D13	WAM C71809		MW427589	MW364766		MW427424	Hosie et al. 2021
Neoacasta D13	WAM C71810		MW427590	MW364767		MW427425	Hosie et al. 2021
Neoacasta D13	WAM C71813		MW427593	MW364770		MW427428	Hosie et al. 2021
Neoacasta D13	WAM C71814		MW427594	MW364771		MW427429	Hosie et al. 2021
Neoacasta D14	QM W29526		MW427434				Hosie et al. 2021
Neoacasta D14	WAM C61514	MW374024	MW427512	MW364698		MW427368	Hosie et al. 2021
Neoacasta D14	WAM C61515	MW374025	MW427513	MW364699		MW427369	Hosie et al. 2021
Neoacasta D14	WAM C61516		MW427514	MW364700			Hosie et al. 2021
Neoacasta D14	WAM C61519	MW374027	MW427516	MW364701			Hosie et al. 2021
Neoacasta D14	WAM C61520	MW374028	MW427517	MW364702		MW427370	Hosie et al. 2021
Neoacasta D14	WAM C61521	MW374029	MW427518	MW364703		MW427371	Hosie et al. 2021
Neoacasta D14	WAM C61536		MW427526	MW364710		MW427375	Hosie et al. 2021
Neoacasta D14	WAM C71757		MW427586	MW364764			Hosie et al. 2021
Neoacasta D14	WAM C71758		MW427587	MW364765		MW427422	Hosie et al. 2021
Neoacasta D14	WAM C71759		MW427588			MW427423	Hosie et al. 2021
Neoacasta D14	WAM C71811	MW374078	MW427591	MW364768		MW427426	Hosie et al. 2021

Species	**Specimen ID**	***COI***	***12S***	***H3***	***RPII***	***28S***	**References**
Neoacasta D14	WAM C71812	MW374079	MW427592	MW364769		MW427427	Hosie et al. 2021
Neoacasta D14	WAM C72917	MW374081		MW364772			Hosie et al. 2021
Neoacasta D17	WAM C67630	MW374037	MW427527	MW364711		MW427376	Hosie et al. 2021
Neoacasta D17	WAM C67631	MW374038	MW427528	MW364712		MW427377	Hosie et al. 2021
Neoacasta D17	WAM C67632		MW427529	MW364713		MW427378	Hosie et al. 2021
Neoacasta D19	WAM C67640	MW374043	MW427534	MW364718			Hosie et al. 2021
Neoacasta D2	WAM C54067	MW373967	MW427440	MW364645		MW427313	Hosie et al. 2021
Neoacasta D2	WAM C54301	MW373968	MW427442	MW364647		MW427315	Hosie et al. 2021
Neoacasta D2	WAM C55249	MW373969	MW427445	MW364648		MW427316	Hosie et al. 2021
Neoacasta D2	WAM C55250	MW373970	MW427446			MW427317	Hosie et al. 2021
Neoacasta D2	WAM C55265	MW373971	MW427447			MW427318	Hosie et al. 2021
Neoacasta D2	WAM C55266	MW373972					Hosie et al. 2021
Neoacasta D2	WAM C55267	MW373973	MW427448	MW364649		MW427319	Hosie et al. 2021
Neoacasta D2	WAM C55268	MW373974	MW427449	MW364650		MW427320	Hosie et al. 2021
Neoacasta D2	WAM C55269	MW373975	MW427450			MW427321	Hosie et al. 2021
Neoacasta D21	WAM C67665	MW374046	MW427542	MW364725		MW427387	Hosie et al. 2021
Neoacasta D21	WAM C67666	MW374047		MW364726		MW427388	Hosie et al. 2021
Neoacasta D21	WAM C67667	MW374048	MW427543	MW364727		MW427389	Hosie et al. 2021
Neoacasta D21	WAM C67731	MW374062	MW427571	MW364748		MW427407	Hosie et al. 2021
Neoacasta D21	WAM C67732	MW374063	MW427572	MW364749		MW427408	Hosie et al. 2021
Neoacasta D22	WAM C67657		MW427540	MW364724			Hosie et al. 2021
Neoacasta D22	WAM C67658		MW427541				Hosie et al. 2021
Neoacasta D22	WAM C67673	MW374049	MW427545	MW364729		MW427391	Hosie et al. 2021
Neoacasta D22	WAM C67675	MW374050	MW427546	MW364730		MW427392	Hosie et al. 2021
Neoacasta D22	WAM C67679	MW374051	MW427549	MW364732		MW427394	Hosie et al. 2021
Neoacasta D22	WAM C67680		MW427550	MW364733			Hosie et al. 2021
Neoacasta D22	WAM C67682		MW427551	MW364734		MW427395	Hosie et al. 2021

Species	**Specimen ID**	***COI***	***12S***	***H3***	***RPII***	***28S***	**References**
Neoacasta D22	WAM C67692	MW374055	MW427558	MW364740		MW427401	Hosie et al. 2021
Neoacasta D22	WAM C67693	MW374056	MW427559	MW364741		MW427402	Hosie et al. 2021
Neoacasta D22	WAM C67694	MW374057	MW427560	MW364742		MW427403	Hosie et al. 2021
Neoacasta D22	WAM C71751	MW374076	MW427584	MW364762		MW427421	Hosie et al. 2021
Neoacasta D23	WAM C67683	MW374052	MW427552	MW364735		MW427396	Hosie et al. 2021
Neoacasta D23	WAM C67685	MW374053	MW427553	MW364736		MW427397	Hosie et al. 2021
Neoacasta D24	WAM C67690		MW427556			MW427399	Hosie et al. 2021
Neoacasta D24	WAM C67691	MW374054	MW427557	MW364739		MW427400	Hosie et al. 2021
Neoacasta D25	WAM C67695	MW374058	MW427561	MW364743		MW427404	Hosie et al. 2021
Neoacasta D27	WAM C72920	MW374082		MW364773			Hosie et al. 2021
Neoacasta D27	WAM C72927	MW374086		MW364776			Hosie et al. 2021
Neoacasta D28	WAM C72922	MW374083		MW364774			Hosie et al. 2021
Neoacasta D29	WAM C72924	MW374084					Hosie et al. 2021
Neoacasta D29	WAM C72925	MW374085		MW364775			Hosie et al. 2021
Neoacasta D3	WAM C43665		MW427438				Hosie et al. 2021
Neoacasta D3	WAM C55284		MW427451	MW364651		MW427322	Hosie et al. 2021
Neoacasta D3	WAM C55285		MW427452			MW427323	Hosie et al. 2021
Neoacasta D3	WAM C55286	MW373976	MW427453	MW364652		MW427324	Hosie et al. 2021
Neoacasta D3	WAM C55287		MW427454				Hosie et al. 2021
Neoacasta D3	WAM C55288		MW427455			MW427325	Hosie et al. 2021
Neoacasta D3	WAM C55410		MW427461	MW364659		MW427332	Hosie et al. 2021
Neoacasta D3	WAM C55411		MW427462	MW364660		MW427333	Hosie et al. 2021
Neoacasta D3	WAM C58797	MW373988					Hosie et al. 2021
Neoacasta D3	WAM C58798	MW373989					Hosie et al. 2021
Neoacasta D3	WAM C58799	MW373990					Hosie et al. 2021
Neoacasta D3	WAM C58800	MW373991					Hosie et al. 2021
Neoacasta D3	WAM C58801	MW373992					Hosie et al. 2021

Species	**Specimen ID**	***COI***	***12S***	***H3***	***RPII***	***28S***	**References**
Neoacasta D3	WAM C58886	MW373996	MW427474	MW364670		MW427344	Hosie et al. 2021
Neoacasta D3	WAM C58887	MW373997	MW427475	MW364671		MW427345	Hosie et al. 2021
Neoacasta D3	WAM C58888	MW373998	MW427476	MW364672		MW427346	Hosie et al. 2021
Neoacasta D3	WAM C58889	MW373999	MW427477	MW364673		MW427347	Hosie et al. 2021
Neoacasta D3	WAM C58891		MW427478				Hosie et al. 2021
Neoacasta D3	WAM C58892		MW427479				Hosie et al. 2021
Neoacasta D3	WAM C61433	MW374009					Hosie et al. 2021
Neoacasta D3	WAM C61500	MW374016	MW427500	MW364688		MW427362	Hosie et al. 2021
Neoacasta D3	WAM C61501	MW374017	MW427501	MW364689			Hosie et al. 2021
Neoacasta D3	WAM C61502	MW374018	MW427502	MW364690		MW427363	Hosie et al. 2021
Neoacasta D3	WAM C61517	MW374026	MW427515				Hosie et al. 2021
Neoacasta D3	WAM C71746	MW374071		MW364757		MW427416	Hosie et al. 2021
Neoacasta D3	WAM C71747	MW374072	MW427580	MW364758		MW427417	Hosie et al. 2021
Neoacasta D3	WAM C71748	MW374073	MW427581	MW364759		MW427418	Hosie et al. 2021
Neoacasta D3	WAM C71749	MW374074	MW427582	MW364760		MW427419	Hosie et al. 2021
Neoacasta D3	WAM C71750	MW374075	MW427583	MW364761		MW427420	Hosie et al. 2021
Neoacasta D3	WAM C71756	MW374077	MW427585	MW364763			Hosie et al. 2021
Neoacasta D31	WAM C72913	MW374080				MW427430	Hosie et al. 2021
Neoacasta D32	SAMA C14356		MW427435				Hosie et al. 2021
Neoacasta D32	SAMA C14357		MW427436				Hosie et al. 2021
Neoacasta D33	SAMA C14358		MW427437				Hosie et al. 2021
Neoacasta D33	WAM C67688		MW427555	MW364738		MW427398	Hosie et al. 2021
Neoacasta D33	WAM C67707		MW427566				Hosie et al. 2021
Neoacasta D33	WAM C67708		MW427567	MW364746			Hosie et al. 2021
Neoacasta D33	WAM C67709		MW427568				Hosie et al. 2021
Neoacasta D35	WAM C61511		MW427509				Hosie et al. 2021
Neoacasta D38	WAM C55156		MW427443				Hosie et al. 2021

Species	**Specimen ID**	***COI***	***12S***	***H3***	***RPII***	***28S***	**References**
Neoacasta D38	WAM C55157		MW427444				Hosie et al. 2021
Neoacasta D41	QM W29523		MW427431				Hosie et al. 2021
Neoacasta D41	QM W29524		MW427432				Hosie et al. 2021
Neoacasta D41	QM W29525		MW427433				Hosie et al. 2021
Neoacasta D42	WAM C61503		MW427503				Hosie et al. 2021
Neoacasta D7	WAM C55426	MW373983	MW427463	MW364661		MW427334	Hosie et al. 2021
Neoacasta D7	WAM C55427		MW427464	MW364662		MW427335	Hosie et al. 2021
Neoacasta D7	WAM C55428	MW373984	MW427465	MW364663		MW427336	Hosie et al. 2021
Nobia grandis	CEL_KT100	MG878749	KF776166	KF776314	KF776365		Chan et al., 2017; Tsang et al., 2014
Nobia grandis	CEL-KT52		KF776165	KF776313	KF776364		Tsang et al., 2014
Pecitnoacasta sculpturata	WAM C61394	MZ086827					Hosie et al. 2021
Pecitnoacasta sculpturata	WAM C61395	MZ086828					Hosie et al. 2021
Pecitnoacasta sculpturata	WAM C61396	MZ086829					Hosie et al. 2021
Pectinoacasta cancellorum	WAM C50791	MZ086798					Hosie et al. 2021
Pectinoacasta cancellorum	WAM C55302	MZ086801					Hosie et al. 2021
Pectinoacasta cancellorum	WAM C55303	MZ086802					Hosie et al. 2021
Pectinoacasta cancellorum	WAM C55304	MZ086803					Hosie et al. 2021
Pectinoacasta cancellorum	WAM C55305	MZ086804					Hosie et al. 2021
Pectinoacasta cancellorum	WAM C55306	MZ086805					Hosie et al. 2021
Pectinoacasta cancellorum	WAM C55307	MZ086806					Hosie et al. 2021
Pectinoacasta cancellorum	WAM C55308	MZ086807					Hosie et al. 2021
Pectinoacasta pectinipes	WAM C58873	MZ086826					Hosie et al. 2021
Pectinoacasta pectinipes	WAM C67748	MZ086835					Hosie et al. 2021
Pectinoacasta pectinipes	WAM C67749	MZ086836					Hosie et al. 2021
Pectinoacasta pectinipes	WAM C67750	MZ086837					Hosie et al. 2021
Pectinoacasta pectinipes	WAM C67772	MZ086838					Hosie et al. 2021

Species	**Specimen ID**	***COI***	***12S***	***H3***	***RPII***	***28S***	**References**
Pectinoacasta sculpturata	SGI131-1	MN842042					Yu et al. 2020
Perforatus perforatus	KACb0004		AY520697	AY520663		AY520595	Pérez-Losada et al., 2004
Pyrgoma cancellatum	CEL-KT78-4		KF776167	KF776316	KF776366		Tsang et al., 2014
Semibalanus balanoides	KACb0005		AY520660	AY520694		AY520592	Pérez-Losada et al., 2004
Semibalanus cariosus	KACb0006		AY520661	AY520695		AY520593	Pérez-Losada et al., 2004
Striatobalanus amaryllis	WAM C55372	MW373978	MW427457	MW364654	MW427327		Hosie et al. 2021
Trevathana dentata	CEL-RYU166-1		KF776177	KF776325	KF776376		Tsang et al., 2014
Wanella sp.2	UF12617		HG970502	HG970618		HG970560	Malay & Michonneau, 2014
Chthamaloidea							
Catomerus polymerus			AY520682	AY520716		AY520614	Pérez-Losada et al., 2004
Chamaesipho tasmanica	KACb0024		AY520681	AY520715		AY520613	Pérez-Losada et al., 2004
Chthamalus stellatus	KACb0018		AY520675	AY520709		AY520607	Pérez-Losada et al., 2004
Coronuloidea							
Austrobalanus imperator	KACb400		AB723876	AB723948		AB723930	Pérez-Losada et al., 2008
Chelonibia testudinaria	CEL-BB-45	KM974417	KM974279	KM974508	KM974552		Hayashi et al., 2013
Epopella plicata	CEL-Tetra-13-1	KM974418	KM974280	KM974509		KM974553	Chan et al., 2017
Tetraclitella purpurascens	KACb15		AY520672	AY520706		AY520604	Pérez-Losada et al., 2004
Elminioidea							
Austrominius modestus	KACb12		AY520669	AY520703		AY520601	Pérez-Losada et al., 2004
Elminius kingii	KACB13		AY520670	AY520704		AY520602	Pérez-Losada et al., 2004

Appendix IV. Pairwise genetic distances between primary species hypotheses using Kimura 2-parameter model (below diagonal) and uncorrected p-distances (above diagonal).

PSH	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
1		0.1339	0.1667	0.1518	0.1399	0.1369	0.1488	0.1369	0.1458	0.1637	0.1815	0.1815	0.1548	0.1607	0.119	0.1548
2	0.1498		0.1905	0.1667	0.1531	0.1399	0.1696	0.1696	0.1637	0.1636	0.1845	0.1815	0.1616	0.1458	0.1227	0.124
3	0.1925	0.2255		0.1667	0.1607	0.1726	0.1667	0.1607	0.1756	0.1786	0.1905	0.1845	0.1696	0.1786	0.1667	0.1696
4	0.1728	0.1925	0.1925		0.1696	0.1458	0.1726	0.1726	0.1518	0.1786	0.1845	0.1815	0.1607	0.1875	0.1607	0.1667
5	0.1574	0.1745	0.1845	0.1966		0.1518	0.1369	0.1607	0.1399	0.181	0.1577	0.1429	0.1533	0.107	0.1369	0.1435
6	0.1536	0.1574	0.2006	0.165	0.1728		0.1369	0.1429	0.128	0.1994	0.1696	0.1786	0.1786	0.1607	0.128	0.1488
7	0.1689	0.1966	0.1925	0.2006	0.1536	0.1536		0.1637	0.1488	0.1875	0.1935	0.1786	0.1964	0.1637	0.1458	0.1548
8	0.1536	0.1966	0.1845	0.2006	0.1845	0.1612	0.1885		0.1458	0.1786	0.1756	0.1875	0.1905	0.1756	0.131	0.1815
9	0.165	0.1885	0.2047	0.1728	0.1574	0.1424	0.1689	0.165		0.2083	0.1548	0.1696	0.2024	0.1726	0.1518	0.1429
10	0.1885	0.1883	0.2088	0.2088	0.2122	0.2384	0.2213	0.2088	0.2516		0.2054	0.1726	0.1697	0.1605	0.1412	0.1537
11	0.213	0.2171	0.2255	0.2171	0.1806	0.1966	0.2298	0.2047	0.1767	0.2471		0.1786	0.2054	0.1518	0.1607	0.1845
12	0.213	0.213	0.2171	0.213	0.1612	0.2088	0.2088	0.2213	0.1966	0.2006	0.2088		0.2143	0.1726	0.1786	0.1488
13	0.1767	0.1857	0.1966	0.1845	0.1747	0.2088	0.2341	0.2255	0.2428	0.1967	0.2471	0.2605		0.1513	0.1391	0.1822
14	0.1845	0.1649	0.2088	0.2213	0.1168	0.1845	0.1885	0.2047	0.2006	0.1843	0.1728	0.2006	0.1722		0.131	0.1472
15	0.1314	0.1358	0.1925	0.1845	0.1536	0.1424	0.165	0.1461	0.1728	0.159	0.1845	0.2088	0.1563	0.1462		0.129
16	0.1767	0.1374	0.1966	0.1925	0.1621	0.1689	0.1767	0.213	0.1612	0.1753	0.2171	0.1689	0.2139	0.1668	0.1437	
17	0.1932	0.1837	0.1972	0.2137	0.175	0.1852	0.1812	0.2349	0.1852	0.1986	0.2179	0.1812	0.2199	0.1921	0.1647	0.09817
18	0.1767	0.171	0.1966	0.2213	0.156	0.1689	0.08909	0.1966	0.1728	0.2156	0.2088	0.213	0.2226	0.1791	0.1415	0.1582
19	0.1767	0.1847	0.1767	0.1925	0.1745	0.1689	0.1574	0.2255	0.1728	0.2086	0.2341	0.2171	0.2339	0.2171	0.1868	0.1667
20	0.1612	0.1439	0.2006	0.1728	0.1715	0.1689	0.1728	0.2171	0.213	0.1789	0.2298	0.1885	0.1884	0.1673	0.1448	0.1075
21	0.1277	0.175	0.1885	0.2006	0.1536	0.1574	0.1728	0.2171	0.1689	0.2151	0.2171	0.2298	0.2023	0.1818	0.1512	0.1753
22	0.1767	0.1603	0.1574	0.2047	0.2133	0.1806	0.1612	0.1574	0.1885	0.1818	0.256	0.2341	0.2052	0.1791	0.1459	0.1519
23	0.1767	0.1581	0.1925	0.2213	0.1745	0.1728	0.1925	0.1966	0.1689	0.1915	0.2171	0.1966	0.2429	0.2119	0.1405	0.1173
24	0.1966	0.184	0.1689	0.2341	0.1683	0.1966	0.2047	0.1966	0.1498	0.1951	0.1845	0.2255	0.2255	0.1619	0.155	0.1395
25	0.2088	0.1582	0.213	0.2255	0.1904	0.1767	0.1845	0.2255	0.1885	0.1862	0.2341	0.1885	0.2285	0.1917	0.1619	0.09974
26	0.1925	0.1736	0.1885	0.1767	0.2122	0.1885	0.2298	0.2213	0.2088	0.2064	0.2255	0.2696	0.1358	0.1673	0.1384	0.1862
27	0.1461	0.1592	0.1612	0.1885	0.1477	0.1689	0.1728	0.1689	0.1806	0.1748	0.2088	0.2088	0.1616	0.1415	0.1384	0.1519
28	0.1925	0.1802	0.2171	0.2006	0.1806	0.1806	0.2006	0.1767	0.2213	0.183	0.2428	0.2171	0.2023	0.1745	0.1465	0.184

PSH	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**
29	0.1612	0.1639	0.1925	0.1612	0.1478	0.165	0.1966	0.1767	0.1885	0.2237	0.2006	0.2006	0.1984	0.1778	0.1671	0.1843
30	0.1498	0.1382	0.2088	0.2171	0.1745	0.1728	0.2006	0.2006	0.2171	0.1978	0.165	0.2341	0.1695	0.1347	0.1427	0.1731
31	0.1728	0.1932	0.1461	0.1966	0.2025	0.2047	0.2088	0.2047	0.2384	0.1646	0.2171	0.2213	0.2079	0.1967	0.1755	0.211
32	0.1966	0.2015	0.2006	0.2213	0.1745	0.2047	0.213	0.2341	0.2047	0.2129	0.1806	0.08569	0.2369	0.1892	0.171	0.1753
33	0.1574	0.169	0.165	0.2006	0.1806	0.1806	0.1767	0.1885	0.1767	0.1487	0.1925	0.1925	0.1857	0.1673	0.1688	0.1753
34	0.1966	0.1871	0.1574	0.2213	0.2187	0.2213	0.2171	0.2341	0.2428	0.1566	0.2213	0.2255	0.2136	0.1967	0.1755	0.1907
35	0.1728	0.1592	0.1689	0.165	0.1806	0.1612	0.1806	0.1064	0.1536	0.2	0.1966	0.2255	0.1995	0.177	0.1534	0.171
36	0.1767	0.179	0.1806	0.1845	0.1685	0.1536	0.1536	0.1536	0.1689	0.181	0.2088	0.2255	0.1695	0.1818	0.1427	0.1731
37	0.1424	0.1496	0.2088	0.2298	0.122	0.1574	0.1536	0.1966	0.1767	0.2021	0.1845	0.2006	0.1857	0.108	0.13	0.171
38	0.1845	0.198	0.1767	0.1966	0.1994	0.1728	0.1925	0.1845	0.1925	0.2086	0.2384	0.2047	0.1884	0.2171	0.18	0.1929
39	0.1387	0.169	0.1728	0.1925	0.1837	0.1728	0.1885	0.1767	0.1885	0.1936	0.2255	0.1966	0.1884	0.1794	0.1197	0.1582
40	0.1767	0.1458	0.2006	0.2171	0.1806	0.1461	0.1845	0.2171	0.213	0.1748	0.2341	0.2088	0.2136	0.1917	0.1599	0.1273
41	0.1925	0.1973	0.2341	0.2384	0.1776	0.2298	0.2171	0.2471	0.213	0.1978	0.2006	0.1728	0.2489	0.2017	0.196	0.184
42	0.1574	0.1496	0.2255	0.2171	0.1625	0.1612	0.1966	0.1966	0.213	0.1915	0.1689	0.2255	0.1802	0.1393	0.1384	0.1818
43	0.165	0.177	0.1966	0.2171	0.2025	0.1925	0.1728	0.1728	0.1966	0.1626	0.2384	0.213	0.1939	0.1602	0.1491	0.1731
44	0.2171	0.173	0.213	0.2213	0.1806	0.1689	0.2384	0.2605	0.2047	0.2021	0.1885	0.256	0.1939	0.1578	0.1621	0.1731
45	0.1574	0.1612	0.2047	0.2006	0.1745	0.1498	0.1728	0.1612	0.1966	0.2064	0.2428	0.2171	0.1857	0.1745	0.1534	0.1862
46	0.1574	0.177	0.1925	0.2047	0.2025	0.165	0.1536	0.1387	0.1728	0.2086	0.2213	0.2384	0.1995	0.2043	0.1688	0.1862
47	0.1574	0.1496	0.2171	0.1806	0.1837	0.1574	0.1387	0.165	0.1574	0.2043	0.2006	0.1925	0.2165	0.1917	0.1427	0.1624
48	0.165	0.1671	0.2006	0.165	0.1745	0.165	0.1885	0.1689	0.165	0.1831	0.1885	0.2428	0.1695	0.1578	0.1491	0.1884
49	0.1536	0.1554	0.2047	0.2006	0.1448	0.1806	0.1806	0.1689	0.1925	0.1873	0.1728	0.2006	0.1695	0.1279	0.1217	0.1775
50	0.1314	0.1473	0.1612	0.1845	0.1514	0.1424	0.1536	0.1925	0.165	0.1785	0.2047	0.1925	0.2028	0.1585	0.1419	0.1055
51	0.135	0.1554	0.2006	0.1966	0.1745	0.1885	0.2088	0.2006	0.1767	0.1687	0.1767	0.1925	0.2136	0.1745	0.1448	0.1193
52	0.1767	0.175	0.2088	0.1966	0.1962	0.165	0.165	0.2298	0.1767	0.2108	0.213	0.2006	0.2281	0.1843	0.1578	0.1603
53	0.2006	0.1816	0.2213	0.213	0.1868	0.1845	0.2047	0.2088	0.1885	0.2155	0.2384	0.1845	0.2581	0.1967	0.1777	0.1255
54	0.1536	0.169	0.1728	0.1689	0.1536	0.1767	0.2213	0.1925	0.1966	0.2021	0.2255	0.2006	0.1857	0.1745	0.1578	0.1293
55	0.1498	0.1651	0.1885	0.1925	0.1776	0.165	0.1885	0.2213	0.1767	0.2021	0.2213	0.1767	0.1967	0.1818	0.1491	0.1374
56	0.1064	0.1496	0.2255	0.1925	0.1419	0.165	0.1612	0.1966	0.1767	0.1852	0.2171	0.2171	0.1722	0.1555	0.1176	0.1456
57	0.1806	0.1973	0.2213	0.2428	0.2089	0.213	0.1845	0.2047	0.1966	0.2086	0.2341	0.213	0.2222	0.2276	0.1822	0.2064
58	0.1845	0.2184	0.1885	0.2516	0.2089	0.2088	0.265	0.2171	0.2255	0.181	0.2516	0.2255	0.2222	0.2119	0.1868	0.1907
59	0.2341	0.1973	0.2384	0.2428	0.2187	0.2341	0.2047	0.2088	0.2428	0.1936	0.2171	0.2088	0.2251	0.1942	0.2101	0.2064
60	0.1612	0.1994	0.2171	0.2088	0.1994	0.165	0.1689	0.2341	0.1966	0.2064	0.2171	0.213	0.2165	0.1917	0.1755	0.1796
61	0.1806	0.1576	0.165	0.2171	0.1565	0.165	0.1966	0.2213	0.1845	0.1876	0.1925	0.2047	0.1857	0.1721	0.1512	0.1193
62	0.1767	0.1912	0.1728	0.1885	0.1715	0.1845	0.1689	0.1925	0.1689	0.2129	0.2471	0.1767	0.2193	0.1818	0.1891	0.1688

PSH	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
63	0.1277	0.1612	0.1885	0.1689	0.1461	0.1536	0.165	0.1536	0.1498	0.1925	0.1845	0.2088	0.1767	0.1806	0.1424	0.1925
64	0.1728	0.1536	0.2047	0.1885	0.165	0.1277	0.1612	0.1728	0.165	0.213	0.1689	0.2006	0.2047	0.1689	0.1424	0.1845
65	0.1241	0.1567	0.1806	0.1806	0.1588	0.1314	0.1277	0.1241	0.1498	0.1796	0.213	0.2213	0.193	0.1594	0.1062	0.1567
66	0.1885	0.1731	0.1885	0.2171	0.1745	0.2006	0.1806	0.2384	0.2047	0.2087	0.213	0.213	0.2197	0.1816	0.1711	0.1561
67	0.1574	0.1475	0.1806	0.1845	0.1634	0.1806	0.1885	0.2088	0.2171	0.1741	0.165	0.213	0.193	0.1531	0.1466	0.1569
68	0.2088	0.173	0.2006	0.1966	0.1625	0.1767	0.213	0.2047	0.1767	0.1936	0.09594	0.1885	0.1967	0.1578	0.1643	0.1775
69	0.1612	0.1756	0.1728	0.1885	0.1625	0.2171	0.1966	0.1689	0.2006	0.2108	0.2047	0.2428	0.1136	0.1697	0.1448	0.2087
70	0.1536	0.1496	0.2088	0.2088	0.1137	0.1689	0.1574	0.1885	0.1689	0.1852	0.1806	0.1806	0.1616	0.08873	0.13	0.1688
71	0.1767	0.173	0.1845	0.2171	0.1837	0.2047	0.1728	0.2255	0.1925	0.1831	0.2255	0.1806	0.1995	0.177	0.1621	0.1603
72	0.2516	0.2099	0.2006	0.2516	0.2285	0.1806	0.2516	0.2047	0.2213	0.2021	0.2741	0.2471	0.2136	0.2197	0.1937	0.1907
73	0.1767	0.1796	0.1885	0.1966	0.1776	0.2088	0.1728	0.2047	0.2171	0.1957	0.213	0.2428	0.1358	0.1649	0.1448	0.2019
74	0.1806	0.1671	0.2171	0.1689	0.1595	0.2298	0.1767	0.2006	0.2047	0.1957	0.2213	0.1925	0.116	0.1462	0.1578	0.1731
75	0.1689	0.1477	0.1845	0.2088	0.1536	0.1806	0.2006	0.2088	0.1536	0.1586	0.1767	0.2471	0.1695	0.1555	0.1363	0.154
76	0.1885	0.1435	0.1806	0.2006	0.1655	0.213	0.2088	0.2047	0.2471	0.1904	0.213	0.2471	0.1333	0.1602	0.1379	0.1862
77	0.1689	0.1592	0.1689	0.1925	0.1506	0.2006	0.2171	0.1845	0.2088	0.1936	0.213	0.2341	0.09912	0.1555	0.13	0.1907
78	0.1498	0.1612	0.1806	0.1925	0.09197	0.1806	0.1574	0.1689	0.1767	0.1978	0.1689	0.1767	0.1442	0.1179	0.1423	0.1695
79	0.1728	0.1845	0.2047	0.2047	0.1205	0.2006	0.165	0.1885	0.2047	0.2088	0.2088	0.1966	0.1536	0.1205	0.1498	0.2006
80	0.1387	0.1498	0.1728	0.1099	0.1536	0.1387	0.1728	0.165	0.1536	0.2047	0.2047	0.165	0.165	0.1925	0.1424	0.1387
81	0.213	0.1925	0.213	0.2341	0.1885	0.1885	0.1728	0.2047	0.1806	0.2605	0.2255	0.2428	0.2605	0.2171	0.1966	0.1728
82	0.2047	0.1862	0.2088	0.2298	0.1808	0.2047	0.1767	0.2006	0.1612	0.1974	0.2006	0.2255	0.2466	0.1841	0.1688	0.1519
83	0.1925	0.1496	0.1767	0.2213	0.1477	0.1574	0.1574	0.2006	0.1728	0.1769	0.213	0.1966	0.1995	0.1673	0.1427	0.09782
84	0.1845	0.1645	0.2088	0.2047	0.2133	0.1767	0.2255	0.213	0.1767	0.1996	0.2213	0.2255	0.2139	0.2045	0.1735	0.1415
85	0.2006	0.1688	0.2171	0.2047	0.2167	0.1767	0.2088	0.2255	0.1885	0.1974	0.2213	0.2384	0.2081	0.1866	0.1735	0.1313
86	0.2006	0.1667	0.1925	0.2255	0.1714	0.1885	0.2471	0.2171	0.1767	0.1974	0.2088	0.2088	0.1856	0.1692	0.1805	0.1477
87	0.1536	0.1707	0.1612	0.2006	0.1776	0.1424	0.1767	0.1925	0.1498	0.1789	0.1966	0.1806	0.1829	0.1721	0.1491	0.1153
88	0.1767	0.162	0.2006	0.1728	0.1837	0.1612	0.1767	0.1728	0.1728	0.1936	0.213	0.2047	0.1829	0.1818	0.1315	0.1645
89	0.1612	0.1496	0.1689	0.1885	0.1595	0.1574	0.1461	0.1574	0.1728	0.1957	0.2047	0.1806	0.1775	0.1508	0.1448	0.1603
90	0.165	0.1592	0.1767	0.1806	0.1776	0.1689	0.165	0.0994	0.1498	0.181	0.2047	0.2047	0.2079	0.1892	0.1534	0.1731
91	0.1277	0.1623	0.1925	0.1767	0.1305	0.1498	0.135	0.1728	0.1612	0.1707	0.1966	0.2006	0.1589	0.1462	0.1217	0.1333
92	0.1314	0.1515	0.2255	0.1966	0.1745	0.1966	0.1728	0.1845	0.1612	0.1936	0.1966	0.2516	0.1884	0.1555	0.1279	0.1603
93	0.1461	0.1439	0.213	0.2047	0.1625	0.1885	0.165	0.1966	0.1689	0.1873	0.1885	0.2471	0.1857	0.137	0.1197	0.1519
94	0.1498	0.169	0.1806	0.1845	0.1868	0.165	0.1966	0.165	0.2047	0.2021	0.2006	0.1925	0.1884	0.1721	0.1279	0.1667
95	0.1424	0.173	0.1885	0.2213	0.1994	0.1806	0.1885	0.2255	0.1925	0.1852	0.2255	0.2298	0.2107	0.1843	0.1621	0.1094
96	0.1728	0.1554	0.1689	0.2213	0.1506	0.1966	0.2088	0.1845	0.2088	0.1894	0.2171	0.2428	0.1748	0.1347	0.1279	0.1582

PSH	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
97	0.1885	0.185	0.2171	0.2341	0.193	0.2047	0.2047	0.2006	0.2255	0.1894	0.2471	0.2298	0.2079	0.1917	0.1556	0.1884
98	0.1925	0.1773	0.2213	0.2341	0.1967	0.1966	0.2298	0.1925	0.2384	0.1897	0.2741	0.2471	0.2113	0.1971	0.1603	0.1933
99	0.165	0.1871	0.213	0.2213	0.1745	0.1806	0.1845	0.1728	0.2006	0.1957	0.2255	0.2213	0.1857	0.1917	0.1512	0.1775
100	0.1728	0.175	0.1885	0.2255	0.1868	0.1925	0.2006	0.1728	0.2341	0.2108	0.2471	0.2255	0.1967	0.1843	0.1578	0.1862
101	0.1767	0.1592	0.1767	0.213	0.193	0.1806	0.1885	0.1728	0.213	0.2	0.256	0.2298	0.1939	0.1697	0.1491	0.1624
102	0.1845	0.156	0.1612	0.1845	0.2094	0.1845	0.1728	0.1845	0.2006	0.1799	0.2255	0.2384	0.1935	0.1913	0.1547	0.1627
103	0.1498	0.1651	0.2006	0.1885	0.2154	0.165	0.1689	0.2088	0.1885	0.1789	0.2088	0.2047	0.2079	0.1917	0.1578	0.1561
104	0.1424	0.1624	0.213	0.1845	0.1652	0.1966	0.1885	0.2088	0.1574	0.1818	0.1689	0.1966	0.211	0.1643	0.1573	0.1333
105	0.1536	0.1708	0.1845	0.2088	0.1776	0.1925	0.2255	0.2006	0.1574	0.1964	0.1966	0.1925	0.2079	0.1757	0.1535	0.1201
106	0.1205	0.1459	0.1966	0.1806	0.1362	0.1498	0.165	0.1387	0.1536	0.1665	0.2047	0.213	0.1616	0.1393	0.09424	0.1413
107	0.2047	0.1912	0.2047	0.256	0.1994	0.1806	0.213	0.2255	0.2213	0.2017	0.2213	0.2171	0.1884	0.1808	0.1708	0.1421
108	0.1728	0.173	0.2006	0.2605	0.1745	0.1689	0.213	0.2047	0.1806	0.2064	0.2213	0.2384	0.2165	0.1818	0.1688	0.1436
109	0.1461	0.1554	0.1767	0.1925	0.1868	0.1612	0.1966	0.2213	0.1806	0.1957	0.1966	0.1925	0.1884	0.1602	0.1512	0.1354
110	0.1925	0.1477	0.1806	0.2171	0.1715	0.165	0.1806	0.1925	0.1885	0.1667	0.2213	0.1767	0.2079	0.177	0.1578	0.1134
111	0.1885	0.1606	0.1806	0.2171	0.1376	0.1424	0.1689	0.1966	0.1612	0.1715	0.2047	0.1925	0.2001	0.1693	0.1526	0.09461
112	0.1612	0.1677	0.2047	0.2088	0.1745	0.2006	0.2341	0.1925	0.1806	0.181	0.165	0.2088	0.2107	0.1721	0.1512	0.1395
113	0.1498	0.1582	0.1925	0.1885	0.1808	0.1806	0.2088	0.1845	0.1689	0.184	0.1806	0.1845	0.2168	0.1668	0.1573	0.1114
114	0.1574	0.1582	0.1966	0.1925	0.1776	0.1845	0.2213	0.1845	0.1806	0.1862	0.1767	0.213	0.1996	0.1619	0.1619	0.1333
115	0.213	0.183	0.2171	0.2213	0.1868	0.1885	0.1845	0.1885	0.1925	0.1957	0.2047	0.2298	0.2369	0.1818	0.18	0.1645

PSH	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32
1	0.1672	0.1548	0.1548	0.1429	0.1161	0.1548	0.1548	0.1696	0.1786	0.1667	0.131	0.1667	0.1429	0.1339	0.1518	0.1696
2	0.1601	0.1504	0.1608	0.1292	0.1535	0.1421	0.1404	0.1603	0.1405	0.1524	0.1413	0.1574	0.145	0.1246	0.1672	0.1733
3	0.1701	0.1696	0.1548	0.1726	0.1637	0.1399	0.1667	0.1488	0.1815	0.1637	0.1429	0.1845	0.1667	0.1786	0.131	0.1726
4	0.1821	0.1875	0.1667	0.1518	0.1726	0.1756	0.1875	0.1964	0.1905	0.1548	0.1637	0.1726	0.1429	0.1845	0.1696	0.1875
5	0.1535	0.1388	0.1531	0.1508	0.1369	0.1818	0.1531	0.1483	0.1651	0.181	0.1323	0.1578	0.1323	0.1531	0.174	0.1531
6	0.1612	0.1488	0.1488	0.1488	0.1399	0.1577	0.1518	0.1696	0.1548	0.1637	0.1488	0.1577	0.1458	0.1518	0.1756	0.1756
7	0.1582	0.0833	0.1399	0.1518	0.1518	0.1429	0.1667	0.1756	0.1607	0.1935	0.1518	0.1726	0.1696	0.1726	0.1786	0.1815
8	0.197	0.1696	0.1905	0.1845	0.1845	0.1399	0.1696	0.1696	0.1905	0.1875	0.1488	0.1548	0.1548	0.1726	0.1756	0.1964
9	0.1612	0.1518	0.1518	0.1815	0.1488	0.1637	0.1488	0.1339	0.1637	0.1786	0.1577	0.1875	0.1637	0.1845	0.1994	0.1756
10	0.1711	0.1835	0.1784	0.1565	0.1831	0.1587	0.1659	0.1686	0.162	0.1768	0.1534	0.1596	0.1892	0.1706	0.1455	0.1815

PSH	**17**	**18**	**19**	**20**	**21**	**22**	**23**	**24**	**25**	**26**	**27**	**28**	**29**	**30**	**31**	**32**
11	0.1851	0.1786	0.1964	0.1935	0.1845	0.2113	0.1845	0.1607	0.1964	0.1905	0.1786	0.2024	0.1726	0.1458	0.1845	0.1577
12	0.1582	0.1815	0.1845	0.1637	0.1935	0.1964	0.1696	0.1905	0.1637	0.2202	0.1786	0.1845	0.1726	0.1964	0.1875	0.0804
13	0.1865	0.1884	0.1963	0.1636	0.1738	0.176	0.2025	0.1905	0.1925	0.1227	0.1431	0.1738	0.171	0.1493	0.1779	0.1984
14	0.1664	0.1566	0.1845	0.1476	0.1587	0.1566	0.1808	0.1434	0.166	0.1476	0.1273	0.1531	0.1556	0.1218	0.1697	0.1642
15	0.1455	0.1272	0.1624	0.1299	0.135	0.1308	0.1265	0.138	0.1434	0.1248	0.1248	0.1313	0.1474	0.1282	0.1538	0.1504
16	0.0912	0.1405	0.1471	0.0992	0.1537	0.1355	0.1074	0.1256	0.0926	0.162	0.1355	0.1603	0.1605	0.1521	0.1802	0.1537
17		0.1609	0.1481	0.1082	0.1387	0.1559	0.1223	0.1327	0.1012	0.1835	0.1463	0.1579	0.1601	0.1509	0.1799	0.1601
18	0.1847		0.162	0.1554	0.1587	0.1438	0.1636	0.1372	0.1537	0.162	0.1471	0.1636	0.1763	0.1818	0.1835	0.1521
19	0.1679	0.1862		0.1492	0.1187	0.1587	0.1605	0.1587	0.1438	0.1985	0.1507	0.1623	0.1671	0.1796	0.1735	0.1735
20	0.1183	0.1775	0.1693		0.1337	0.1388	0.1219	0.1256	0.0992	0.1585	0.1246	0.1373	0.1622	0.1353	0.1717	0.155
21	0.1559	0.1818	0.131	0.1496		0.1421	0.1528	0.1554	0.1405	0.1616	0.1398	0.1497	0.1499	0.1657	0.1687	0.1672
22	0.1781	0.1624	0.1818	0.1561	0.1603		0.1388	0.1405	0.1504	0.1471	0.1421	0.1421	0.1684	0.1636	0.1669	0.1818
23	0.1353	0.1884	0.1842	0.1349	0.1741	0.1561		0.1223	0.1273	0.1651	0.1451	0.1651	0.1622	0.1512	0.1636	0.1682
24	0.1483	0.154	0.1818	0.1395	0.1775	0.1582	0.1354		0.1289	0.1405	0.1372	0.1537	0.1816	0.1372	0.1669	0.1488
25	0.1098	0.1753	0.1624	0.1075	0.1582	0.171	0.1415	0.1436		0.1653	0.1339	0.1554	0.1895	0.1587	0.1785	0.157
26	0.2157	0.1862	0.2371	0.1816	0.1857	0.1667	0.1904	0.1582	0.1907		0.1418	0.1698	0.1744	0.1448	0.1646	0.1662
27	0.1657	0.1667	0.1713	0.1382	0.1573	0.1603	0.164	0.154	0.1498	0.1598		0.1451	0.1572	0.1261	0.155	0.1596
28	0.1808	0.1884	0.1866	0.1542	0.17	0.1603	0.1904	0.1753	0.1775	0.1967	0.164		0.1596	0.1528	0.1744	0.1559
29	0.1837	0.2057	0.1931	0.1865	0.1703	0.1949	0.1865	0.213	0.2241	0.2031	0.1799	0.1831		0.1499	0.1769	0.1794
30	0.1716	0.2133	0.2102	0.1515	0.1912	0.1884	0.172	0.154	0.1818	0.1637	0.1401	0.1741	0.1703		0.1626	0.1717
31	0.2106	0.2156	0.2018	0.1994	0.1953	0.1929	0.1884	0.1929	0.2087	0.1898	0.177	0.203	0.2065	0.1871		0.1748
32	0.1837	0.1731	0.2018	0.177	0.1932	0.2133	0.1946	0.1688	0.1796	0.1918	0.183	0.1781	0.2099	0.1994	0.2036	
33	0.1776	0.1884	0.1833	0.1932	0.185	0.1519	0.1802	0.1775	0.2064	0.1756	0.169	0.1601	0.1832	0.185	0.1631	0.1871
34	0.198	0.211	0.2039	0.185	0.185	0.1951	0.1925	0.1818	0.1974	0.1796	0.177	0.1863	0.1998	0.1891	0.0946	0.1912
35	0.1939	0.1775	0.2018	0.1651	0.1871	0.1519	0.1822	0.1667	0.1884	0.1696	0.1477	0.1464	0.1639	0.175	0.1891	0.183
36	0.1776	0.1753	0.1874	0.1671	0.1439	0.1498	0.1761	0.1796	0.1582	0.1618	0.1458	0.1503	0.1607	0.169	0.181	0.1912
37	0.1939	0.1498	0.1773	0.1651	0.1631	0.1519	0.1741	0.1561	0.184	0.1776	0.1477	0.168	0.1703	0.1307	0.1953	0.183
38	0.1905	0.1667	0.1901	0.196	0.1918	0.1862	0.2246	0.1796	0.1667	0.1857	0.1618	0.162	0.1931	0.2043	0.2106	0.1696

PSH	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32
39	0.1816	0.1561	0.1915	0.1554	0.169	0.1519	0.1863	0.1731	0.1796	0.1637	0.1573	0.172	0.1576	0.183	0.181	0.1592
40	0.1312	0.1688	0.1793	0.1326	0.177	0.1667	0.1425	0.1603	0.1134	0.1796	0.1496	0.17	0.1735	0.1631	0.1871	0.171
41	0.1939	0.1951	0.1813	0.183	0.175	0.1951	0.2073	0.2087	0.2019	0.2433	0.1932	0.1781	0.1931	0.2015	0.2036	0.1912
42	0.1677	0.1667	0.2124	0.1554	0.1554	0.1603	0.1988	0.1603	0.1603	0.1696	0.1439	0.162	0.1735	0.1307	0.1871	0.175
43	0.1898	0.1753	0.1874	0.1671	0.183	0.1273	0.1761	0.1862	0.184	0.1756	0.1382	0.1406	0.2133	0.179	0.1932	0.1932
44	0.1837	0.1818	0.2081	0.1651	0.175	0.2087	0.2073	0.1775	0.1862	0.1618	0.1612	0.172	0.1671	0.1671	0.1932	0.1953
45	0.198	0.184	0.1977	0.185	0.175	0.1519	0.2052	0.1996	0.1731	0.1776	0.1515	0.1444	0.1671	0.1612	0.2184	0.2057
46	0.2001	0.1498	0.2124	0.185	0.175	0.1667	0.2052	0.1688	0.2087	0.1898	0.1592	0.1464	0.1639	0.2015	0.2036	0.1953
47	0.1776	0.154	0.2018	0.179	0.1554	0.1395	0.172	0.1753	0.1753	0.1776	0.177	0.1425	0.1832	0.1932	0.2078	0.175
48	0.2043	0.184	0.1895	0.177	0.1573	0.1603	0.2073	0.1951	0.1667	0.1657	0.1534	0.166	0.1931	0.175	0.2078	0.2015
49	0.1756	0.1561	0.1936	0.1612	0.169	0.1775	0.1946	0.1561	0.1561	0.1578	0.1382	0.166	0.1735	0.1382	0.173	0.1631
50	0.0905	0.1796	0.1475	0.0885	0.1377	0.1519	0.1249	0.1193	0.1055	0.1815	0.1302	0.1558	0.1535	0.1265	0.1789	0.1789
51	0.1387	0.184	0.1753	0.1252	0.1592	0.1753	0.1162	0.1436	0.1456	0.198	0.1631	0.1842	0.1545	0.1573	0.1994	0.181
52	0.1637	0.2019	0.1385	0.1554	0.1326	0.1775	0.17	0.1951	0.1688	0.2085	0.175	0.2009	0.1703	0.181	0.2141	0.1891
53	0.1335	0.2023	0.1739	0.1406	0.196	0.1822	0.1606	0.1459	0.1336	0.2178	0.1796	0.1666	0.1998	0.1677	0.2235	0.2106
54	0.1238	0.1974	0.1518	0.1215	0.1477	0.1645	0.1444	0.1436	0.1374	0.1898	0.142	0.168	0.1832	0.1612	0.1994	0.185
55	0.1238	0.1974	0.1576	0.1197	0.1534	0.171	0.1425	0.1354	0.1153	0.1736	0.1496	0.166	0.1865	0.1554	0.185	0.1592
56	0.1857	0.1624	0.1753	0.1477	0.169	0.1645	0.164	0.1731	0.171	0.1716	0.1307	0.1741	0.1964	0.1439	0.179	0.171
57	0.2257	0.2042	0.1977	0.1994	0.2036	0.1907	0.203	0.1974	0.1929	0.2064	0.177	0.2073	0.1865	0.1973	0.2205	0.1912
58	0.1918	0.2226	0.206	0.1871	0.1973	0.2156	0.2116	0.1929	0.1796	0.2278	0.1932	0.1761	0.1865	0.2141	0.1871	0.2162
59	0.2085	0.1996	0.2209	0.2099	0.1932	0.2064	0.2224	0.1796	0.2087	0.2085	0.179	0.1822	0.1735	0.1912	0.2015	0.2078
60	0.2001	0.1951	0.1956	0.175	0.2057	0.1884	0.1988	0.2019	0.1884	0.196	0.1554	0.2009	0.1931	0.169	0.1994	0.1912
61	0.1314	0.1951	0.133	0.1236	0.1595	0.1624	0.1466	0.1498	0.1233	0.1719	0.1576	0.1805	0.1767	0.1479	0.1833	0.1915
62	0.1918	0.1753	0.1998	0.173	0.181	0.171	0.1904	0.1796	0.1996	0.1939	0.177	0.1761	0.1703	0.183	0.1973	0.1631
63	0.1932	0.1966	0.1314	0.165	0.1536	0.1689	0.1925	0.1767	0.1925	0.1728	0.1536	0.1689	0.1845	0.1728	0.1806	0.2088
64	0.1579	0.2006	0.1689	0.1845	0.165	0.1845	0.1767	0.1885	0.1845	0.1925	0.1387	0.1925	0.1461	0.165	0.1845	0.1845
65	0.1596	0.15	0.1726	0.1635	0.1726	0.1238	0.1796	0.1433	0.1749	0.1657	0.15	0.1478	0.1529	0.1544	0.2082	0.1937
66	0.1673	0.1884	0.1456	0.154	0.1354	0.1907	0.184	0.1796	0.1667	0.2133	0.1818	0.1996	0.2021	0.1951	0.2019	0.211

PSH	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32
67	0.1835	0.1526	0.2006	0.168	0.1786	0.1655	0.1819	0.1743	0.1854	0.19	0.1556	0.1929	0.1687	0.1556	0.1701	0.1958
68	0.1877	0.1796	0.1854	0.181	0.1973	0.1818	0.1842	0.1667	0.218	0.1696	0.1651	0.1761	0.1576	0.1496	0.179	0.177
69	0.2178	0.1974	0.2068	0.196	0.2022	0.1796	0.2137	0.1929	0.218	0.1368	0.1578	0.1863	0.1799	0.1578	0.1796	0.2149
70	0.1796	0.1561	0.1793	0.1651	0.1612	0.1688	0.1802	0.1624	0.171	0.1696	0.127	0.166	0.1735	0.1458	0.185	0.179
71	0.1857	0.1974	0.1977	0.183	0.169	0.171	0.1802	0.1667	0.1884	0.1756	0.1554	0.1761	0.1671	0.179	0.179	0.1631
72	0.2001	0.249	0.2231	0.2036	0.2036	0.1818	0.1904	0.2087	0.2042	0.1857	0.1932	0.1967	0.2343	0.2141	0.1994	0.2205
73	0.1803	0.1796	0.1984	0.1716	0.1756	0.1884	0.1988	0.1884	0.2019	0.1425	0.154	0.1863	0.1703	0.1578	0.196	0.2043
74	0.1898	0.1688	0.1956	0.181	0.1973	0.1753	0.203	0.1775	0.1974	0.1275	0.1515	0.1822	0.1671	0.1671	0.1932	0.177
75	0.1657	0.1775	0.1854	0.1671	0.183	0.171	0.166	0.1775	0.171	0.1637	0.142	0.1741	0.1671	0.1363	0.185	0.1891
76	0.2149	0.1884	0.2244	0.1891	0.1891	0.154	0.1988	0.1753	0.1884	0.1387	0.1496	0.1822	0.1964	0.171	0.177	0.1953
77	0.2043	0.1862	0.2231	0.177	0.2036	0.1582	0.1741	0.1775	0.1996	0.133	0.1363	0.168	0.1767	0.1651	0.1631	0.1912
78	0.1755	0.1875	0.2007	0.1667	0.1722	0.2028	0.1949	0.1725	0.1966	0.1722	0.1344	0.1891	0.1545	0.1722	0.1978	0.1978
79	0.2096	0.1925	0.2213	0.1885	0.213	0.213	0.2171	0.2213	0.2428	0.1885	0.1689	0.2213	0.1925	0.2006	0.2255	0.213
80	0.1812	0.1806	0.1767	0.1574	0.1612	0.1767	0.1806	0.2006	0.2213	0.1461	0.165	0.213	0.1612	0.1925	0.1845	0.1966
81	0.1932	0.1767	0.1767	0.2213	0.1925	0.1925	0.1885	0.2213	0.1767	0.2384	0.2255	0.2384	0.1925	0.2298	0.2428	0.2428
82	0.1609	0.1731	0.1645	0.1884	0.171	0.171	0.1907	0.1753	0.154	0.1996	0.1731	0.1753	0.2093	0.1996	0.1929	0.1929
83	0.1128	0.1561	0.1654	0.1252	0.1592	0.1498	0.1217	0.1293	0.1233	0.1857	0.1477	0.168	0.1767	0.173	0.1871	0.1871
84	0.1483	0.1884	0.1907	0.1477	0.1862	0.2019	0.1688	0.1582	0.1436	0.1796	0.1582	0.184	0.1985	0.1907	0.2019	0.1907
85	0.142	0.1951	0.1862	0.1273	0.1775	0.1818	0.1498	0.1519	0.1415	0.1951	0.1519	0.1862	0.2204	0.1884	0.2064	0.2019
86	0.14	0.2019	0.1667	0.1415	0.1603	0.1667	0.154	0.1395	0.1293	0.1775	0.1519	0.1796	0.1808	0.1667	0.2064	0.1907
87	0.1074	0.1796	0.1382	0.116	0.1345	0.1415	0.1368	0.1374	0.1075	0.1696	0.1534	0.164	0.1545	0.1651	0.175	0.183
88	0.1706	0.1688	0.1723	0.162	0.1781	0.1395	0.1658	0.184	0.1688	0.168	0.1503	0.118	0.1603	0.166	0.1946	0.164
89	0.1482	0.1645	0.1713	0.1477	0.1534	0.1173	0.1741	0.154	0.1753	0.1637	0.1477	0.1311	0.1514	0.1631	0.1891	0.169
90	0.1756	0.1731	0.1977	0.1534	0.1891	0.154	0.172	0.1688	0.1731	0.1857	0.1458	0.1368	0.1703	0.177	0.1912	0.177
91	0.1559	0.1582	0.1648	0.1439	0.1363	0.1561	0.164	0.1436	0.1645	0.1482	0.1307	0.1292	0.1576	0.1554	0.179	0.183
92	0.1696	0.1667	0.1874	0.1671	0.1651	0.1667	0.1781	0.1796	0.1603	0.1796	0.1307	0.168	0.1865	0.171	0.2015	0.1891
93	0.1696	0.154	0.1895	0.1573	0.1671	0.1561	0.164	0.1667	0.1603	0.1677	0.1289	0.1601	0.1865	0.1534	0.183	0.181
94	0.196	0.1645	0.1813	0.1671	0.183	0.1561	0.1904	0.1818	0.1796	0.1736	0.1573	0.172	0.1735	0.173	0.181	0.1612

PSH	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32
95	0.1482	0.1929	0.1854	0.1124	0.1671	0.1498	0.1406	0.1415	0.1395	0.1939	0.1534	0.1988	0.2168	0.1592	0.171	0.2099
96	0.1857	0.1645	0.1956	0.179	0.1871	0.1603	0.1842	0.1667	0.1996	0.1816	0.142	0.17	0.1576	0.142	0.1871	0.1953
97	0.2043	0.1796	0.2124	0.1973	0.2057	0.1498	0.1761	0.1775	0.1907	0.1657	0.1671	0.1483	0.2272	0.1671	0.2078	0.2015
98	0.2153	0.1822	0.2022	0.1936	0.206	0.1627	0.195	0.1955	0.1933	0.162	0.1634	0.1486	0.235	0.1773	0.206	0.206
99	0.1939	0.1688	0.1936	0.1932	0.2015	0.1561	0.1761	0.1688	0.1884	0.1501	0.169	0.1464	0.1998	0.1651	0.2078	0.1973
100	0.196	0.1818	0.1733	0.1671	0.1612	0.1436	0.1863	0.1667	0.1688	0.1637	0.1651	0.1503	0.1865	0.185	0.2036	0.2057
101	0.1796	0.1818	0.1674	0.1631	0.1631	0.1233	0.1781	0.1582	0.1731	0.1578	0.1439	0.1503	0.1931	0.175	0.2078	0.1891
102	0.1806	0.1542	0.1799	0.1711	0.1978	0.1606	0.1733	0.1914	0.1914	0.1777	0.1455	0.1624	0.2014	0.1711	0.1955	0.2001
103	0.1756	0.1645	0.2081	0.1554	0.2099	0.154	0.162	0.1667	0.1796	0.1657	0.1573	0.1967	0.1767	0.1592	0.1671	0.1871
104	0.1441	0.1667	0.1603	0.1354	0.1775	0.1907	0.1354	0.1253	0.1603	0.1907	0.171	0.1862	0.1878	0.1796	0.2087	0.1907
105	0.1489	0.1832	0.1708	0.1342	0.1835	0.1885	0.1414	0.1249	0.1546	0.1991	0.1683	0.1809	0.1747	0.1658	0.215	0.1658
106	0.1762	0.1505	0.1805	0.1504	0.1688	0.1436	0.1665	0.1505	0.1646	0.1415	0.1282	0.1504	0.1598	0.1392	0.1665	0.1711
107	0.1369	0.202	0.1912	0.139	0.1708	0.2103	0.151	0.17	0.1446	0.1886	0.1535	0.2043	0.1914	0.1784	0.2232	0.1938
108	0.1598	0.184	0.1793	0.1554	0.171	0.154	0.166	0.0901	0.1519	0.1857	0.1496	0.1761	0.1931	0.1651	0.1953	0.1891
109	0.1146	0.1907	0.146	0.1052	0.1345	0.1688	0.1503	0.1354	0.1293	0.1816	0.1382	0.1483	0.1832	0.1477	0.1592	0.1554
110	0.1256	0.154	0.1753	0.1326	0.171	0.1374	0.1273	0.1313	0.1354	0.1857	0.1554	0.172	0.1799	0.175	0.1912	0.173
111	0.1009	0.1606	0.1715	0.1288	0.1671	0.1434	0.1145	0.1226	0.1165	0.1849	0.1584	0.1562	0.1776	0.1606	0.1895	0.1804
112	0.1604	0.1884	0.1854	0.1444	0.1736	0.184	0.1425	0.1436	0.1603	0.1864	0.1918	0.1908	0.1767	0.1877	0.217	0.1918
113	0.1483	0.1929	0.171	0.1293	0.1862	0.1753	0.1354	0.154	0.1561	0.1996	0.184	0.1907	0.1602	0.1731	0.2087	0.1884
114	0.1545	0.1907	0.1818	0.1415	0.1753	0.184	0.1415	0.1395	0.1603	0.1929	0.1862	0.1929	0.1739	0.171	0.1996	0.1951
115	0.1716	0.1775	0.1977	0.185	0.173	0.171	0.168	0.1929	0.1667	0.1837	0.185	0.1822	0.1576	0.1912	0.183	0.212

PSH	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48
1	0.1399	0.1696	0.1518	0.1548	0.128	0.1607	0.125	0.1548	0.1667	0.1399	0.1458	0.1845	0.1399	0.1399	0.1399	0.1458
2	0.1489	0.1626	0.1413	0.1565	0.1337	0.1707	0.1489	0.1307	0.1702	0.1337	0.155	0.152	0.1429	0.155	0.1337	0.1474
3	0.1458	0.1399	0.1488	0.1577	0.1786	0.1548	0.1518	0.1726	0.1964	0.1905	0.1696	0.1815	0.1756	0.1667	0.1845	0.1726
4	0.1726	0.1875	0.1458	0.1607	0.1935	0.1696	0.1667	0.1845	0.1994	0.1845	0.1845	0.1875	0.1726	0.1756	0.1577	0.1458
5	0.1578	0.1856	0.1578	0.1485	0.1114	0.1717	0.1601	0.1578	0.1555	0.1439	0.174	0.1578	0.1531	0.174	0.1601	0.1531

PSH	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48
6	0.1577	0.1875	0.1429	0.1369	0.1399	0.1518	0.1518	0.131	0.1935	0.1429	0.1667	0.1488	0.1339	0.1458	0.1399	0.1458
7	0.1548	0.1845	0.1577	0.1369	0.1369	0.1667	0.1637	0.1607	0.1845	0.1696	0.1518	0.1994	0.1518	0.1369	0.125	0.1637
8	0.1637	0.1964	0.0982	0.1369	0.1696	0.1607	0.1548	0.1845	0.2054	0.1696	0.1518	0.2143	0.1429	0.125	0.1458	0.1488
9	0.1548	0.2024	0.1369	0.1488	0.1548	0.1667	0.1637	0.1815	0.1815	0.1815	0.1696	0.1756	0.1696	0.1518	0.1399	0.1458
10	0.133	0.1393	0.1721	0.1581	0.1737	0.1784	0.1674	0.1534	0.1706	0.1659	0.144	0.1737	0.1768	0.1784	0.1753	0.1596
11	0.1667	0.1875	0.1696	0.1786	0.1607	0.1994	0.1905	0.1964	0.1726	0.1488	0.1994	0.1637	0.2024	0.1875	0.1726	0.1637
12	0.1667	0.1905	0.1905	0.1905	0.1726	0.1756	0.1696	0.1786	0.1518	0.1905	0.1815	0.2113	0.1845	0.1994	0.1667	0.2024
13	0.1616	0.182	0.1718	0.1493	0.1616	0.1636	0.1636	0.182	0.2065	0.1575	0.1677	0.1677	0.1616	0.1718	0.184	0.1493
14	0.1476	0.1697	0.155	0.1587	0.0996	0.1845	0.1568	0.1661	0.1734	0.1255	0.1421	0.1402	0.1531	0.1753	0.1661	0.1402
15	0.1487	0.1538	0.1368	0.1282	0.1179	0.1573	0.1094	0.1419	0.1692	0.1248	0.1333	0.1436	0.1368	0.1487	0.1282	0.1333
16	0.1537	0.1653	0.1504	0.1521	0.1504	0.1669	0.1405	0.1157	0.1603	0.1587	0.1521	0.1521	0.162	0.162	0.1438	0.1636
17	0.1555	0.1707	0.1677	0.1555	0.1677	0.1651	0.1585	0.1189	0.1677	0.1479	0.1646	0.1601	0.1707	0.1723	0.1555	0.1753
18	0.1636	0.1802	0.1554	0.1537	0.1339	0.1471	0.1388	0.1488	0.1686	0.1471	0.1537	0.1587	0.1603	0.1339	0.1372	0.1603
19	0.1598	0.175	0.1735	0.1629	0.1553	0.1649	0.1659	0.1568	0.1583	0.1811	0.1629	0.1781	0.1705	0.1811	0.1735	0.1644
20	0.1672	0.1611	0.1459	0.1474	0.1459	0.1692	0.1383	0.1201	0.1596	0.1383	0.1474	0.1459	0.1611	0.1611	0.1565	0.155
21	0.1611	0.1611	0.1626	0.1292	0.1444	0.1662	0.1489	0.155	0.1535	0.1383	0.1596	0.1535	0.1535	0.1535	0.1383	0.1398
22	0.1355	0.1686	0.1355	0.1339	0.1355	0.162	0.1355	0.1471	0.1686	0.1421	0.1157	0.1785	0.1355	0.1471	0.1256	0.1421
23	0.1574	0.1667	0.159	0.1543	0.1528	0.1898	0.162	0.1281	0.1775	0.1713	0.1543	0.1775	0.1759	0.1759	0.1512	0.1775
24	0.1554	0.1587	0.1471	0.157	0.1388	0.157	0.1521	0.1421	0.1785	0.1421	0.162	0.1554	0.1719	0.1488	0.1537	0.1686
25	0.1769	0.1702	0.1636	0.1405	0.1603	0.1471	0.157	0.1041	0.1736	0.1421	0.1603	0.162	0.1521	0.1785	0.1537	0.1471
26	0.154	0.157	0.1494	0.1433	0.1555	0.1616	0.1448	0.157	0.2027	0.1494	0.154	0.1433	0.1555	0.1646	0.1555	0.1463
27	0.1489	0.155	0.1322	0.1307	0.1322	0.1433	0.1398	0.1337	0.1672	0.1292	0.1246	0.1429	0.1353	0.1413	0.155	0.1368
28	0.142	0.162	0.1312	0.1343	0.1481	0.1435	0.1512	0.1497	0.1559	0.1435	0.1265	0.1512	0.1296	0.1312	0.1281	0.1466
29	0.1597	0.172	0.145	0.1425	0.1499	0.1671	0.14	0.1523	0.1671	0.1523	0.1818	0.1474	0.1474	0.145	0.1597	0.1671
30	0.1611	0.1641	0.1535	0.1489	0.1185	0.1753	0.1596	0.1444	0.1733	0.1185	0.1565	0.1474	0.1429	0.1733	0.1672	0.1535
31	0.1444	0.0882	0.1641	0.1581	0.1687	0.1799	0.1581	0.1626	0.1748	0.1626	0.1672	0.1672	0.1854	0.1748	0.1778	0.1778
32	0.1626	0.1657	0.1596	0.1657	0.1596	0.1494	0.1413	0.1505	0.1657	0.1535	0.1672	0.1687	0.1763	0.1687	0.1535	0.1733
33		0.1444	0.1474	0.1489	0.1535	0.1662	0.1459	0.1641	0.1626	0.155	0.1489	0.1565	0.1763	0.1657	0.1565	0.1596

PSH	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48
34	0.1631		0.1489	0.1596	0.1641	0.1631	0.1626	0.1596	0.1657	0.1581	0.1596	0.1657	0.1733	0.1702	0.1763	0.1672
35	0.1671	0.169		0.117	0.1429	0.1418	0.1322	0.1459	0.1565	0.1444	0.1429	0.152	0.1246	0.1292	0.1353	0.1429
36	0.169	0.183	0.1289		0.1444	0.1448	0.1444	0.1429	0.1702	0.1353	0.1277	0.1535	0.1261	0.1413	0.1261	0.1459
37	0.175	0.1891	0.1612	0.1631		0.157	0.1413	0.1459	0.1641	0.1246	0.1322	0.152	0.1383	0.1413	0.1322	0.1565
38	0.1918	0.1877	0.1598	0.1637	0.1796		0.1753	0.1463	0.1875	0.1616	0.1448	0.1768	0.1418	0.1448	0.1448	0.1662
39	0.1651	0.1871	0.1477	0.1631	0.1592	0.2043		0.1368	0.1717	0.1535	0.1413	0.1596	0.1459	0.1489	0.1459	0.1611
40	0.1891	0.183	0.1651	0.1612	0.1651	0.1657	0.1534		0.1763	0.1459	0.1353	0.1626	0.1489	0.1641	0.1292	0.1657
41	0.1871	0.1912	0.179	0.1973	0.1891	0.2213	0.1994	0.2057		0.1748	0.1672	0.155	0.1702	0.1763	0.1657	0.1809
42	0.177	0.181	0.1631	0.1515	0.1382	0.1857	0.175	0.1651	0.2036		0.1505	0.1383	0.1413	0.1535	0.1444	0.1049
43	0.169	0.183	0.1612	0.142	0.1477	0.1637	0.1592	0.1515	0.1932	0.171		0.1581	0.1216	0.152	0.1261	0.1429
44	0.179	0.1912	0.173	0.175	0.173	0.2064	0.183	0.1871	0.177	0.1554	0.181		0.1611	0.1626	0.1641	0.1535
45	0.2057	0.2015	0.1382	0.1401	0.1554	0.1598	0.1651	0.169	0.1973	0.1592	0.1345	0.185		0.1398	0.1216	0.1565
46	0.1912	0.1973	0.1439	0.1592	0.1592	0.1637	0.169	0.1891	0.2057	0.175	0.173	0.1871	0.1573		0.1413	0.1535
47	0.179	0.2057	0.1515	0.1401	0.1477	0.1637	0.1651	0.1439	0.1912	0.1631	0.1401	0.1891	0.1345	0.1592		0.155
48	0.183	0.1932	0.1612	0.1651	0.179	0.1918	0.185	0.1912	0.212	0.1142	0.1612	0.175	0.179	0.175	0.177	
49	0.173	0.177	0.1671	0.1382	0.1234	0.1857	0.1573	0.1515	0.2078	0.0825	0.1458	0.1592	0.1554	0.177	0.1592	0.1179
50	0.1708	0.1891	0.1708	0.1748	0.1512	0.1775	0.1629	0.1136	0.2037	0.1531	0.1649	0.1688	0.1748	0.1728	0.1649	0.1649
51	0.179	0.1912	0.177	0.1871	0.175	0.1939	0.175	0.1345	0.169	0.177	0.1912	0.1891	0.2015	0.2015	0.1651	0.1953
52	0.2078	0.2162	0.1912	0.1891	0.1612	0.198	0.179	0.175	0.175	0.1932	0.1871	0.2078	0.185	0.1973	0.173	0.1953
53	0.1918	0.2149	0.1837	0.1837	0.1816	0.1988	0.1918	0.1444	0.2001	0.1918	0.2085	0.2106	0.2001	0.2106	0.1877	0.2192
54	0.1953	0.185	0.169	0.1631	0.169	0.1756	0.1631	0.1439	0.2015	0.169	0.169	0.1891	0.177	0.183	0.1671	0.1651
55	0.169	0.181	0.173	0.173	0.175	0.1837	0.1401	0.1215	0.1994	0.1631	0.1871	0.1953	0.173	0.177	0.1871	0.181
56	0.1592	0.181	0.1554	0.177	0.1215	0.1796	0.1496	0.1592	0.1912	0.1363	0.1671	0.1631	0.1671	0.1891	0.1612	0.1515
57	0.1953	0.227	0.1932	0.185	0.1871	0.2235	0.1953	0.1573	0.2036	0.2057	0.1953	0.227	0.181	0.1932	0.1631	0.212
58	0.1953	0.179	0.2015	0.1973	0.2057	0.1756	0.173	0.183	0.1912	0.2036	0.1994	0.2078	0.2036	0.2099	0.2248	0.1994
59	0.2036	0.212	0.1891	0.173	0.179	0.1857	0.2141	0.212	0.2036	0.2036	0.183	0.1953	0.179	0.169	0.1973	0.2036
60	0.1891	0.2015	0.2057	0.2036	0.185	0.2128	0.181	0.173	0.227	0.185	0.2078	0.1953	0.183	0.1932	0.175	0.2099
61	0.1833	0.1956	0.1813	0.1813	0.1499	0.1779	0.1833	0.1236	0.1874	0.1854	0.1773	0.1693	0.1773	0.1956	0.1813	0.1874

PSH	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48
62	0.1871	0.1871	0.177	0.177	0.175	0.1918	0.1651	0.177	0.2078	0.1912	0.181	0.2099	0.185	0.185	0.173	0.212
63	0.165	0.1885	0.1498	0.1574	0.1461	0.1728	0.1885	0.1966	0.1767	0.1689	0.1424	0.1885	0.165	0.1966	0.1612	0.165
64	0.1536	0.2088	0.1612	0.1689	0.1574	0.1845	0.1767	0.1728	0.1806	0.1461	0.1689	0.1728	0.1574	0.1806	0.1767	0.1806
65	0.1567	0.1866	0.1029	0.1368	0.126	0.1567	0.1303	0.1544	0.2009	0.1346	0.126	0.1703	0.1346	0.1281	0.1346	0.1455
66	0.1731	0.2226	0.1929	0.1929	0.1796	0.2019	0.1818	0.1775	0.1667	0.2087	0.2064	0.1818	0.218	0.218	0.1929	0.2064
67	0.168	0.168	0.1618	0.1659	0.1701	0.2032	0.1764	0.168	0.1659	0.1577	0.1764	0.1639	0.2024	0.1893	0.1536	0.1807
68	0.1612	0.1891	0.171	0.1671	0.1534	0.1877	0.171	0.185	0.1932	0.1439	0.181	0.1671	0.175	0.181	0.173	0.183
69	0.1918	0.1837	0.1776	0.1756	0.1559	0.1736	0.1816	0.196	0.2106	0.1637	0.1716	0.1756	0.1716	0.1796	0.1898	0.1637
70	0.1592	0.171	0.1592	0.1515	0.0911	0.1837	0.175	0.1554	0.2036	0.127	0.1515	0.1671	0.1573	0.1631	0.1612	0.1345
71	0.1671	0.169	0.177	0.169	0.1671	0.1756	0.1671	0.171	0.1891	0.179	0.175	0.1912	0.177	0.1912	0.1496	0.2036
72	0.2078	0.181	0.2036	0.177	0.2078	0.2022	0.2205	0.2036	0.2205	0.1973	0.1973	0.2184	0.1891	0.2141	0.2015	0.1932
73	0.1796	0.1716	0.1736	0.1637	0.1559	0.1857	0.1618	0.1877	0.2128	0.1637	0.1736	0.1657	0.1618	0.1756	0.1837	0.1618
74	0.169	0.1871	0.1592	0.1651	0.142	0.1677	0.171	0.1932	0.1994	0.171	0.1671	0.169	0.177	0.183	0.183	0.1671
75	0.1573	0.183	0.1592	0.173	0.1612	0.2043	0.1671	0.173	0.181	0.1534	0.1592	0.1142	0.171	0.185	0.181	0.1671
76	0.181	0.171	0.1554	0.1651	0.1554	0.1857	0.1671	0.1631	0.2184	0.1534	0.169	0.181	0.1573	0.173	0.177	0.1515
77	0.1871	0.1612	0.1458	0.1651	0.1534	0.1677	0.1573	0.1651	0.1994	0.1573	0.1573	0.1671	0.1496	0.175	0.183	0.1515
78	0.1585	0.1949	0.1722	0.1722	0.1163	0.1806	0.1806	0.1892	0.1978	0.1477	0.1722	0.1585	0.1695	0.1892	0.1695	0.1585
79	0.1806	0.2384	0.1885	0.1885	0.117	0.2088	0.2171	0.2088	0.2255	0.1612	0.2006	0.1966	0.1925	0.1885	0.1845	0.1806
80	0.1574	0.2006	0.1612	0.1574	0.1728	0.165	0.1574	0.2006	0.2255	0.1966	0.1767	0.1885	0.1845	0.1498	0.165	0.1574
81	0.2006	0.2213	0.2341	0.1767	0.213	0.1925	0.1966	0.1767	0.2516	0.2428	0.2088	0.2341	0.1966	0.2088	0.2088	0.2171
82	0.1561	0.1731	0.1951	0.154	0.1907	0.1818	0.1775	0.1645	0.2133	0.1753	0.1731	0.1974	0.1884	0.1907	0.1862	0.1929
83	0.1651	0.171	0.171	0.1671	0.1573	0.1857	0.1651	0.1382	0.183	0.1631	0.171	0.1891	0.1871	0.171	0.1477	0.1671
84	0.1929	0.1951	0.1907	0.1731	0.1929	0.1818	0.1731	0.154	0.2203	0.1775	0.2064	0.1884	0.2133	0.1796	0.1907	0.1775
85	0.1974	0.2087	0.1907	0.1688	0.1907	0.1775	0.184	0.154	0.2226	0.1818	0.1974	0.1884	0.1996	0.1951	0.1907	0.1996
86	0.1929	0.2133	0.1951	0.1561	0.1775	0.1907	0.2064	0.1374	0.2156	0.1775	0.1796	0.1884	0.1818	0.1951	0.1753	0.1884
87	0.1651	0.173	0.1671	0.1515	0.142	0.1716	0.169	0.1106	0.171	0.1631	0.169	0.1651	0.179	0.183	0.1573	0.1671
88	0.1802	0.172	0.1143	0.1444	0.1311	0.1349	0.1581	0.1503	0.1781	0.1522	0.118	0.172	0.1162	0.1464	0.1255	0.1741
89	0.1554	0.171	0.1252	0.1382	0.1458	0.152	0.142	0.1458	0.179	0.142	0.1088	0.177	0.1289	0.1477	0.1142	0.1439

PSH	**33**	**34**	**35**	**36**	**37**	**38**	**39**	**40**	**41**	**42**	**43**	**44**	**45**	**46**	**47**	**48**
90	0.177	0.1671	0.0620	0.127	0.1671	0.1559	0.1651	0.1631	0.183	0.1534	0.1534	0.1953	0.1554	0.1573	0.1534	0.1496
91	0.1612	0.181	0.1496	0.1382	0.1363	0.1756	0.1458	0.1554	0.1631	0.1345	0.1458	0.1326	0.1326	0.1363	0.1534	0.1554
92	0.177	0.1932	0.1458	0.173	0.1573	0.1776	0.1592	0.171	0.1994	0.1496	0.142	0.1592	0.171	0.169	0.1612	0.142
93	0.1554	0.1651	0.1401	0.1458	0.1345	0.1796	0.1592	0.1612	0.1994	0.1401	0.1401	0.1592	0.1554	0.1592	0.1612	0.1401
94	0.171	0.177	0.1515	0.1631	0.1592	0.2106	0.0555	0.1612	0.2036	0.1891	0.1612	0.1973	0.169	0.175	0.1631	0.179
95	0.181	0.183	0.171	0.1912	0.179	0.2257	0.171	0.1326	0.1912	0.1912	0.179	0.1932	0.2057	0.2036	0.179	0.1973
96	0.1534	0.1651	0.1592	0.1671	0.142	0.2001	0.1458	0.173	0.1912	0.1458	0.1671	0.1554	0.1592	0.177	0.177	0.169
97	0.1871	0.1953	0.1612	0.1401	0.1554	0.1837	0.1612	0.1592	0.1953	0.169	0.1439	0.1891	0.142	0.179	0.1363	0.1973
98	0.1773	0.2039	0.1713	0.146	0.1615	0.1799	0.1674	0.1576	0.1956	0.1753	0.1422	0.1956	0.1556	0.1773	0.1518	0.1793
99	0.173	0.1871	0.1534	0.1382	0.1458	0.1716	0.1554	0.1612	0.1871	0.1671	0.1345	0.175	0.1477	0.175	0.1439	0.1912
100	0.169	0.2184	0.1612	0.1612	0.1458	0.1677	0.169	0.1671	0.177	0.177	0.1515	0.183	0.1363	0.1534	0.1458	0.185
101	0.175	0.2205	0.1496	0.1651	0.1477	0.1898	0.1592	0.1573	0.1932	0.173	0.142	0.181	0.1345	0.1573	0.127	0.173
102	0.1755	0.1843	0.1733	0.1667	0.1799	0.1865	0.1603	0.1434	0.2047	0.1667	0.1497	0.1821	0.1711	0.1689	0.1497	0.1581
103	0.169	0.185	0.177	0.1631	0.175	0.1877	0.1363	0.142	0.1994	0.1651	0.1573	0.185	0.1631	0.2099	0.1651	0.1871
104	0.1667	0.1951	0.1884	0.2087	0.1796	0.211	0.1775	0.1519	0.1951	0.1884	0.1796	0.1929	0.2321	0.2203	0.1818	0.1996
105	0.1809	0.2097	0.1835	0.2097	0.1809	0.2017	0.2017	0.1633	0.1938	0.2017	0.2205	0.1938	0.2315	0.2043	0.1809	0.1886
106	0.1642	0.1688	0.1326	0.1282	0.1392	0.1688	0.1348	0.1527	0.195	0.1261	0.1348	0.1437	0.1415	0.1437	0.1459	0.1217
107	0.1938	0.215	0.2287	0.1784	0.1912	0.2043	0.2124	0.1584	0.2178	0.1784	0.2017	0.1991	0.1912	0.1964	0.1964	0.1912
108	0.183	0.183	0.179	0.185	0.175	0.1816	0.183	0.1439	0.2036	0.1631	0.1912	0.177	0.181	0.1871	0.171	0.1953
109	0.175	0.169	0.169	0.177	0.1631	0.1618	0.1496	0.127	0.183	0.1496	0.1671	0.173	0.169	0.185	0.1631	0.169
110	0.1671	0.181	0.183	0.171	0.1631	0.1796	0.169	0.1363	0.1891	0.169	0.175	0.2015	0.1871	0.181	0.1631	0.1932
111	0.1455	0.1584	0.1627	0.1541	0.1541	0.1737	0.1627	0.1186	0.1693	0.1737	0.1627	0.1715	0.1872	0.1872	0.1519	0.1804
112	0.1877	0.2043	0.1857	0.1877	0.1776	0.1925	0.1939	0.1618	0.1716	0.1877	0.2149	0.2001	0.2106	0.2128	0.1857	0.1837
113	0.1818	0.2087	0.1862	0.1996	0.1775	0.211	0.1951	0.154	0.184	0.1862	0.1996	0.1775	0.211	0.211	0.1907	0.2087
114	0.1862	0.2087	0.1818	0.1951	0.1796	0.1929	0.2064	0.1645	0.1862	0.184	0.2133	0.1996	0.2156	0.2133	0.1884	0.1818
115	0.169	0.175	0.173	0.1651	0.1932	0.1939	0.183	0.1631	0.1994	0.181	0.183	0.181	0.181	0.183	0.1932	0.1994

PSH	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64
1	0.1369	0.119	0.122	0.1548	0.1726	0.1369	0.1339	0.0982	0.1577	0.1607	0.1964	0.1429	0.1577	0.1548	0.1161	0.1518
2	0.1383	0.1319	0.1383	0.1535	0.1585	0.1489	0.1459	0.1337	0.1702	0.1854	0.1702	0.1717	0.14	0.1657	0.1429	0.1369
3	0.1756	0.1429	0.1726	0.1786	0.1875	0.1518	0.1637	0.1905	0.1875	0.1637	0.1994	0.1845	0.1458	0.1518	0.1637	0.1756
4	0.1726	0.1607	0.1696	0.1696	0.1815	0.1488	0.1667	0.1667	0.2024	0.2083	0.2024	0.1786	0.1845	0.1637	0.1488	0.1637
5	0.1299	0.1352	0.1531	0.1694	0.1624	0.1369	0.1555	0.1276	0.1787	0.1787	0.1856	0.1717	0.1392	0.1508	0.131	0.1458
6	0.1577	0.128	0.1637	0.1458	0.1607	0.1548	0.1458	0.1458	0.1815	0.1786	0.1964	0.1458	0.1458	0.1607	0.1369	0.1161
7	0.1577	0.1369	0.1786	0.1458	0.1756	0.1875	0.1637	0.1429	0.1607	0.2173	0.1756	0.1488	0.1696	0.1488	0.1458	0.1429
8	0.1488	0.1667	0.1726	0.1935	0.1786	0.1667	0.1875	0.1696	0.1756	0.1845	0.1786	0.1964	0.1875	0.1667	0.1369	0.1518
9	0.1667	0.1458	0.1548	0.1548	0.1637	0.1696	0.1548	0.1548	0.1696	0.1905	0.2024	0.1696	0.1607	0.1488	0.1339	0.1458
10	0.1628	0.1562	0.1487	0.18	0.1834	0.1737	0.1737	0.1612	0.1784	0.1581	0.1674	0.1768	0.163	0.1815	0.1667	0.1815
11	0.1518	0.1756	0.1548	0.1815	0.1994	0.1905	0.1875	0.1845	0.1964	0.2083	0.1845	0.1845	0.1667	0.2054	0.1607	0.1488
12	0.1726	0.1667	0.1667	0.1726	0.1607	0.1726	0.1548	0.1845	0.1815	0.1905	0.1786	0.1815	0.1756	0.1548	0.1786	0.1726
13	0.1493	0.1742	0.182	0.1922	0.2127	0.1616	0.1697	0.1513	0.1881	0.1881	0.1902	0.184	0.1616	0.1861	0.1548	0.1756
14	0.1162	0.1407	0.1531	0.1605	0.1697	0.1531	0.1587	0.1384	0.1919	0.1808	0.1679	0.1661	0.1513	0.1587	0.1577	0.1488
15	0.1111	0.1276	0.1299	0.1402	0.1556	0.1402	0.1333	0.1077	0.159	0.1624	0.1795	0.1538	0.135	0.1641	0.128	0.128
16	0.1554	0.0975	0.1091	0.1421	0.1142	0.1174	0.124	0.1306	0.1769	0.1653	0.1769	0.157	0.1091	0.1488	0.1667	0.1607
17	0.154	0.0846	0.125	0.1448	0.1208	0.1128	0.1128	0.1616	0.1905	0.1662	0.1784	0.1723	0.1191	0.1662	0.1672	0.1403
18	0.1388	0.157	0.1603	0.1736	0.1738	0.1702	0.1702	0.1438	0.1752	0.1884	0.1719	0.1686	0.1686	0.1537	0.1696	0.1726
19	0.1674	0.1321	0.1537	0.1248	0.1527	0.1355	0.14	0.1537	0.1705	0.1766	0.1872	0.1689	0.1204	0.172	0.119	0.1488
20	0.1429	0.0828	0.114	0.1383	0.1265	0.1109	0.1094	0.1322	0.1717	0.1626	0.1793	0.1535	0.1126	0.152	0.1458	0.1607
21	0.1489	0.1242	0.1413	0.1201	0.1692	0.1322	0.1368	0.1489	0.1748	0.1702	0.1672	0.1763	0.1416	0.1581	0.1369	0.1458
22	0.1554	0.1355	0.1537	0.1554	0.1589	0.1455	0.1504	0.1455	0.1653	0.1835	0.1769	0.1636	0.1438	0.1504	0.1488	0.1607
23	0.1682	0.1137	0.1065	0.1497	0.1424	0.1296	0.1281	0.1451	0.1744	0.1806	0.1883	0.1713	0.1314	0.1651	0.1667	0.1548
24	0.1388	0.1091	0.1289	0.1686	0.1308	0.1289	0.1223	0.1521	0.1702	0.1669	0.157	0.1736	0.1339	0.157	0.1548	0.1637
25	0.1388	0.0975	0.1306	0.1488	0.1209	0.124	0.1058	0.1504	0.1669	0.157	0.1785	0.1636	0.1124	0.1719	0.1667	0.1607
26	0.1402	0.1585	0.1707	0.1784	0.185	0.1646	0.1524	0.1509	0.1768	0.1921	0.1784	0.1692	0.1511	0.1677	0.1518	0.1667
27	0.1246	0.1181	0.1444	0.1535	0.157	0.1277	0.1337	0.1185	0.155	0.1672	0.1565	0.1383	0.14	0.155	0.1369	0.125
28	0.1466	0.1386	0.1605	0.1728	0.1471	0.1481	0.1466	0.1528	0.1775	0.1543	0.159	0.1728	0.1577	0.1543	0.1488	0.1667

PSH	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64
29	0.1523	0.1368	0.1376	0.1499	0.172	0.1597	0.1622	0.1695	0.1622	0.1622	0.1523	0.1671	0.1548	0.1499	0.1607	0.131
30	0.1246	0.115	0.1398	0.1581	0.1479	0.1429	0.1383	0.1292	0.1702	0.1824	0.1657	0.1489	0.1324	0.1596	0.1518	0.1458
31	0.152	0.1564	0.1717	0.1824	0.189	0.1717	0.1611	0.1565	0.1869	0.1626	0.1733	0.1717	0.1598	0.1702	0.1577	0.1607
32	0.1444	0.1564	0.1581	0.1641	0.1799	0.1611	0.1413	0.1505	0.1657	0.1839	0.1778	0.1657	0.1659	0.1444	0.1786	0.1607
33	0.152	0.1503	0.1565	0.1778	0.1662	0.1687	0.1489	0.1413	0.1687	0.1687	0.1748	0.1641	0.1598	0.1626	0.1458	0.1369
34	0.155	0.1641	0.1657	0.1839	0.1829	0.1611	0.1581	0.1581	0.1915	0.1565	0.1809	0.1733	0.1689	0.1626	0.1637	0.1786
35	0.1474	0.1503	0.155	0.1657	0.1601	0.1489	0.152	0.1383	0.1672	0.1733	0.1641	0.1763	0.1583	0.155	0.1339	0.1429
36	0.1246	0.1534	0.1626	0.1641	0.1601	0.1444	0.152	0.155	0.1611	0.1702	0.152	0.1748	0.1583	0.155	0.1399	0.1488
37	0.1125	0.135	0.1535	0.1429	0.1585	0.1489	0.1535	0.1109	0.1626	0.1763	0.1565	0.1611	0.1339	0.1535	0.131	0.1399
38	0.1616	0.1554	0.1677	0.1707	0.1713	0.154	0.1601	0.157	0.189	0.154	0.1616	0.1814	0.1557	0.1662	0.1518	0.1607
39	0.1398	0.1442	0.1535	0.1565	0.1662	0.1444	0.1261	0.1337	0.1687	0.152	0.1824	0.1581	0.1598	0.1459	0.1637	0.1548
40	0.1353	0.1043	0.1216	0.1535	0.1296	0.1292	0.1109	0.1413	0.1398	0.1596	0.1809	0.152	0.1126	0.155	0.1696	0.1518
41	0.1778	0.1748	0.1489	0.1535	0.1723	0.1733	0.1717	0.1657	0.1748	0.1657	0.1748	0.1915	0.1629	0.1778	0.1548	0.1577
42	0.0775	0.1365	0.155	0.1672	0.1662	0.1489	0.1444	0.1231	0.1763	0.1748	0.1748	0.1611	0.1613	0.1657	0.1488	0.131
43	0.1307	0.1457	0.1657	0.1626	0.1784	0.1489	0.1626	0.1474	0.1687	0.1717	0.1596	0.1778	0.1553	0.1581	0.128	0.1488
44	0.1413	0.1488	0.1641	0.1778	0.1799	0.1641	0.1687	0.1444	0.1915	0.1778	0.1687	0.1687	0.1492	0.1793	0.1637	0.1518
45	0.1383	0.1534	0.1733	0.1611	0.1723	0.155	0.152	0.1474	0.1581	0.1748	0.1565	0.1596	0.1553	0.1611	0.1458	0.1399
46	0.155	0.1518	0.1733	0.1702	0.1799	0.1596	0.155	0.1641	0.1672	0.1793	0.1489	0.1672	0.1689	0.1611	0.1696	0.1577
47	0.1413	0.1457	0.1459	0.152	0.1631	0.1474	0.1626	0.1429	0.1444	0.19	0.1702	0.1535	0.1583	0.152	0.1429	0.1548
48	0.1079	0.1457	0.1687	0.1687	0.186	0.1459	0.1581	0.1353	0.1809	0.1717	0.1748	0.1793	0.1629	0.1809	0.1458	0.1577
49		0.1411	0.1489	0.1687	0.1692	0.1261	0.1307	0.1201	0.1717	0.1763	0.1596	0.1763	0.1537	0.1763	0.1429	0.1488
50	0.1589		0.1028	0.1273	0.1062	0.0982	0.0936	0.1319	0.1534	0.1426	0.1656	0.1411	0.083	0.1396	0.1399	0.131
51	0.169	0.1117		0.1322	0.1357	0.1201	0.1231	0.1337	0.1581	0.1702	0.1809	0.1596	0.1126	0.1672	0.1518	0.1667
52	0.1953	0.1415	0.1477		0.1585	0.1413	0.1322	0.152	0.1824	0.1778	0.1717	0.1626	0.1324	0.1702	0.1607	0.1339
53	0.196	0.1158	0.152	0.1816		0.1357	0.125	0.1631	0.1753	0.1753	0.1829	0.1799	0.1267	0.1555	0.1726	0.1577
54	0.1401	0.1063	0.1326	0.1592	0.152		0.1155	0.1413	0.1854	0.1717	0.1763	0.1854	0.1142	0.1672	0.1548	0.1696
55	0.1458	0.1009	0.1363	0.1477	0.1387	0.127		0.1474	0.1687	0.152	0.1793	0.1505	0.1111	0.1626	0.1667	0.1607
56	0.1326	0.1473	0.1496	0.173	0.1877	0.1592	0.1671		0.1535	0.1717	0.1884	0.1413	0.1492	0.1641	0.0982	0.1399

PSH	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64
57	0.1994	0.1748	0.181	0.2141	0.2043	0.2184	0.1953	0.175		0.1884	0.1793	0.1094	0.1537	0.1444	0.1696	0.1815
58	0.2057	0.1609	0.1973	0.2078	0.2043	0.1994	0.173	0.1994	0.2227		0.1763	0.1793	0.1492	0.1702	0.1875	0.1905
59	0.183	0.1911	0.212	0.1994	0.2149	0.2057	0.2099	0.2227	0.2099	0.2057		0.1824	0.1583	0.1748	0.1667	0.1696
60	0.2057	0.1589	0.183	0.1871	0.2106	0.2184	0.171	0.1592	0.1197	0.2099	0.2141		0.1476	0.1489	0.1667	0.1726
61	0.1753	0.0887	0.1236	0.1479	0.1408	0.1254	0.1217	0.1693	0.1753	0.1693	0.1813	0.1674		0.1431	0.1458	0.1458
62	0.2057	0.157	0.1932	0.1973	0.1776	0.1932	0.1871	0.1891	0.1631	0.1973	0.2036	0.169	0.1615		0.1607	0.1667
63	0.1612	0.1574	0.1728	0.1845	0.2006	0.1767	0.1925	0.1064	0.1966	0.2213	0.1925	0.1925	0.165	0.1845		0.128
64	0.1689	0.1461	0.1925	0.1498	0.1806	0.1966	0.1845	0.1574	0.213	0.2255	0.1966	0.2006	0.165	0.1925	0.1424	
65	0.1478	0.139	0.1913	0.1866	0.1684	0.1589	0.1657	0.1368	0.1961	0.1842	0.1913	0.1749	0.1635	0.1589	0.1424	0.1387
66	0.2042	0.1519	0.1519	0.0997	0.18	0.1603	0.1603	0.1688	0.2087	0.1862	0.2042	0.211	0.1498	0.2064	0.1728	0.1574
67	0.1536	0.1725	0.1556	0.2024	0.2076	0.1764	0.1743	0.1577	0.1743	0.198	0.2002	0.1639	0.1789	0.198	0.1767	0.1925
68	0.1458	0.1748	0.169	0.1891	0.2064	0.1912	0.1891	0.1651	0.2141	0.1973	0.171	0.1994	0.1693	0.2162	0.1612	0.165
69	0.1463	0.1877	0.198	0.196	0.2178	0.1756	0.196	0.152	0.2064	0.2085	0.198	0.2106	0.1759	0.2064	0.1314	0.1689
70	0.116	0.1396	0.1671	0.173	0.1857	0.1439	0.169	0.1382	0.177	0.2015	0.181	0.1871	0.1499	0.179	0.1689	0.1498
71	0.1891	0.1589	0.181	0.181	0.198	0.1891	0.169	0.183	0.1651	0.2162	0.212	0.1631	0.1753	0.1477	0.2006	0.1845
72	0.2078	0.1708	0.212	0.2141	0.2257	0.2227	0.1994	0.2099	0.2402	0.183	0.2078	0.227	0.2039	0.2248	0.1845	0.2047
73	0.1425	0.1654	0.1857	0.1796	0.2287	0.1716	0.1696	0.1736	0.2149	0.2043	0.198	0.2001	0.1699	0.1898	0.1728	0.1767
74	0.1458	0.1708	0.1994	0.1994	0.2022	0.171	0.1671	0.1631	0.1912	0.2036	0.179	0.1994	0.1556	0.177	0.1612	0.1925
75	0.1554	0.1415	0.1515	0.171	0.1857	0.179	0.1573	0.1534	0.2057	0.2015	0.2015	0.1891	0.1422	0.1891	0.165	0.1612
76	0.1382	0.1769	0.1891	0.1973	0.2149	0.185	0.171	0.1671	0.2184	0.2036	0.1932	0.2184	0.1854	0.2099	0.1885	0.2213
77	0.1382	0.1769	0.1871	0.2078	0.2106	0.1631	0.1631	0.1554	0.2162	0.1994	0.1994	0.212	0.1793	0.1932	0.1612	0.2171
78	0.1266	0.1549	0.1863	0.2037	0.1806	0.1503	0.1778	0.1477	0.1949	0.2096	0.1978	0.2125	0.1612	0.1835	0.135	0.1461
79	0.1314	0.1845	0.213	0.2255	0.213	0.1925	0.213	0.1461	0.2255	0.2696	0.2298	0.2213	0.1925	0.2006	0.165	0.2006
80	0.1885	0.1689	0.1966	0.1728	0.1767	0.1767	0.1767	0.1612	0.2213	0.2171	0.213	0.1885	0.1966	0.1574	0.1461	0.1536
81	0.2213	0.1845	0.2171	0.1845	0.1767	0.1885	0.2088	0.2341	0.2255	0.2088	0.2428	0.2213	0.1689	0.1767	0.2298	0.2047
82	0.1688	0.1603	0.1862	0.184	0.1713	0.1753	0.1519	0.1951	0.1929	0.184	0.2064	0.1796	0.1688	0.1688	0.213	0.2088
83	0.1651	0.0956	0.1252	0.1554	0.1349	0.1234	0.1363	0.1612	0.181	0.1973	0.1912	0.1891	0.1272	0.185	0.1885	0.165
84	0.171	0.1153	0.1796	0.1862	0.1691	0.1456	0.1395	0.1667	0.2226	0.1796	0.211	0.1996	0.1645	0.1818	0.2047	0.1845

PSH	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64
85	0.1907	0.1153	0.154	0.1753	0.1543	0.1415	0.1313	0.1667	0.2273	0.1974	0.2156	0.1996	0.1477	0.2019	0.213	0.1806
86	0.171	0.1094	0.1395	0.1667	0.1418	0.1233	0.1333	0.184	0.1731	0.1775	0.2156	0.1929	0.1134	0.1645	0.1885	0.1845
87	0.1458	0.0868	0.1124	0.1382	0.1444	0.1088	0.1035	0.1592	0.171	0.175	0.183	0.1651	0.0913	0.173	0.1461	0.1574
88	0.1464	0.1658	0.166	0.1542	0.1788	0.1522	0.1741	0.1561	0.2094	0.2246	0.1946	0.1967	0.1683	0.172	0.1424	0.1387
89	0.1307	0.1321	0.177	0.173	0.1696	0.1382	0.1458	0.1671	0.2057	0.1891	0.179	0.2015	0.1713	0.1592	0.1461	0.1461
90	0.1573	0.157	0.179	0.1994	0.1898	0.1612	0.169	0.173	0.1994	0.1994	0.1973	0.2162	0.1854	0.171	0.1387	0.1612
91	0.1234	0.1302	0.1612	0.1631	0.1776	0.1458	0.1554	0.1215	0.175	0.183	0.1554	0.179	0.1366	0.173	0.1064	0.1498
92	0.1554	0.1512	0.173	0.169	0.2064	0.1612	0.183	0.1088	0.1953	0.2162	0.2184	0.1932	0.1733	0.1891	0.1277	0.165
93	0.142	0.1415	0.181	0.173	0.1939	0.1612	0.1612	0.1035	0.171	0.177	0.2036	0.173	0.1576	0.179	0.1277	0.1689
94	0.171	0.1728	0.177	0.183	0.1877	0.1592	0.1458	0.1573	0.1891	0.1932	0.2141	0.169	0.1773	0.175	0.1925	0.1845
95	0.179	0.1154	0.1252	0.1631	0.1482	0.1382	0.1326	0.1534	0.2036	0.1912	0.2162	0.1891	0.1054	0.179	0.1885	0.1845
96	0.1382	0.1589	0.1671	0.179	0.2064	0.175	0.175	0.1326	0.185	0.181	0.2015	0.1651	0.1833	0.1612	0.1806	0.1885
97	0.1592	0.1769	0.1912	0.1912	0.1816	0.1573	0.177	0.177	0.1973	0.2314	0.1932	0.2036	0.1874	0.1953	0.1767	0.2088
98	0.1576	0.1998	0.1998	0.1895	0.1984	0.1634	0.1915	0.1793	0.206	0.2406	0.1936	0.2252	0.196	0.2039	0.1966	0.2298
99	0.1534	0.1708	0.1932	0.1912	0.1696	0.1477	0.173	0.1671	0.185	0.2099	0.1973	0.1953	0.1895	0.1932	0.1689	0.1806
100	0.1671	0.1435	0.1592	0.181	0.198	0.171	0.173	0.169	0.183	0.1994	0.1554	0.1891	0.1556	0.1953	0.165	0.2088
101	0.171	0.1396	0.171	0.177	0.1898	0.1573	0.1671	0.1671	0.1651	0.212	0.1651	0.179	0.1441	0.171	0.1728	0.1845
102	0.1518	0.1646	0.1933	0.2024	0.1914	0.1843	0.1646	0.1667	0.1821	0.1955	0.214	0.1733	0.1624	0.1689	0.1728	0.1885
103	0.1515	0.1473	0.1401	0.1891	0.2022	0.1891	0.1671	0.1592	0.1592	0.1912	0.1932	0.1631	0.1713	0.173	0.1767	0.165
104	0.1645	0.1293	0.0789	0.171	0.1691	0.1233	0.1395	0.1645	0.1974	0.1884	0.218	0.1951	0.1233	0.2019	0.1574	0.2047
105	0.1835	0.1235	0.0689	0.1658	0.151	0.1462	0.1295	0.1683	0.1938	0.1938	0.2232	0.1991	0.1225	0.1835	0.1728	0.2006
106	0.1131	0.1443	0.1619	0.1782	0.1642	0.1482	0.1665	0.086	0.1596	0.2072	0.1974	0.1596	0.1688	0.1758	0.1241	0.1728
107	0.1758	0.1142	0.1608	0.1861	0.1584	0.139	0.1414	0.1708	0.2124	0.2205	0.1938	0.1991	0.1535	0.2017	0.2213	0.1767
108	0.173	0.1396	0.1612	0.175	0.1696	0.142	0.1458	0.171	0.1912	0.1994	0.1953	0.185	0.1537	0.183	0.2006	0.1767
109	0.1439	0.0938	0.1215	0.1345	0.1501	0.1124	0.1035	0.1477	0.2036	0.171	0.2015	0.1871	0.109	0.1534	0.1689	0.165
110	0.171	0.1099	0.142	0.1592	0.1463	0.1401	0.1458	0.177	0.2078	0.1912	0.1973	0.1973	0.146	0.175	0.1885	0.1536
111	0.1693	0.1065	0.1309	0.1671	0.1208	0.1247	0.135	0.1519	0.1964	0.1827	0.208	0.1804	0.1309	0.1671	0.1767	0.1612
112	0.1796	0.1478	0.0572	0.1736	0.1803	0.1463	0.152	0.1696	0.2043	0.1918	0.2001	0.2149	0.124	0.2064	0.1845	0.2047

PSH	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64
113	0.184	0.1293	0.0587	0.171	0.1564	0.154	0.1415	0.1519	0.2019	0.211	0.2203	0.1907	0.1153	0.1862	0.1806	0.1925
114	0.1753	0.1333	0.0605	0.1603	0.1648	0.1415	0.1477	0.1603	0.2203	0.1951	0.2019	0.2203	0.1233	0.1974	0.1767	0.1925
115	0.177	0.157	0.1592	0.1573	0.1816	0.185	0.1612	0.1932	0.1953	0.1932	0.1871	0.2036	0.1595	0.171	0.213	0.1966

PSH	65	66	67	68	69	70	71	72	73	74	75	76	77	78	79	80
1	0.1131	0.1637	0.1399	0.1786	0.1429	0.1369	0.1548	0.2083	0.1548	0.1577	0.1488	0.1637	0.1488	0.1339	0.1518	0.125
2	0.1393	0.1521	0.132	0.152	0.154	0.1337	0.152	0.1793	0.157	0.1474	0.1322	0.1289	0.1413	0.1429	0.1607	0.1339
3	0.1577	0.1637	0.1577	0.1726	0.1518	0.1786	0.1607	0.1726	0.1637	0.1845	0.1607	0.1577	0.1488	0.1577	0.1756	0.1518
4	0.1577	0.1845	0.1607	0.1696	0.1637	0.1786	0.1845	0.2083	0.1696	0.1488	0.1786	0.1726	0.1667	0.1667	0.1756	0.1012
5	0.141	0.1531	0.1446	0.1439	0.1439	0.1044	0.1601	0.1926	0.1555	0.1415	0.1369	0.1462	0.1346	0.0859	0.1101	0.1369
6	0.119	0.1726	0.1577	0.1548	0.1845	0.1488	0.1756	0.1577	0.1786	0.1935	0.1577	0.1815	0.1726	0.1577	0.1726	0.125
7	0.1161	0.1577	0.1637	0.1815	0.1696	0.1399	0.1518	0.2083	0.1518	0.1548	0.1726	0.1786	0.1845	0.1399	0.1458	0.1518
8	0.1131	0.1994	0.1786	0.1756	0.1488	0.1637	0.1905	0.1756	0.1756	0.1726	0.1786	0.1756	0.1607	0.1488	0.1637	0.1458
9	0.1339	0.1756	0.1845	0.1548	0.1726	0.1488	0.1667	0.1875	0.1845	0.1756	0.1369	0.2054	0.1786	0.1548	0.1756	0.1369
10	0.157	0.1785	0.1528	0.1674	0.18	0.1612	0.1596	0.1737	0.169	0.169	0.1408	0.1651	0.1674	0.1706	0.1786	0.1756
11	0.1815	0.1815	0.1458	0.0893	0.1756	0.1577	0.1905	0.2232	0.1815	0.1875	0.1548	0.1815	0.1815	0.1488	0.1786	0.1756
12	0.1875	0.1815	0.1815	0.1637	0.2024	0.1577	0.1577	0.2054	0.2024	0.1667	0.2054	0.2054	0.1964	0.1548	0.1696	0.1458
13	0.167	0.1863	0.167	0.1697	0.1043	0.1431	0.1718	0.182	0.1227	0.1063	0.1493	0.1207	0.09202	0.1295	0.1369	0.1458
14	0.1414	0.1585	0.1365	0.1402	0.1494	0.08303	0.155	0.1863	0.1458	0.131	0.1384	0.1421	0.1384	0.1079	0.1101	0.1667
15	0.0981	0.1505	0.1314	0.1453	0.1299	0.1179	0.1436	0.1675	0.1299	0.1402	0.1231	0.1244	0.1179	0.1279	0.1339	0.128
16	0.1393	0.1388	0.1395	0.1554	0.1785	0.1488	0.1421	0.1653	0.1736	0.1521	0.1372	0.162	0.1653	0.1493	0.1726	0.125
17	0.1416	0.1476	0.1599	0.1631	0.185	0.157	0.1616	0.1723	0.1575	0.1646	0.1463	0.1829	0.1753	0.1538	0.1791	0.1582
18	0.134	0.1636	0.1361	0.157	0.1702	0.1388	0.1702	0.2066	0.157	0.1488	0.1554	0.1636	0.162	0.1629	0.1667	0.1577
19	0.1517	0.1306	0.1726	0.1613	0.1771	0.1568	0.1705	0.1887	0.171	0.1689	0.1613	0.1897	0.1887	0.1727	0.1875	0.1548
20	0.1446	0.1372	0.1481	0.1581	0.1692	0.1459	0.1596	0.1748	0.1509	0.1581	0.1474	0.1641	0.155	0.1471	0.1637	0.1399
21	0.1517	0.1223	0.1562	0.1702	0.1738	0.1429	0.1489	0.1748	0.154	0.1702	0.1596	0.1641	0.1748	0.1514	0.1815	0.1429
22	0.1129	0.1653	0.1462	0.1587	0.157	0.1488	0.1504	0.1587	0.1636	0.1537	0.1504	0.1372	0.1405	0.1742	0.1815	0.1548
23	0.157	0.1603	0.1588	0.1605	0.1821	0.1574	0.1574	0.1651	0.1713	0.1744	0.1466	0.1713	0.1528	0.1684	0.1845	0.1577

PSH	65	66	67	68	69	70	71	72	73	74	75	76	77	78	79	80
24	0.1287	0.157	0.1529	0.1471	0.1669	0.1438	0.1471	0.1785	0.1636	0.1554	0.1554	0.1537	0.1554	0.1516	0.1875	0.1726
25	0.1534	0.1471	0.1613	0.1851	0.1851	0.1504	0.1636	0.1752	0.1736	0.1702	0.1504	0.1636	0.1719	0.1697	0.2024	0.1875
26	0.1464	0.1818	0.1648	0.1494	0.1235	0.1494	0.154	0.1616	0.128	0.1159	0.1448	0.125	0.1204	0.1514	0.1637	0.131
27	0.134	0.1587	0.1385	0.1459	0.1402	0.1155	0.1383	0.1672	0.1372	0.1353	0.1277	0.1337	0.1231	0.1215	0.1488	0.1458
28	0.1323	0.1719	0.1669	0.1543	0.162	0.1466	0.1543	0.1698	0.162	0.159	0.1528	0.159	0.1481	0.1641	0.1875	0.1815
29	0.1364	0.1737	0.1486	0.14	0.1572	0.1523	0.1474	0.1966	0.1499	0.1474	0.1474	0.1695	0.1548	0.1376	0.1667	0.1429
30	0.1376	0.1686	0.1385	0.1337	0.1402	0.1307	0.1565	0.1824	0.1402	0.1474	0.1231	0.1505	0.1459	0.1514	0.1726	0.1667
31	0.1781	0.1736	0.1498	0.1565	0.157	0.1611	0.1565	0.1717	0.1692	0.1672	0.1611	0.155	0.1444	0.1706	0.1905	0.1607
32	0.1675	0.1802	0.1691	0.155	0.1829	0.1565	0.1444	0.1869	0.1753	0.155	0.1641	0.1687	0.1657	0.1706	0.1815	0.1696
33	0.1393	0.1521	0.1481	0.1429	0.1662	0.1413	0.1474	0.1778	0.157	0.1489	0.1398	0.1581	0.1626	0.1407	0.1577	0.1399
34	0.1623	0.1884	0.1481	0.1641	0.1601	0.1505	0.1489	0.1581	0.1509	0.1626	0.1596	0.1505	0.1429	0.1684	0.1994	0.1726
35	0.0952	0.1669	0.1433	0.1505	0.1555	0.1413	0.155	0.1748	0.1524	0.1413	0.1413	0.1383	0.1307	0.1514	0.1637	0.1429
36	0.1235	0.1669	0.1465	0.1474	0.154	0.1353	0.1489	0.155	0.1448	0.1459	0.152	0.1459	0.1459	0.1514	0.1637	0.1399
37	0.1146	0.157	0.1498	0.1368	0.1387	0.08511	0.1474	0.1778	0.1387	0.1277	0.1429	0.1383	0.1368	0.1066	0.1071	0.1518
38	0.1393	0.1736	0.1745	0.1631	0.1524	0.1601	0.154	0.1738	0.1616	0.1479	0.1753	0.1616	0.1479	0.1578	0.1786	0.1458
39	0.1182	0.1587	0.1546	0.1505	0.1585	0.1535	0.1474	0.1869	0.1433	0.1505	0.1474	0.1474	0.1398	0.1578	0.1845	0.1399
40	0.1376	0.1554	0.1481	0.1611	0.1692	0.1383	0.1505	0.1748	0.1631	0.1672	0.152	0.1444	0.1459	0.1642	0.1786	0.1726
41	0.1728	0.1471	0.1465	0.1672	0.1799	0.1748	0.1641	0.1869	0.1814	0.1717	0.1581	0.1854	0.1717	0.1706	0.1905	0.1905
42	0.1217	0.1785	0.1401	0.1292	0.1448	0.1155	0.1565	0.1702	0.1448	0.1505	0.1368	0.1368	0.1398	0.1322	0.1429	0.1696
43	0.1146	0.1769	0.1546	0.1581	0.1509	0.1353	0.1535	0.1702	0.1524	0.1474	0.1413	0.1489	0.1398	0.1514	0.1726	0.1548
44	0.1499	0.1587	0.1449	0.1474	0.154	0.1474	0.1657	0.1854	0.1463	0.1489	0.1049	0.1581	0.1474	0.1407	0.1696	0.1637
45	0.1217	0.1851	0.1739	0.1535	0.1509	0.1398	0.155	0.1641	0.1433	0.155	0.1505	0.1398	0.1337	0.1493	0.1667	0.1607
46	0.1164	0.1851	0.1643	0.1581	0.157	0.1444	0.1657	0.1824	0.154	0.1596	0.1611	0.152	0.1535	0.1642	0.1637	0.1339
47	0.1217	0.1669	0.1369	0.152	0.1646	0.1429	0.1337	0.1733	0.1601	0.1596	0.1581	0.155	0.1596	0.1493	0.1607	0.1458
48	0.1305	0.1769	0.1578	0.1596	0.1448	0.1216	0.1748	0.1672	0.1433	0.1474	0.1474	0.1353	0.1353	0.1407	0.1577	0.1399
49	0.1323	0.1752	0.1369	0.1307	0.1311	0.1064	0.1641	0.1778	0.128	0.1307	0.1383	0.1246	0.1246	0.1151	0.119	0.1637
50	0.1252	0.1355	0.1516	0.1534	0.1631	0.1258	0.1411	0.1503	0.1462	0.1503	0.1273	0.1549	0.1549	0.1379	0.1607	0.1488
51	0.1658	0.1355	0.1385	0.1489	0.1707	0.1474	0.1581	0.1809	0.1616	0.1717	0.1353	0.1641	0.1626	0.162	0.1815	0.1696

PSH	**65**	**66**	**67**	**68**	**69**	**70**	**71**	**72**	**73**	**74**	**75**	**76**	**77**	**78**	**79**	**80**
52	0.1623	0.09256	0.1739	0.1641	0.1692	0.152	0.1581	0.1824	0.157	0.1717	0.1505	0.1702	0.1778	0.1748	0.1905	0.1518
53	0.1484	0.1573	0.1777	0.1768	0.185	0.1616	0.1707	0.1905	0.1927	0.1738	0.1616	0.1829	0.1799	0.1578	0.1815	0.1548
54	0.1411	0.1421	0.1546	0.1657	0.154	0.1292	0.1641	0.1884	0.1509	0.1505	0.1565	0.1611	0.1444	0.1343	0.1667	0.1548
55	0.1464	0.1421	0.153	0.1641	0.1692	0.1489	0.1489	0.1717	0.1494	0.1474	0.1398	0.1505	0.1444	0.1557	0.1815	0.1548
56	0.1235	0.1488	0.1401	0.1459	0.1357	0.1246	0.1596	0.1793	0.1524	0.1444	0.1368	0.1474	0.1383	0.1322	0.131	0.1429
57	0.1693	0.1785	0.153	0.1824	0.1768	0.155	0.1459	0.2006	0.1829	0.1657	0.1763	0.1854	0.1839	0.1684	0.1905	0.1875
58	0.1605	0.162	0.1707	0.1702	0.1784	0.1733	0.1839	0.1596	0.1753	0.1748	0.1733	0.1748	0.1717	0.1791	0.2202	0.1845
59	0.1658	0.1752	0.1723	0.1505	0.1707	0.1581	0.1809	0.1778	0.1707	0.1565	0.1733	0.1672	0.1717	0.1706	0.1935	0.1815
60	0.1534	0.1802	0.1449	0.1717	0.1799	0.1626	0.1444	0.1915	0.1723	0.1717	0.1641	0.1854	0.1809	0.1812	0.1875	0.1637
61	0.1446	0.1339	0.1565	0.1492	0.1542	0.1339	0.1537	0.175	0.1496	0.1385	0.1279	0.1613	0.1568	0.1429	0.1667	0.1696
62	0.1411	0.1769	0.1707	0.1839	0.1768	0.1565	0.1322	0.19	0.1646	0.155	0.1641	0.1793	0.1672	0.1599	0.1726	0.1399
63	0.128	0.1518	0.1548	0.1429	0.119	0.1488	0.1726	0.1607	0.1518	0.1429	0.1458	0.1637	0.1429	0.122	0.1458	0.131
64	0.125	0.1399	0.1667	0.1458	0.1488	0.1339	0.1607	0.1756	0.1548	0.1667	0.1429	0.1875	0.1845	0.131	0.1726	0.1369
65		0.1693	0.1429	0.1446	0.134	0.1217	0.1481	0.1746	0.1358	0.1305	0.134	0.1446	0.134	0.1353	0.1399	0.119
66	0.1961		0.1546	0.1636	0.1769	0.1521	0.1686	0.2	0.1769	0.162	0.1537	0.1769	0.1901	0.1538	0.1875	0.1607
67	0.1612	0.1765		0.1562	0.168	0.153	0.153	0.1916	0.1599	0.1481	0.153	0.153	0.1433	0.1597	0.1786	0.1458
68	0.1635	0.1884	0.1786		0.1479	0.1368	0.1611	0.1596	0.157	0.1505	0.1322	0.1565	0.1489	0.1599	0.1815	0.1548
69	0.15	0.2064	0.1943	0.1677		0.1357	0.1738	0.1601	0.1265	0.09909	0.1524	0.1174	0.09909	0.1258	0.1369	0.1458
70	0.1346	0.1731	0.1743	0.1534	0.152		0.1444	0.1748	0.1326	0.1216	0.1353	0.1353	0.1337	0.096	0.1071	0.1369
71	0.168	0.1951	0.1743	0.185	0.2022	0.1631		0.1733	0.1616	0.1474	0.1535	0.1687	0.152	0.1535	0.1815	0.1488
72	0.2033	0.2393	0.2272	0.183	0.1837	0.2036	0.2015		0.1616	0.1702	0.1748	0.1565	0.1565	0.2004	0.2232	0.1845
73	0.1522	0.2064	0.1835	0.1796	0.1406	0.1482	0.1857	0.1857		0.1143	0.1448	0.125	0.1113	0.1493	0.1607	0.1488
74	0.1455	0.1862	0.168	0.171	0.1074	0.1345	0.1671	0.1973	0.1256		0.1337	0.1216	0.1064	0.1194	0.131	0.131
75	0.15	0.1753	0.1743	0.1477	0.1736	0.1515	0.175	0.2036	0.1637	0.1496		0.1459	0.1444	0.145	0.1488	0.1518
76	0.1635	0.2064	0.1743	0.179	0.1293	0.1515	0.1953	0.179	0.1387	0.1345	0.1651		0.05015	0.1322	0.1458	0.1399
77	0.15	0.225	0.1618	0.169	0.1074	0.1496	0.173	0.179	0.1219	0.116	0.1631	0.0522		0.1173	0.1399	0.1399
78	0.1515	0.1755	0.1832	0.1835	0.1397	0.1037	0.175	0.2399	0.1695	0.1318	0.1639	0.1477	0.1292		0.0625	0.128
79	0.1574	0.2213	0.2088	0.213	0.1536	0.117	0.213	0.2741	0.1845	0.1461	0.1689	0.165	0.1574	0.0657		0.1369

PSH	65	66	67	68	69	70	71	72	73	74	75	76	77	78	79	80
80	0.1314	0.1845	0.165	0.1767	0.165	0.1536	0.1689	0.2171	0.1689	0.1461	0.1728	0.1574	0.1574	0.1424	0.1536	
81	0.1925	0.213	0.2255	0.2213	0.2088	0.1845	0.1806	0.2341	0.213	0.2171	0.213	0.2341	0.2255	0.2213	0.2428	0.2088
82	0.1726	0.184	0.1876	0.184	0.2087	0.1731	0.1603	0.218	0.1974	0.1907	0.1796	0.2019	0.2087	0.1905	0.213	0.2006
83	0.1567	0.1753	0.1597	0.185	0.1918	0.1477	0.1671	0.173	0.1756	0.169	0.1496	0.173	0.169	0.1423	0.1925	0.1845
84	0.1612	0.171	0.1944	0.1818	0.1775	0.1796	0.184	0.1907	0.1818	0.171	0.171	0.2156	0.1951	0.1935	0.1966	0.1612
85	0.1544	0.1624	0.1899	0.1862	0.184	0.1818	0.1862	0.1974	0.1907	0.1753	0.1753	0.2133	0.1951	0.1844	0.2006	0.1612
86	0.1866	0.1624	0.1831	0.1929	0.1775	0.1667	0.1884	0.1929	0.1974	0.171	0.1624	0.1974	0.1731	0.1725	0.2088	0.1925
87	0.1433	0.1436	0.1786	0.179	0.1716	0.1496	0.171	0.175	0.1657	0.1651	0.1515	0.1767	0.1631	0.1639	0.1689	0.1767
88	0.1154	0.1929	0.1714	0.168	0.1561	0.1581	0.164	0.1946	0.1483	0.1601	0.1464	0.1542	0.1406	0.1834	0.1845	0.1728
89	0.0947	0.1884	0.1495	0.1671	0.1463	0.1382	0.1477	0.179	0.152	0.1496	0.1554	0.1477	0.142	0.1585	0.1574	0.1277
90	0.107	0.2087	0.1639	0.177	0.1677	0.1631	0.179	0.1973	0.1559	0.1612	0.169	0.1651	0.1458	0.1806	0.1612	0.1574
91	0.1133	0.1731	0.1556	0.1515	0.1598	0.1363	0.1496	0.177	0.1425	0.1363	0.1439	0.1761	0.1554	0.1318	0.165	0.1461
92	0.1433	0.1753	0.1764	0.1912	0.1677	0.1592	0.173	0.2314	0.1618	0.171	0.1458	0.169	0.1592	0.1503	0.1536	0.1845
93	0.1455	0.1753	0.1536	0.177	0.1559	0.1307	0.175	0.2057	0.1425	0.1458	0.1458	0.1573	0.1477	0.137	0.1574	0.1845
94	0.1346	0.1862	0.1597	0.183	0.1918	0.173	0.1612	0.2248	0.1716	0.173	0.171	0.169	0.1592	0.1949	0.2088	0.1536
95	0.1657	0.1624	0.168	0.1973	0.198	0.173	0.185	0.1932	0.2064	0.1912	0.1651	0.2015	0.1953	0.1978	0.2255	0.1885
96	0.1368	0.1818	0.1475	0.1573	0.1736	0.1289	0.1573	0.1932	0.1387	0.1651	0.1363	0.1534	0.1458	0.1557	0.1806	0.1845
97	0.1522	0.218	0.1743	0.1871	0.1796	0.1631	0.173	0.2057	0.1637	0.179	0.173	0.179	0.1631	0.1978	0.2213	0.2171
98	0.1589	0.2068	0.1807	0.1874	0.1759	0.1576	0.1833	0.2081	0.1699	0.1733	0.1733	0.1773	0.1693	0.2131	0.2298	0.2006
99	0.126	0.2133	0.1701	0.171	0.1637	0.1554	0.177	0.2036	0.1677	0.1573	0.169	0.173	0.1631	0.1695	0.1845	0.1767
100	0.1522	0.1796	0.1786	0.173	0.1796	0.173	0.175	0.185	0.1716	0.173	0.179	0.169	0.173	0.1778	0.1845	0.2006
101	0.1368	0.1907	0.1722	0.179	0.1696	0.169	0.1671	0.1932	0.1816	0.173	0.1651	0.1573	0.1631	0.1722	0.1845	0.1767
102	0.1478	0.1914	0.1442	0.1755	0.1581	0.1711	0.1755	0.1888	0.1955	0.1581	0.1821	0.1821	0.1689	0.172	0.1925	0.1806
103	0.168	0.2133	0.168	0.1573	0.1756	0.177	0.1651	0.1973	0.1756	0.1651	0.1554	0.185	0.175	0.2007	0.2171	0.1845
104	0.1819	0.1624	0.159	0.1624	0.2042	0.1731	0.211	0.2539	0.184	0.1796	0.1624	0.1884	0.1951	0.1875	0.2213	0.1806
105	0.1873	0.1674	0.1767	0.1733	0.1784	0.1758	0.1964	0.2124	0.1938	0.1861	0.1658	0.1912	0.1912	0.1819	0.2213	0.1845
106	0.1073	0.1766	0.1372	0.1348	0.1415	0.1261	0.1596	0.2023	0.1392	0.1415	0.137	0.1415	0.1304	0.1356	0.1574	0.1314
107	0.1902	0.1832	0.193	0.1835	0.2017	0.1784	0.1708	0.1758	0.1835	0.1938	0.1758	0.215	0.1964	0.1848	0.2006	0.1845

PSH	**65**	**66**	**67**	**68**	**69**	**70**	**71**	**72**	**73**	**74**	**75**	**76**	**77**	**78**	**79**	**80**
108	0.1478	0.1862	0.185	0.1973	0.196	0.1671	0.1671	0.1994	0.1918	0.2057	0.181	0.181	0.1671	0.1806	0.2384	0.2428
109	0.1544	0.1519	0.1743	0.1651	0.1637	0.1496	0.171	0.1973	0.1618	0.1592	0.1534	0.173	0.1612	0.1695	0.213	0.1845
110	0.1544	0.1818	0.1639	0.181	0.2001	0.1592	0.1631	0.169	0.1736	0.1651	0.1534	0.177	0.171	0.1722	0.2171	0.1689
111	0.1368	0.1693	0.1637	0.1849	0.1918	0.1562	0.1649	0.176	0.1827	0.1693	0.1519	0.1782	0.1693	0.1608	0.213	0.1806
112	0.1961	0.1731	0.1707	0.1736	0.1925	0.1796	0.2022	0.2149	0.1967	0.1898	0.1657	0.2043	0.1939	0.1778	0.2047	0.2047
113	0.189	0.1667	0.1831	0.1775	0.2019	0.1775	0.2042	0.2273	0.1996	0.1974	0.1561	0.1996	0.2087	0.1844	0.1885	0.1806
114	0.1913	0.1645	0.1634	0.1818	0.1951	0.171	0.2087	0.2297	0.2019	0.1974	0.1645	0.2064	0.1974	0.1844	0.2088	0.1845
115	0.1913	0.1862	0.1958	0.1932	0.1939	0.169	0.181	0.1994	0.1736	0.185	0.169	0.1871	0.1871	0.1949	0.2171	0.1885

PSH	**81**	**82**	**83**	**84**	**85**	**86**	**87**	**88**	**89**	**90**	**91**	**92**	**93**	**94**	**95**
1	0.1815	0.1756	0.1667	0.1607	0.1726	0.1726	0.1369	0.1548	0.1429	0.1458	0.1161	0.119	0.131	0.1339	0.128
2	0.1667	0.162	0.1337	0.1455	0.1488	0.1471	0.1502	0.1435	0.1337	0.1413	0.1437	0.1353	0.1292	0.1489	0.152
3	0.1815	0.1786	0.1548	0.1786	0.1845	0.1667	0.1429	0.1726	0.1488	0.1548	0.1667	0.1905	0.1815	0.1577	0.1637
4	0.1964	0.1935	0.1875	0.1756	0.1756	0.1905	0.1726	0.1518	0.1637	0.1577	0.1548	0.1696	0.1756	0.1607	0.1875
5	0.1637	0.1579	0.1323	0.1818	0.1842	0.1507	0.1555	0.1601	0.1415	0.1555	0.1183	0.1531	0.1439	0.1624	0.1717
6	0.1637	0.1756	0.1399	0.1548	0.1548	0.1637	0.128	0.1429	0.1399	0.1488	0.1339	0.1696	0.1637	0.1458	0.1577
7	0.1518	0.1548	0.1399	0.1905	0.1786	0.2054	0.1548	0.1548	0.131	0.1458	0.122	0.1518	0.1458	0.1696	0.1637
8	0.1756	0.1726	0.1726	0.1815	0.1905	0.1845	0.1667	0.1518	0.1399	0.09226	0.1518	0.1607	0.1696	0.1458	0.1905
9	0.1577	0.1429	0.1518	0.1548	0.1637	0.1548	0.1339	0.1518	0.1518	0.1339	0.1429	0.1429	0.1488	0.1756	0.1667
10	0.2143	0.1702	0.1549	0.1719	0.1702	0.1702	0.1565	0.1675	0.169	0.1581	0.1502	0.1674	0.1628	0.1737	0.1612
11	0.1905	0.1726	0.1815	0.1875	0.1875	0.1786	0.1696	0.1815	0.1756	0.1756	0.1696	0.1696	0.1637	0.1726	0.1905
12	0.2024	0.1905	0.1696	0.1905	0.1994	0.1786	0.1577	0.1756	0.1577	0.1756	0.1726	0.2083	0.2054	0.1667	0.1935
13	0.2143	0.205	0.1718	0.1822	0.1781	0.1615	0.1595	0.1595	0.1554	0.1779	0.1411	0.1636	0.1616	0.1636	0.18
14	0.1845	0.1604	0.1476	0.1755	0.1623	0.1491	0.1513	0.1587	0.1347	0.1642	0.131	0.1384	0.1236	0.1513	0.1605
15	0.1696	0.1487	0.1282	0.1523	0.1523	0.1577	0.1333	0.1192	0.1299	0.1368	0.1111	0.1162	0.1094	0.1162	0.1436
16	0.1518	0.1355	0.09091	0.1273	0.119	0.1322	0.1058	0.1455	0.1421	0.1521	0.1207	0.1421	0.1355	0.1471	0.1008
17	0.1672	0.1426	0.1037	0.1327	0.1277	0.126	0.09909	0.1502	0.1326	0.154	0.1387	0.1494	0.1494	0.1692	0.1326
18	0.1548	0.1521	0.1388	0.1636	0.1686	0.1736	0.157	0.1488	0.1455	0.1521	0.1405	0.1471	0.1372	0.1455	0.1669

PSH	81	82	83	84	85	86	87	88	89	90	91	92	93	94	95
19	0.1548	0.1455	0.1461	0.1653	0.162	0.1471	0.1246	0.1515	0.1507	0.1705	0.1457	0.1629	0.1644	0.1583	0.1613
20	0.1875	0.1636	0.114	0.1322	0.1157	0.1273	0.1064	0.1435	0.1322	0.1368	0.1292	0.1474	0.1398	0.1474	0.1033
21	0.1667	0.1504	0.1413	0.162	0.1554	0.1421	0.1216	0.1559	0.1368	0.1641	0.1231	0.1459	0.1474	0.1596	0.1474
22	0.1667	0.1504	0.1339	0.1736	0.1587	0.1471	0.1273	0.1256	0.1074	0.1372	0.1388	0.1471	0.1388	0.1388	0.1339
23	0.1637	0.1653	0.1111	0.1488	0.1339	0.1372	0.1235	0.1464	0.1528	0.1512	0.1451	0.1559	0.1451	0.1651	0.1265
24	0.1875	0.1537	0.1174	0.1405	0.1355	0.1256	0.124	0.1603	0.1372	0.1488	0.1289	0.157	0.1471	0.1587	0.1273
25	0.1548	0.1372	0.1124	0.1289	0.1273	0.1174	0.09917	0.1488	0.1537	0.1521	0.1455	0.1421	0.1421	0.157	0.1256
26	0.1994	0.1719	0.1616	0.157	0.1686	0.1554	0.1494	0.1481	0.1448	0.1616	0.1326	0.157	0.1479	0.1524	0.1677
27	0.1905	0.1521	0.1322	0.1405	0.1355	0.1355	0.1368	0.1343	0.1322	0.1307	0.1185	0.1185	0.117	0.1398	0.1368
28	0.1994	0.1537	0.1481	0.1603	0.162	0.157	0.1451	0.108	0.1188	0.1235	0.1173	0.1481	0.142	0.1512	0.1713
29	0.1667	0.1789	0.1548	0.1711	0.1868	0.1579	0.1376	0.1421	0.1351	0.1499	0.14	0.1622	0.1622	0.1523	0.1843
30	0.1935	0.1719	0.152	0.1653	0.1636	0.1471	0.1459	0.1466	0.1444	0.155	0.1383	0.1505	0.1368	0.152	0.1413
31	0.2024	0.1669	0.1626	0.1736	0.1769	0.1769	0.1535	0.1682	0.1641	0.1657	0.1565	0.1733	0.1596	0.1581	0.1505
32	0.2024	0.1669	0.1626	0.1653	0.1736	0.1653	0.1596	0.1451	0.1489	0.155	0.1596	0.1641	0.1581	0.1429	0.1793
33	0.1726	0.1388	0.1459	0.1669	0.1702	0.1669	0.1459	0.1574	0.1383	0.155	0.1429	0.155	0.1383	0.1505	0.1581
34	0.1875	0.1521	0.1505	0.1686	0.1785	0.1818	0.152	0.1512	0.1505	0.1474	0.1581	0.1672	0.1459	0.155	0.1596
35	0.1964	0.1686	0.1505	0.1653	0.1653	0.1686	0.1474	0.1049	0.114	0.05927	0.1337	0.1307	0.1261	0.1353	0.1505
36	0.1548	0.1372	0.1474	0.1521	0.1488	0.1388	0.1353	0.1296	0.1246	0.1155	0.1246	0.152	0.1307	0.1444	0.1657
37	0.1815	0.1653	0.1398	0.1669	0.1653	0.1554	0.1277	0.1188	0.1307	0.1474	0.1231	0.1398	0.1216	0.1413	0.1565
38	0.1667	0.1587	0.1616	0.1587	0.1554	0.1653	0.1509	0.1219	0.1357	0.1387	0.154	0.1555	0.157	0.1799	0.1905
39	0.1696	0.1554	0.1459	0.1521	0.1603	0.1769	0.1489	0.1404	0.1277	0.1459	0.1307	0.1413	0.1413	0.05319	0.1505
40	0.1548	0.1455	0.1246	0.1372	0.1372	0.124	0.1018	0.1343	0.1307	0.1444	0.1383	0.1505	0.1429	0.1429	0.1201
41	0.2083	0.1818	0.1596	0.1868	0.1884	0.1835	0.1505	0.1559	0.1565	0.1596	0.1444	0.1717	0.1717	0.1748	0.1657
42	0.2024	0.1537	0.1444	0.1554	0.1587	0.1554	0.1444	0.1358	0.1277	0.1368	0.1216	0.1337	0.1261	0.1641	0.1657
43	0.1786	0.1521	0.1505	0.1769	0.1702	0.157	0.1489	0.108	0.1003	0.1368	0.1307	0.1277	0.1261	0.1429	0.1565
44	0.1964	0.1702	0.1641	0.1636	0.1636	0.1636	0.1459	0.1512	0.155	0.1687	0.1201	0.1413	0.1413	0.1702	0.1672
45	0.1696	0.1636	0.1626	0.1818	0.1719	0.1587	0.1565	0.1065	0.117	0.1383	0.1201	0.1505	0.1383	0.1489	0.1763
46	0.1786	0.1653	0.1505	0.157	0.1686	0.1686	0.1596	0.1312	0.1322	0.1398	0.1231	0.1489	0.1413	0.1535	0.1748

PSH	81	82	83	84	85	86	87	88	89	90	91	92	93	94	95
47	0.1786	0.162	0.1322	0.1653	0.1653	0.1537	0.1398	0.1142	0.1049	0.1368	0.1368	0.1429	0.1429	0.1444	0.1565
48	0.1845	0.1669	0.1474	0.1554	0.1719	0.1636	0.1474	0.1528	0.1292	0.1337	0.1383	0.1277	0.1261	0.1565	0.1702
49	0.1875	0.1488	0.1459	0.1504	0.1653	0.1504	0.1307	0.1312	0.1185	0.1398	0.1125	0.1383	0.1277	0.1505	0.1565
50	0.1607	0.1421	0.08896	0.1058	0.1058	0.1008	0.08129	0.1464	0.1196	0.1396	0.1181	0.135	0.1273	0.1518	0.1058
51	0.1845	0.162	0.114	0.157	0.1372	0.1256	0.1033	0.1466	0.155	0.1565	0.1429	0.152	0.1581	0.155	0.114
52	0.1607	0.1603	0.1383	0.162	0.1537	0.1471	0.1246	0.1373	0.152	0.1717	0.1444	0.1489	0.152	0.1596	0.1444
53	0.1548	0.1507	0.122	0.149	0.1374	0.1275	0.1296	0.1563	0.1494	0.1646	0.1555	0.1768	0.1677	0.1631	0.1326
54	0.1637	0.1537	0.1125	0.1306	0.1273	0.1124	0.1003	0.1358	0.1246	0.1429	0.1307	0.1429	0.1429	0.1413	0.1246
55	0.1786	0.1355	0.1231	0.1256	0.119	0.1207	0.09574	0.1528	0.1307	0.1489	0.1383	0.1596	0.1429	0.1307	0.1201
56	0.1964	0.1686	0.1429	0.1471	0.1471	0.1603	0.1413	0.1389	0.1474	0.152	0.1109	0.1003	0.09574	0.1398	0.1368
57	0.1905	0.1669	0.1581	0.1884	0.1917	0.1521	0.1505	0.179	0.1763	0.1717	0.1535	0.1687	0.1505	0.1641	0.1748
58	0.1786	0.1603	0.1702	0.157	0.1702	0.1554	0.1535	0.1898	0.1641	0.1717	0.1596	0.1839	0.155	0.1672	0.1657
59	0.2024	0.1769	0.1657	0.1802	0.1835	0.1835	0.1596	0.1682	0.1565	0.1702	0.1383	0.1854	0.1748	0.1824	0.1839
60	0.1875	0.157	0.1641	0.1719	0.1719	0.1669	0.1459	0.1698	0.1733	0.1839	0.1565	0.1672	0.152	0.1489	0.1641
61	0.1488	0.1488	0.1157	0.1455	0.1322	0.1041	0.08524	0.1484	0.1507	0.1613	0.1233	0.1522	0.14	0.1553	0.09741
62	0.1548	0.1488	0.1611	0.1587	0.1736	0.1455	0.152	0.1512	0.1413	0.1505	0.152	0.1641	0.1565	0.1535	0.1565
63	0.1935	0.1815	0.1637	0.1756	0.1815	0.1637	0.131	0.128	0.131	0.125	0.0982	0.1161	0.1161	0.1667	0.1637
64	0.1756	0.1786	0.1458	0.1607	0.1577	0.1607	0.1399	0.125	0.131	0.1429	0.1339	0.1458	0.1488	0.1607	0.1607
65	0.1667	0.1517	0.1393	0.1429	0.1376	0.1623	0.1287	0.1058	0.08818	0.09877	0.1041	0.1287	0.1305	0.1217	0.1464
66	0.1815	0.1603	0.1537	0.1504	0.1438	0.1438	0.1289	0.1669	0.1636	0.1785	0.1521	0.1537	0.1537	0.162	0.1438
67	0.1905	0.163	0.1417	0.1681	0.1647	0.1597	0.1562	0.1507	0.1337	0.1449	0.1385	0.1546	0.1369	0.1417	0.1481
68	0.1875	0.1603	0.1611	0.1587	0.162	0.1669	0.1565	0.1481	0.1474	0.155	0.1353	0.1657	0.155	0.1596	0.1702
69	0.1786	0.1785	0.1662	0.1554	0.1603	0.1554	0.1509	0.1389	0.1311	0.1479	0.1418	0.1479	0.1387	0.1662	0.1707
70	0.1607	0.1521	0.1322	0.157	0.1587	0.1471	0.1337	0.1404	0.1246	0.1444	0.1231	0.1413	0.1185	0.152	0.152
71	0.1577	0.1421	0.1474	0.1603	0.162	0.1636	0.1505	0.1451	0.1322	0.1565	0.1337	0.152	0.1535	0.1429	0.1611
72	0.1964	0.1851	0.152	0.1653	0.1702	0.1669	0.1535	0.1682	0.1565	0.1702	0.155	0.1945	0.1763	0.19	0.1672
73	0.1815	0.1702	0.154	0.1587	0.1653	0.1702	0.1463	0.1327	0.1357	0.1387	0.128	0.1433	0.128	0.1509	0.1768
74	0.1845	0.1653	0.1489	0.1504	0.1537	0.1504	0.1459	0.142	0.1337	0.1429	0.1231	0.1505	0.1307	0.152	0.1657

PSH	81	82	83	84	85	86	87	88	89	90	91	92	93	94	95
75	0.1815	0.157	0.1337	0.1504	0.1537	0.1438	0.1353	0.1312	0.1383	0.1489	0.1292	0.1307	0.1307	0.1505	0.1459
76	0.1964	0.1736	0.152	0.1835	0.1818	0.1702	0.1548	0.1373	0.1322	0.1459	0.1543	0.1489	0.1398	0.1489	0.1733
77	0.1905	0.1785	0.1489	0.1686	0.1686	0.1521	0.1444	0.1265	0.1277	0.1307	0.1383	0.1413	0.1322	0.1413	0.1687
78	0.1875	0.1652	0.1279	0.1674	0.1606	0.1516	0.145	0.1598	0.1407	0.1578	0.1194	0.1343	0.1237	0.1684	0.1706
79	0.2024	0.1815	0.1667	0.1696	0.1726	0.1786	0.1488	0.1607	0.1399	0.1429	0.1458	0.1369	0.1399	0.1786	0.1905
80	0.1786	0.1726	0.1607	0.1429	0.1429	0.1667	0.1548	0.1518	0.1161	0.1399	0.131	0.1607	0.1607	0.1369	0.1637
81		0.0506	0.1637	0.1845	0.1815	0.1786	0.1548	0.1815	0.1518	0.1964	0.1726	0.1786	0.1548	0.1518	0.1518
82	0.0526		0.1438	0.157	0.162	0.1471	0.1388	0.1554	0.1372	0.1686	0.1471	0.1554	0.1355	0.1504	0.1388
83	0.1885	0.1624		0.1306	0.1306	0.1207	0.1018	0.1451	0.1322	0.1459	0.1307	0.1459	0.1368	0.1444	0.1201
84	0.2171	0.1796	0.1456		0.06612	0.1471	0.1223	0.1603	0.1488	0.1504	0.1355	0.1636	0.1669	0.1603	0.1504
85	0.213	0.1862	0.1456	0.06966		0.1438	0.1174	0.1587	0.1488	0.157	0.1421	0.1686	0.1587	0.1636	0.1355
86	0.2088	0.1667	0.1333	0.1667	0.1624		0.09752	0.157	0.1488	0.1636	0.1488	0.1587	0.1537	0.1686	0.1289
87	0.1767	0.1561	0.1106	0.1354	0.1293	0.1055		0.1358	0.1216	0.1459	0.1335	0.1444	0.1429	0.1459	0.1079
88	0.213	0.1775	0.164	0.184	0.1818	0.1796	0.1522		0.08796	0.108	0.1173	0.1219	0.1327	0.1389	0.1559
89	0.1728	0.154	0.1477	0.1688	0.1688	0.1688	0.1345	0.09441		0.1125	0.1292	0.1353	0.1444	0.1322	0.1459
90	0.2341	0.1951	0.1651	0.171	0.1796	0.1884	0.1651	0.118	0.1234		0.1368	0.1307	0.1231	0.1429	0.1596
91	0.2006	0.1667	0.1458	0.1519	0.1603	0.1688	0.1493	0.1292	0.1439	0.1534		0.1216	0.114	0.1398	0.1398
92	0.2088	0.1775	0.1651	0.1884	0.1951	0.1818	0.1631	0.1349	0.1515	0.1458	0.1345		0.05927	0.1459	0.1535
93	0.1767	0.1519	0.1534	0.1929	0.1818	0.1753	0.1612	0.1483	0.1631	0.1363	0.1252	0.06209		0.1413	0.1459
94	0.1728	0.171	0.1631	0.184	0.1884	0.1951	0.1651	0.1561	0.1477	0.1612	0.1573	0.1651	0.1592		0.1535
95	0.1728	0.1561	0.1326	0.171	0.1519	0.1436	0.1179	0.1781	0.1651	0.183	0.1573	0.175	0.1651	0.175	
96	0.2341	0.1731	0.1671	0.1974	0.2064	0.1818	0.175	0.1581	0.1515	0.171	0.1458	0.1345	0.1307	0.1477	0.185
97	0.2006	0.1884	0.177	0.2042	0.2042	0.184	0.177	0.1368	0.142	0.181	0.1515	0.1932	0.171	0.1592	0.1932
98	0.213	0.1866	0.1895	0.2068	0.2068	0.191	0.1793	0.1408	0.1422	0.1693	0.146	0.1854	0.1674	0.1537	0.1998
99	0.1885	0.1688	0.1612	0.1974	0.1974	0.1775	0.171	0.1406	0.1382	0.1671	0.1307	0.185	0.1612	0.1592	0.1953
100	0.2171	0.1929	0.183	0.1907	0.1884	0.1796	0.142	0.1425	0.1307	0.183	0.1496	0.181	0.171	0.169	0.185
101	0.2171	0.1884	0.1671	0.184	0.1796	0.171	0.142	0.1406	0.116	0.1631	0.1496	0.1612	0.1612	0.1612	0.1671
102	0.1925	0.1736	0.156	0.1627	0.1802	0.1914	0.1539	0.1755	0.1539	0.1539	0.1539	0.1799	0.1646	0.1539	0.1777

PSH	81	82	83	84	85	86	87	88	89	90	91	92	93	94	95
103	0.2384	0.1796	0.1554	0.1731	0.1884	0.1775	0.1592	0.17	0.171	0.173	0.1612	0.1891	0.179	0.1534	0.1515
104	0.2006	0.1775	0.1519	0.1731	0.1561	0.1519	0.1313	0.1818	0.184	0.1907	0.1667	0.1645	0.1862	0.1775	0.1395
105	0.2047	0.1993	0.1414	0.1674	0.1496	0.1446	0.1179	0.1861	0.1784	0.1809	0.1835	0.1758	0.1886	0.1938	0.1319
106	0.1966	0.1528	0.1459	0.1598	0.1693	0.1742	0.1596	0.1437	0.1348	0.1482	0.1047	0.1217	0.1131	0.1348	0.1665
107	0.213	0.1993	0.1414	0.09195	0.08057	0.1521	0.1319	0.1809	0.1608	0.2124	0.1559	0.1991	0.1886	0.2097	0.1683
108	0.213	0.1731	0.1345	0.1775	0.1688	0.1456	0.1307	0.1781	0.1592	0.183	0.1496	0.177	0.169	0.183	0.1592
109	0.2213	0.1731	0.142	0.1436	0.1354	0.1354	0.1035	0.1444	0.1289	0.1651	0.142	0.1477	0.142	0.169	0.1382
110	0.2006	0.1753	0.06712	0.1519	0.154	0.1333	0.1234	0.162	0.1573	0.169	0.1592	0.181	0.169	0.1871	0.1477
111	0.1767	0.1606	0.05107	0.1649	0.1519	0.1309	0.1025	0.1541	0.1392	0.1649	0.1541	0.1737	0.1627	0.1693	0.1226
112	0.2255	0.2042	0.1559	0.1775	0.1561	0.1436	0.1219	0.1971	0.2085	0.1837	0.1696	0.1776	0.1816	0.1939	0.1482
113	0.2213	0.1929	0.1456	0.1796	0.154	0.1519	0.1213	0.1974	0.1951	0.1862	0.1688	0.1862	0.1884	0.1974	0.1456
114	0.2255	0.2019	0.1374	0.1667	0.1456	0.1436	0.1273	0.1907	0.1974	0.1818	0.171	0.1818	0.1884	0.2064	0.1354
115	0.1099	0.1036	0.1631	0.1974	0.1884	0.1775	0.1573	0.1581	0.1573	0.175	0.1631	0.177	0.1477	0.179	0.169

PSH	96	97	98	99	100	101	102	103	104	105	106	107	108	109	110
1	0.1518	0.1637	0.1667	0.1458	0.1518	0.1548	0.1607	0.1339	0.128	0.1369	0.1101	0.1756	0.1518	0.131	0.1667
2	0.1383	0.1611	0.1553	0.1626	0.1535	0.1413	0.1388	0.1459	0.1438	0.1503	0.1308	0.1657	0.152	0.1383	0.1322
3	0.1488	0.1845	0.1875	0.1815	0.1637	0.1548	0.1429	0.1726	0.1815	0.1607	0.1696	0.1756	0.1726	0.1548	0.1577
4	0.1875	0.1964	0.1964	0.1875	0.1905	0.1815	0.1607	0.1637	0.1607	0.1786	0.1577	0.2113	0.2143	0.1667	0.1845
5	0.1346	0.1671	0.1698	0.1531	0.1624	0.1671	0.179	0.1833	0.1459	0.1555	0.123	0.1717	0.1531	0.1624	0.1508
6	0.1696	0.1756	0.1696	0.1577	0.1667	0.1577	0.1607	0.1458	0.1696	0.1667	0.1339	0.1577	0.1488	0.1429	0.1458
7	0.1786	0.1756	0.1935	0.1607	0.1726	0.1637	0.1518	0.1488	0.1637	0.1905	0.1458	0.1815	0.1815	0.1696	0.1577
8	0.1607	0.1726	0.1667	0.1518	0.1518	0.1518	0.1607	0.1786	0.1786	0.1726	0.125	0.1905	0.1756	0.1875	0.1667
9	0.1786	0.1905	0.1994	0.1726	0.1964	0.1815	0.1726	0.1637	0.1399	0.1399	0.1369	0.1875	0.1577	0.1577	0.1637
10	0.1643	0.1643	0.1646	0.169	0.18	0.1721	0.1572	0.1565	0.1587	0.1696	0.147	0.1734	0.1768	0.169	0.1471
11	0.1845	0.2054	0.2232	0.1905	0.2054	0.2113	0.1905	0.1786	0.1488	0.1696	0.1756	0.1875	0.1875	0.1696	0.1875
12	0.2024	0.1935	0.2054	0.1875	0.1905	0.1935	0.1994	0.1756	0.1696	0.1667	0.1815	0.1845	0.1994	0.1667	0.1548
13	0.1534	0.1779	0.1803	0.1616	0.1697	0.1677	0.1674	0.1779	0.1801	0.1779	0.1431	0.1636	0.184	0.1636	0.1779

PSH	96	97	98	99	100	101	102	103	104	105	106	107	108	109	110
14	0.1218	0.1661	0.1701	0.1661	0.1605	0.1494	0.1657	0.1661	0.1453	0.154	0.1255	0.1579	0.1587	0.1421	0.155
15	0.1162	0.1385	0.1421	0.135	0.1402	0.1333	0.1377	0.1402	0.1398	0.1368	0.08781	0.1503	0.1487	0.135	0.1402
16	0.1405	0.1636	0.1672	0.1554	0.162	0.1438	0.1441	0.1388	0.1207	0.1098	0.1271	0.1277	0.1289	0.1223	0.1041
17	0.1616	0.1753	0.1832	0.1677	0.1692	0.157	0.1577	0.154	0.1294	0.1332	0.1544	0.1236	0.1418	0.1052	0.1143
18	0.1455	0.157	0.1589	0.1488	0.1587	0.1587	0.1374	0.1455	0.1471	0.1597	0.1344	0.1737	0.1603	0.1653	0.1372
19	0.1689	0.1811	0.1738	0.1674	0.1522	0.1476	0.1572	0.1781	0.1421	0.1503	0.1577	0.1657	0.1568	0.1309	0.1537
20	0.1565	0.1702	0.1674	0.1672	0.1474	0.1444	0.1505	0.1383	0.1223	0.1214	0.1344	0.1252	0.1383	0.09726	0.1201
21	0.1626	0.1763	0.1766	0.1733	0.1429	0.1444	0.1706	0.1793	0.1554	0.1599	0.1487	0.1503	0.1505	0.1216	0.1505
22	0.1421	0.1339	0.144	0.1388	0.1289	0.1124	0.1424	0.1372	0.1653	0.1637	0.1289	0.1796	0.1372	0.1488	0.124
23	0.1605	0.1543	0.1685	0.1543	0.162	0.1559	0.1522	0.1435	0.1223	0.1272	0.147	0.1349	0.1466	0.1343	0.1157
24	0.1471	0.1554	0.1689	0.1488	0.1471	0.1405	0.1658	0.1471	0.114	0.1138	0.1344	0.1497	0.0843	0.1223	0.119
25	0.1719	0.1653	0.1672	0.1636	0.1488	0.1521	0.1658	0.157	0.1421	0.1377	0.1455	0.1297	0.1355	0.1174	0.1223
26	0.1585	0.1463	0.1435	0.1341	0.1448	0.1402	0.1555	0.1463	0.1653	0.1715	0.1272	0.1638	0.1616	0.1585	0.1616
27	0.1277	0.1474	0.1446	0.1489	0.1459	0.1292	0.1304	0.1398	0.1504	0.1484	0.1165	0.1368	0.1337	0.1246	0.1383
28	0.1497	0.1327	0.1329	0.1312	0.1343	0.1343	0.1438	0.1698	0.162	0.158	0.1344	0.1753	0.1543	0.1327	0.1512
29	0.14	0.1916	0.197	0.172	0.1622	0.1671	0.1732	0.1548	0.1632	0.1533	0.1418	0.1658	0.1671	0.1597	0.1572
30	0.1277	0.1474	0.1553	0.1459	0.1611	0.1535	0.1505	0.1413	0.157	0.1464	0.1254	0.1561	0.1459	0.1322	0.1535
31	0.1626	0.1778	0.1766	0.1778	0.1748	0.1778	0.1689	0.1474	0.1785	0.183	0.147	0.1888	0.1687	0.1413	0.1657
32	0.1687	0.1733	0.1766	0.1702	0.1763	0.1641	0.1722	0.1626	0.1653	0.1464	0.1505	0.1676	0.1641	0.1383	0.152
33	0.1368	0.1626	0.1553	0.152	0.1489	0.1535	0.1538	0.1489	0.1471	0.158	0.1452	0.1676	0.1596	0.1535	0.1474
34	0.1459	0.1687	0.175	0.1626	0.1854	0.1869	0.1605	0.1611	0.1686	0.1792	0.1487	0.183	0.1596	0.1489	0.1581
35	0.1413	0.1429	0.1507	0.1368	0.1429	0.1337	0.1522	0.155	0.1636	0.1599	0.1201	0.1927	0.1565	0.1489	0.1596
36	0.1474	0.1261	0.1309	0.1246	0.1429	0.1459	0.1472	0.1444	0.1785	0.1792	0.1165	0.1561	0.1611	0.155	0.1505
37	0.1277	0.1383	0.1431	0.1307	0.1307	0.1322	0.1572	0.1535	0.157	0.158	0.1254	0.1657	0.1535	0.1444	0.1444
38	0.1723	0.1601	0.1573	0.1509	0.1479	0.1646	0.1622	0.1631	0.1802	0.1734	0.1487	0.1753	0.1585	0.1433	0.157
39	0.1307	0.1429	0.1476	0.1383	0.1489	0.1413	0.1421	0.1231	0.1554	0.1734	0.1219	0.1811	0.1596	0.1337	0.1489
40	0.152	0.1413	0.14	0.1429	0.1474	0.1398	0.1288	0.1277	0.1355	0.1445	0.1362	0.1407	0.1292	0.1155	0.1231
41	0.1657	0.1687	0.1689	0.1626	0.155	0.1672	0.1756	0.1717	0.1686	0.1676	0.1685	0.185	0.1748	0.1596	0.1641

PSH	96	97	98	99	100	101	102	103	104	105	106	107	108	109	110
42	0.1307	0.1489	0.1537	0.1474	0.155	0.152	0.1472	0.1459	0.1636	0.1734	0.1147	0.1561	0.1444	0.1337	0.1489
43	0.1474	0.1292	0.1279	0.1216	0.1353	0.1277	0.1338	0.1398	0.157	0.1869	0.1219	0.1734	0.1657	0.1474	0.1535
44	0.1383	0.1641	0.1689	0.1535	0.1596	0.1581	0.1589	0.1611	0.1669	0.1676	0.129	0.1715	0.155	0.152	0.1733
45	0.1413	0.1277	0.1385	0.1322	0.1231	0.1216	0.1505	0.1444	0.195	0.1946	0.1272	0.1657	0.1581	0.1489	0.1626
46	0.155	0.1565	0.1553	0.1535	0.1368	0.1398	0.1488	0.1793	0.1868	0.1753	0.129	0.1696	0.1626	0.1611	0.1581
47	0.155	0.1231	0.1355	0.1292	0.1307	0.1155	0.1338	0.1459	0.1587	0.158	0.1308	0.1696	0.1505	0.1444	0.1444
48	0.1489	0.1702	0.1568	0.1657	0.1611	0.152	0.1405	0.1626	0.1719	0.1638	0.1111	0.1657	0.1687	0.1489	0.1672
49	0.1246	0.1413	0.14	0.1368	0.1474	0.1505	0.1355	0.1353	0.1455	0.1599	0.1039	0.1541	0.152	0.1292	0.1505
50	0.1411	0.1549	0.172	0.1503	0.1288	0.1258	0.1455	0.1319	0.1174	0.1126	0.1295	0.1049	0.1258	0.08742	0.1012
51	0.1474	0.1657	0.172	0.1672	0.1413	0.1505	0.1672	0.1261	0.07438	0.06551	0.1434	0.1426	0.1429	0.1109	0.1277
52	0.1565	0.1657	0.1644	0.1657	0.1581	0.155	0.1739	0.1641	0.1504	0.1464	0.1559	0.1618	0.1535	0.1216	0.1413
53	0.1768	0.1585	0.171	0.1494	0.1707	0.1646	0.1658	0.1738	0.149	0.1349	0.1452	0.1407	0.1494	0.1341	0.1311
54	0.1535	0.1398	0.1446	0.1322	0.1505	0.1398	0.1605	0.1641	0.1124	0.131	0.1326	0.1252	0.1277	0.1033	0.1261
55	0.1535	0.155	0.1659	0.152	0.152	0.1474	0.1455	0.1474	0.1256	0.1175	0.147	0.1272	0.1307	0.09574	0.1307
56	0.1201	0.155	0.1568	0.1474	0.1489	0.1474	0.1472	0.1413	0.1455	0.1484	0.08065	0.1503	0.1505	0.1322	0.155
57	0.1611	0.1702	0.1766	0.1611	0.1596	0.1459	0.1589	0.1413	0.1702	0.1676	0.1416	0.1811	0.1657	0.1748	0.1778
58	0.1581	0.1945	0.2009	0.1793	0.1717	0.1809	0.1689	0.1657	0.1636	0.1676	0.1774	0.1869	0.1717	0.1505	0.1657
59	0.1733	0.1672	0.1674	0.1702	0.1383	0.1459	0.1823	0.1672	0.1851	0.1888	0.1703	0.1676	0.1687	0.1733	0.1702
60	0.1459	0.1748	0.1903	0.1687	0.1641	0.1565	0.1522	0.1444	0.1686	0.1715	0.1416	0.1715	0.1611	0.1626	0.1702
61	0.1598	0.1629	0.1692	0.1644	0.1385	0.1294	0.1438	0.1507	0.1124	0.1118	0.1487	0.1368	0.137	0.1005	0.1309
62	0.1429	0.1687	0.175	0.1672	0.1687	0.1505	0.1488	0.152	0.1736	0.1599	0.1541	0.1734	0.1596	0.1368	0.1535
63	0.1577	0.1548	0.1696	0.1488	0.1458	0.1518	0.1518	0.1548	0.1399	0.1518	0.1131	0.1875	0.1726	0.1488	0.1637
64	0.1637	0.1786	0.1935	0.1577	0.1786	0.1607	0.1637	0.1458	0.1756	0.1726	0.1518	0.1548	0.1548	0.1458	0.1369
65	0.1235	0.1358	0.1411	0.1146	0.1358	0.1235	0.1323	0.1481	0.1587	0.1628	0.09903	0.1649	0.1323	0.1376	0.1376
66	0.1587	0.1851	0.1772	0.1818	0.157	0.1653	0.1658	0.1818	0.1438	0.1477	0.1547	0.1597	0.162	0.1355	0.1587
67	0.132	0.153	0.1578	0.1498	0.1562	0.1514	0.1295	0.1481	0.1412	0.1548	0.1238	0.167	0.161	0.153	0.1449
68	0.1398	0.1626	0.1629	0.1505	0.152	0.1565	0.1538	0.1398	0.1438	0.1522	0.1219	0.1599	0.1702	0.1459	0.1581
69	0.1524	0.157	0.1542	0.1448	0.157	0.1494	0.1405	0.154	0.1752	0.1561	0.1272	0.1734	0.1692	0.1448	0.1723

PSH	96	97	98	99	100	101	102	103	104	105	106	107	108	109	110
70	0.117	0.1444	0.14	0.1383	0.152	0.1489	0.1505	0.155	0.1521	0.1541	0.1147	0.1561	0.1474	0.1337	0.1413
71	0.1398	0.152	0.1598	0.155	0.1535	0.1474	0.1538	0.1459	0.1802	0.1696	0.1416	0.1503	0.1474	0.1505	0.1444
72	0.1672	0.1763	0.1781	0.1748	0.1611	0.1672	0.1639	0.1702	0.2099	0.1811	0.1738	0.1541	0.1717	0.1702	0.1489
73	0.125	0.1448	0.1496	0.1479	0.1509	0.1585	0.1689	0.154	0.1603	0.1676	0.1254	0.1599	0.1662	0.1433	0.1524
74	0.1459	0.1565	0.1522	0.1398	0.152	0.152	0.1405	0.1459	0.157	0.1618	0.1272	0.1676	0.1763	0.1413	0.1459
75	0.1231	0.152	0.1522	0.1489	0.1565	0.1459	0.1589	0.1383	0.1438	0.1464	0.1237	0.1541	0.1581	0.1368	0.1368
76	0.1368	0.1565	0.1553	0.152	0.1489	0.1398	0.1589	0.1611	0.1636	0.1657	0.1272	0.183	0.1581	0.152	0.155
77	0.1307	0.1444	0.1492	0.1444	0.152	0.1444	0.1488	0.1535	0.1686	0.1657	0.1183	0.1696	0.1474	0.1429	0.1505
78	0.1386	0.1706	0.1816	0.1493	0.1557	0.1514	0.1512	0.1727	0.1629	0.1587	0.1225	0.1609	0.1578	0.1493	0.1514
79	0.1577	0.1875	0.1935	0.1607	0.1607	0.1607	0.1667	0.1845	0.1875	0.1875	0.1399	0.1726	0.1994	0.1815	0.1845
80	0.1607	0.1845	0.1726	0.1548	0.1726	0.1548	0.1577	0.1607	0.1577	0.1607	0.119	0.1607	0.2024	0.1607	0.1488
81	0.1964	0.1726	0.1815	0.1637	0.1845	0.1845	0.1667	0.1994	0.1726	0.1756	0.1696	0.1815	0.1815	0.1875	0.1726
82	0.1521	0.1636	0.1623	0.1488	0.1669	0.1636	0.1524	0.157	0.1554	0.1717	0.1363	0.1717	0.1521	0.1521	0.1537
83	0.1474	0.155	0.1644	0.1429	0.1596	0.1474	0.1388	0.1383	0.1355	0.1272	0.1308	0.1272	0.1216	0.1277	0.06383
84	0.1702	0.1752	0.1772	0.1702	0.1653	0.1603	0.1441	0.1521	0.1521	0.1477	0.1418	0.08583	0.1554	0.1289	0.1355
85	0.1769	0.1752	0.1772	0.1702	0.1636	0.157	0.1575	0.1636	0.1388	0.1337	0.1492	0.07585	0.1488	0.1223	0.1372
86	0.1587	0.1603	0.1656	0.1554	0.157	0.1504	0.1658	0.1554	0.1355	0.1297	0.1529	0.1357	0.1306	0.1223	0.1207
87	0.1535	0.155	0.1568	0.1505	0.1277	0.1277	0.1371	0.1413	0.119	0.1079	0.1416	0.1195	0.1185	0.09574	0.1125
88	0.1404	0.1235	0.1267	0.1265	0.1281	0.1265	0.1538	0.1497	0.1587	0.1618	0.129	0.158	0.1559	0.1296	0.1435
89	0.1353	0.1277	0.1279	0.1246	0.1185	0.1064	0.1371	0.1505	0.1603	0.1561	0.1219	0.1426	0.1413	0.117	0.1398
90	0.1505	0.1581	0.1492	0.1474	0.1596	0.1444	0.1371	0.152	0.1653	0.158	0.1326	0.1811	0.1596	0.1459	0.1489
91	0.1307	0.1353	0.1309	0.1185	0.1337	0.1337	0.1371	0.1429	0.1471	0.1599	0.09677	0.1387	0.1337	0.1277	0.1413
92	0.1216	0.1672	0.1613	0.1611	0.1581	0.1429	0.1572	0.1641	0.1455	0.1541	0.1111	0.1715	0.155	0.1322	0.1581
93	0.1185	0.1505	0.1476	0.1429	0.1505	0.1429	0.1455	0.1565	0.162	0.1638	0.1039	0.1638	0.1489	0.1277	0.1489
94	0.1322	0.1413	0.137	0.1413	0.1489	0.1429	0.1371	0.1368	0.1554	0.1676	0.1219	0.1792	0.1596	0.1489	0.1626
95	0.1611	0.1672	0.172	0.1687	0.1611	0.1474	0.1555	0.1353	0.1256	0.1195	0.147	0.1484	0.1413	0.1246	0.1322
96		0.1489	0.1492	0.155	0.1581	0.1505	0.1522	0.1368	0.1521	0.158	0.1075	0.1734	0.1383	0.1383	0.1489
97	0.169		0.06088	0.05927	0.1307	0.1337	0.1639	0.1489	0.1736	0.185	0.1344	0.185	0.1626	0.1596	0.1626

PSH	96	97	98	99	100	101	102	103	104	105	106	107	108	109	110
98	0.1693	0.0639		0.07915	0.137	0.137	0.1642	0.1568	0.1788	0.1853	0.1293	0.1911	0.1644	0.1583	0.1705
99	0.177	0.0621	0.08431		0.1307	0.1383	0.1488	0.1535	0.1669	0.1792	0.1147	0.1734	0.155	0.1611	0.1535
100	0.181	0.1458	0.1537	0.1458		0.04711	0.1589	0.1611	0.1736	0.1599	0.1398	0.1541	0.1596	0.1505	0.1733
101	0.171	0.1496	0.1537	0.1554	0.04887		0.1455	0.1581	0.1669	0.1522	0.1398	0.1522	0.1429	0.1383	0.1581
102	0.1733	0.1888	0.1891	0.1689	0.1821	0.1646		0.1304	0.1742	0.1753	0.136	0.1653	0.1656	0.1405	0.1472
103	0.1534	0.169	0.1793	0.175	0.185	0.181	0.1455		0.1306	0.1503	0.1308	0.1773	0.1565	0.1383	0.1398
104	0.1731	0.2019	0.2091	0.1929	0.2019	0.1929	0.2028	0.1456		0.07186	0.1473	0.1537	0.1521	0.1107	0.1388
105	0.1809	0.2178	0.2183	0.2097	0.1835	0.1733	0.2043	0.1708	0.07607		0.155	0.1407	0.1387	0.1021	0.1368
106	0.1174	0.1504	0.144	0.1261	0.1573	0.1573	0.1525	0.1459	0.167	0.177		0.1434	0.1487	0.1416	0.1434
107	0.2017	0.2178	0.2265	0.2017	0.1758	0.1733	0.1907	0.207	0.1753	0.1584	0.1619		0.1599	0.1329	0.1387
108	0.1554	0.1871	0.1895	0.177	0.183	0.1612	0.191	0.179	0.1731	0.1559	0.1688	0.1835		0.1155	0.1368
109	0.1554	0.183	0.1813	0.185	0.171	0.1554	0.1581	0.1554	0.1213	0.111	0.1596	0.1486	0.127		0.1277
110	0.169	0.1871	0.1977	0.175	0.2015	0.181	0.1667	0.1573	0.1561	0.1535	0.1619	0.1559	0.1534	0.142	
111	0.1693	0.1671	0.1872	0.1498	0.1918	0.1849	0.1649	0.1541	0.1455	0.1368	0.148	0.1571	0.1392	0.1371	0.06029
112	0.1816	0.2106	0.2047	0.2085	0.1736	0.1756	0.2024	0.1618	0.09209	0.06685	0.1925	0.1608	0.1696	0.1425	0.1618
113	0.1796	0.2064	0.2114	0.2019	0.171	0.171	0.1982	0.1582	0.08453	0.06276	0.1646	0.1726	0.1775	0.1374	0.1582
114	0.1818	0.2087	0.1978	0.211	0.1688	0.1645	0.1914	0.1582	0.1017	0.06717	0.1839	0.1521	0.1603	0.1374	0.1519
115	0.1612	0.169	0.1833	0.173	0.1871	0.1871	0.191	0.1671	0.1818	0.2043	0.1619	0.1964	0.2057	0.171	0.175

PSH	111	112	113	114	115
1	0.1637	0.1429	0.1339	0.1399	0.1815
2	0.1424	0.1479	0.1405	0.1405	0.1596
3	0.1577	0.1756	0.1667	0.1696	0.1845
4	0.1845	0.1786	0.1637	0.1667	0.1875
5	0.1241	0.1531	0.1579	0.1555	0.1624
6	0.128	0.1726	0.1577	0.1607	0.1637
7	0.1488	0.1964	0.1786	0.1875	0.1607
8	0.1696	0.1667	0.1607	0.1607	0.1637

PSH	111	112	113	114	115
9	0.1429	0.1577	0.1488	0.1577	0.1667
10	0.1508	0.1581	0.1603	0.162	0.169
11	0.1756	0.1458	0.1577	0.1548	0.1756
12	0.1667	0.1786	0.1607	0.1815	0.1935
13	0.1723	0.18	0.1843	0.1718	0.1984
14	0.1491	0.1513	0.1472	0.1434	0.1587
15	0.1361	0.135	0.1398	0.1434	0.1573
16	0.08814	0.1256	0.1025	0.1207	0.1455
17	0.09354	0.1422	0.1327	0.1376	0.1509
18	0.1424	0.1636	0.1669	0.1653	0.1554
19	0.1508	0.1613	0.1504	0.1587	0.1705
20	0.1169	0.1296	0.1174	0.1273	0.1611
21	0.1475	0.1524	0.162	0.1537	0.152
22	0.1288	0.1603	0.1537	0.1603	0.1504
23	0.1051	0.1281	0.1223	0.1273	0.1481
24	0.1119	0.1289	0.1372	0.1256	0.1669
25	0.1068	0.1421	0.1388	0.1421	0.1471
26	0.161	0.1621	0.1719	0.1669	0.1601
27	0.1407	0.1662	0.1603	0.162	0.1611
28	0.139	0.1654	0.1653	0.1669	0.159
29	0.1555	0.1548	0.1421	0.1526	0.14
30	0.1424	0.1631	0.1521	0.1504	0.1657
31	0.1644	0.1845	0.1785	0.1719	0.1596
32	0.1576	0.1662	0.1636	0.1686	0.1809
33	0.1305	0.1631	0.1587	0.162	0.1489
34	0.1407	0.1753	0.1785	0.1785	0.1535
35	0.1441	0.1616	0.162	0.1587	0.152
36	0.1373	0.1631	0.1719	0.1686	0.1459

PSH	111	112	113	114	115
37	0.1373	0.1555	0.1554	0.157	0.1672
38	0.1525	0.1667	0.1802	0.1669	0.1677
39	0.1441	0.1677	0.1686	0.1769	0.1596
40	0.1085	0.1433	0.1372	0.1455	0.1444
41	0.1492	0.1509	0.1603	0.162	0.1717
42	0.1525	0.1631	0.162	0.1603	0.1581
43	0.1441	0.1829	0.1719	0.1818	0.1596
44	0.1508	0.1723	0.1554	0.1719	0.1581
45	0.1627	0.1799	0.1802	0.1835	0.1581
46	0.1627	0.1814	0.1802	0.1818	0.1596
47	0.1356	0.1616	0.1653	0.1636	0.1672
48	0.1576	0.1601	0.1785	0.1587	0.1717
49	0.1492	0.157	0.1603	0.1537	0.155
50	0.09831	0.1323	0.1174	0.1207	0.1396
51	0.1186	0.05488	0.0562	0.05785	0.1413
52	0.1475	0.1524	0.1504	0.1421	0.1398
53	0.1104	0.1575	0.1391	0.1457	0.1585
54	0.1136	0.1311	0.1372	0.1273	0.1611
55	0.122	0.1357	0.1273	0.1322	0.1429
56	0.1356	0.1494	0.1355	0.1421	0.1672
57	0.1695	0.1753	0.1736	0.1868	0.1687
58	0.1593	0.1662	0.1802	0.1686	0.1672
59	0.178	0.1723	0.1868	0.1736	0.1626
60	0.1576	0.1829	0.1653	0.1868	0.1748
61	0.1186	0.113	0.1058	0.1124	0.1416
62	0.1475	0.1768	0.162	0.1702	0.1505
63	0.1548	0.1607	0.1577	0.1548	0.1815
64	0.1429	0.1756	0.1667	0.1667	0.1696

PSH	111	112	113	114	115
65	0.1235	0.1693	0.164	0.1658	0.1658
66	0.1492	0.1521	0.1471	0.1455	0.162
67	0.1448	0.1502	0.1597	0.1445	0.1691
68	0.161	0.1524	0.1554	0.1587	0.1672
69	0.1661	0.1667	0.1736	0.1686	0.1677
70	0.139	0.157	0.1554	0.1504	0.1489
71	0.1458	0.1738	0.1752	0.1785	0.1581
72	0.1542	0.1829	0.1917	0.1934	0.1717
73	0.1593	0.1697	0.1719	0.1736	0.1524
74	0.1492	0.1646	0.1702	0.1702	0.1611
75	0.1356	0.1463	0.1388	0.1455	0.1489
76	0.1559	0.1753	0.1719	0.1769	0.1626
77	0.1492	0.1677	0.1785	0.1702	0.1626
78	0.1425	0.1557	0.1606	0.1606	0.1684
79	0.1815	0.1756	0.1637	0.1786	0.1845
80	0.1577	0.1756	0.1577	0.1607	0.1637
81	0.1548	0.1905	0.1875	0.1905	0.1012
82	0.1424	0.1752	0.1669	0.1736	0.09587
83	0.04915	0.1387	0.1306	0.124	0.1444
84	0.1458	0.1554	0.157	0.1471	0.1702
85	0.1356	0.1388	0.1372	0.1306	0.1636
86	0.1186	0.1289	0.1355	0.1289	0.1554
87	0.09492	0.1113	0.1107	0.1157	0.1398
88	0.1373	0.17	0.1702	0.1653	0.1404
89	0.1254	0.1784	0.1686	0.1702	0.1398
90	0.1458	0.1601	0.162	0.1587	0.1535
91	0.1373	0.1494	0.1488	0.1504	0.1444
92	0.1525	0.1555	0.162	0.1587	0.155

PSH	**111**	**112**	**113**	**114**	**115**
93	0.1441	0.1585	0.1636	0.1636	0.1322
94	0.1492	0.1677	0.1702	0.1769	0.1565
95	0.1119	0.1326	0.1306	0.1223	0.1489
96	0.1492	0.1585	0.157	0.1587	0.1429
97	0.1475	0.1799	0.1769	0.1785	0.1489
98	0.1627	0.1756	0.1805	0.1705	0.1598
99	0.1339	0.1784	0.1736	0.1802	0.152
100	0.1661	0.1524	0.1504	0.1488	0.1626
101	0.161	0.154	0.1504	0.1455	0.1626
102	0.1458	0.1739	0.1709	0.1658	0.1656
103	0.1373	0.1433	0.1405	0.1405	0.1474
104	0.1305	0.08595	0.07934	0.09421	0.1587
105	0.1235	0.06358	0.05988	0.06387	0.1753
106	0.1325	0.1667	0.1455	0.1602	0.1434
107	0.1397	0.1426	0.1517	0.1357	0.1696
108	0.1254	0.1494	0.1554	0.1421	0.1763
109	0.1237	0.128	0.124	0.124	0.1505
110	0.05763	0.1433	0.1405	0.1355	0.1535
111		0.139	0.1305	0.1356	0.1458
112	0.1562		0.0595	0.02975	0.1616
113	0.1455	0.06235		0.06777	0.162
114	0.1519	0.03044	0.0715		0.1603
115	0.1649	0.1857	0.1862	0.184	

Appendix V. Author attribution statements

To Whom It May Concern,

I, Andrew M Hosie as the first author of the unpublished Chapter 2. “Barcoding Barnacle Biodiversity: Assessing Australia’s Acastinae and Allies”, declare that I was primarily responsible for the design, execution, interpretation, and writing for this chapter.

I, as a co-author, endorse that this level of contribution by the candidate indicated above is appropriate.

Jane Fromont

Co-author 1 (Signature of Co-author 1)

Kylie A. Munyard

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Diana S. Jones

Co-author 3 (Signature of Co-author 3)

To Whom It May Concern,

I, Andrew M Hosie as the first author of the 2019 publication "Description of a new species of *Membranobalanus* (Crustacea, Cirripedia) from southern Australia. *ZooKeys, 873*, 25–42 https://doi.org/10.3897/zookeys.873.35421", declare that I was primarily responsible for the design, execution, interpretation, and writing for this manuscript.

I, as a co-author, endorse that this level of contribution by the candidate indicated above is appropriate.

Jane Fromont

Co-author 1 (Signature of Co-author 1)

Kylie A. Munyard

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Diana S. Jones

Co-author 3 (Signature of Co-author 3)

To Whom It May Concern,

I, Andrew M Hosie as the first author of the 2021 publication "New species and new records of sponge-inhabiting barnacles from Australia. *Diversity, 13*, 290. https://doi.org/10.3390/d13070290", declare that I was primarily responsible for the design, analyses, interpretation, and writing for this manuscript.

I, as a co-author, endorse that this level of contribution by the candidate indicated above is appropriate.

Jane Fromont

Co-author 1 (Signature of Co-author 1)

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Diana S. Jones

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To Whom It May Concern,

I, Andrew M Hosie as the first author of the 2021 publication "Surveying keratose sponges (Porifera, Demospongiae, Dictyoceratida) reveals hidden diversity of host specialist barnacles (Crustacea, Cirripedia, Balanidae). *Molecular Phylogenetics and Evolution, 161*, 107179. https://doi.org/10.1016/j.ympev.2021.107179", declare that I was primarily responsible for the design, analyses, interpretation, and writing for this manuscript.

I, as a co-author, endorse that this level of contribution by the candidate indicated above is appropriate.

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To Whom It May Concern,

I, Andrew M Hosie as the first author of the unpublished Chapter 5 “Origins of sponge symbiosis and phylogenetic placement of the sponge-inhabiting barnacles”, declare that I was primarily responsible for the design, execution, interpretation, and writing for this chapter.

I, as a co-author, endorse that this level of contribution by the candidate indicated above is appropriate.

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Hosie, A. M., Fromont, J., Munyard, K. & Jones, D. S. (2019) Description of a new species of *Membranobalanus* (Crustacea, Cirripedia) from southern Australia. *ZooKeys, 873*, 25–42. https://doi.org/10.3897/zookeys.873.35421.

Hosie, A. M., Fromont, J., Munyard, K. & Jones, D. S. (2021) New species and new records of sponge-inhabiting barnacles from Australia. *Diversity, 13*, 290. https://doi.org/10.3390/d13070290.

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