Integrative taxonomy and phylogeny of barnacles (Crustacea: Cirripedia) from the Moluccas, eastern Indonesia

Dissertation

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Abstract

Barnacles (Cirripedia) are crustaceans, with sessile adult forms that are permanently attached to hard substrata or to other living organisms. They are adjusted to various lifestyles, from parasites of decapod crustaceans to free-living groups. As cosmopolite animals, barnacles are abundant, with over 1000 species found worldwide in polar, tropical, and temperate waters, from the ocean shore to its depths. However, knowledge of the barnacle fauna of the Maluku Islands, eastern Indonesia (also known as the Moluccas), remains sparse. The lack of studies on barnacles in the Moluccas is unfortunate, given that the exceptionally high marine biodiversity of this region—part of the global epicentre of marine biodiversity—suggests that many barnacle species may not yet have been discovered.

In the doctoral thesis presented here, barnacles from the Moluccas Islands were studied to establish a taxonomic checklist, including information on their morphology, distribution, and substrate. This doctoral thesis is divided into three major sections. In its first section, it focuses on integrative biodiversity discovery of barnacles from the Moluccas, including morphological and molecular data of recently collected material. In the second section, deep-sea barnacles collected from the Moluccas by previous scientific expedition and deposited in the Muséum National d'Histoire Naturelle, Paris were investigated. In the third section of this thesis, a modern non-destructive imaging method, X-ray micro-computed tomography (Micro-CT scanning), was used to study sponge-dwelling barnacles from the Moluccas that still embedded in their sponge host.

The first section provides the most comprehensive overview of barnacle species from the Moluccas Islands to date. Morphological analysis of recently collected material revealed 24 intertidal species and one deep-water species from three families of stalked barnacles (Heteralepadidae: one genus and species; Lepadidae: two genera and species; Pollicipedidae: one genus and species) and four families of acorn barnacles (Pachylasmatidae: one genus and species; Chthamalidae: five genera and species; Tetraclitidae: five genera and eight species; Balanidae: two genera and seven species). Including previous records from the literature, a total of 97 species from the Moluccas Islands are recorded from the superorder Thoracica (free living or epizoic). Of these, 21 species are new records, and two (*Amphibalanus* sp. and *Microeuraphia* sp.) are currently unidentified.

The second section examines the deep-sea barnacles collected by the Karubar expedition (1991) and deposited in the Muséum National d'Histoire Naturelle, Paris. It identifies 40 species from three families of stalked barnacles (Heteralepadidae: two genera, three species; Poecilasmatidae: four genera, five species; Scalpellidae: 12 genera, 21 species) and five families of acorn barnacles (Verrucidae: two genera and species; Pachylasmatidae: one genus and species; Archaeobalanidae: three genera, six species; Pyrgomatidae: one genus and species; Balanidae: one genus and species). Thirty of the species are new records for the Indonesian

Kei Islands and Tanimbar Island, which increases the total number of species recorded from Kei, Aru, and Tanimbar to 40.

The third section explores the sponge-dwelling barnacles of the Moluccas using a modern non-destructive imaging method, X-ray micro-computed tomography (Micro-CT scanning). The results reveal the advantage of using micro-CT scanning when examining sponge barnacles, as their deep anchors in sponge tissue makes it almost impossible to pull out the barnacle without breaking it. Although there are some methodological limitations regarding contrast-enhancing techniques, this study demonstrates that micro-CT is a useful non-destructive technique for the integrative taxonomy of the sponge-inhabiting barnacles.

Overall, this doctoral thesis demonstrates that 126 species now are recorded from the Moluccas Islands, including 46 new records; five further species are proposed. This shows that the Indo-Malayan region (including the Moluccas) has not been replaced by other areas as the centre of benthic biodiversity. However, a comparison of the number of species previously recorded from the Moluccas with those recorded in this study indicates that species diversity for each island has been heavily underestimated. Molecular results also indicate that the barnacle fauna of the region is understudied. Nonetheless, a modern non-destructive imaging method, X-ray micro-computed tomography (Micro-CT scanning) is proven to be a very useful technique for studying the morphology and taxonomy of barnacles from the Moluccas. When paired with classic morphological examination, this technique has the potential to be an extremely useful tool for understanding the integrative taxonomy of barnacles and helping identify further species of barnacles.

Kurzfassung

Rankenfußkrebse (Cirripedia) sind Krustentiere mit festsitzenden adulten Formen, welche dauerhaft an harte Substrate oder an andere lebende Organismen gebunden sind. Sie sind an verschiedene Lebensstile angepasst, vom Parasiten der Zehnfußkrebse bis hin zu den frei lebenden Gruppen. Als kosmopolitische Tiere sind Seepocken in über 1000 Arten weltweit reichlich vorhanden. Sie sind lokalisiert von der Meeresküste bis in die Tiefe des Ozeans, in polaren, tropischen sowie gemäßigten Gewässern. Dennoch sind die Kenntnisse über die Seepockenfauna der Maluku-Inseln im Osten Indonesiens (ebenfalls bekannt als die Molukken) spärlich und lückenhaft. Das Fehlen von Studien über jene Seepockenart auf den Molukken stellt ein Problem von wissenschaftlicher Relevanz dar, denn die bemerkenswert hohe marine Biodiversität dieser Region, die einen Teil des globalen Epizentrums dieser Biodiversität darstellt, deutet darauf hin, dass eine Vielfalt an Seepockenarten möglicherweise unentdeckt geblieben sind.

Im Rahmen der vorliegenden Doktorarbeit wurden Seepocken von den Molukkeninseln untersucht, um eine taxonomische Prüfliste mit Information über deren Morphologie, Verbreitung und dem jeweiligen Substrat zu erstellen. Die Doktorarbeit gliedert sich in drei Hauptabschnitten. Der erste Teil fokussiert sich auf das Material der kürzlich gesammelten molekularen und biogeographischen Daten über die Seepocken und die darauf aufbauende Erstellung der taxonomischen Liste. Der zweite Teil der Dissertation behandelt die Analyse von Tiefsee-Rankenfußkrebsen, die in früheren wissenschaftlichen Expeditionen auf den Molukken gesammelt und in Museumssammlungen deponiert wurden. Im dritten Abschnitt wurde eine moderne zerstörungsfrei Bildgebungsmethode, die Mikro-Röntgen-Computertomographie (Mikro-CT-Scanning), zur Erforschung von schwammbewohnenden Seepocken der Molukken verwendet.

Den bisher umfangreichsten Überblick über die auf den Molukken lebenden Seepockenarten, bietet der erste Abschnitt. Eine morphologische Analyse des kürzlich angeeigneten Materials ergab sowohl vierundzwanzig intertidale Arten, als auch eine Tiefseeart aus drei Familien von gestielten Seepocken (Heteralepadidae: eine Gattung und Art; Lepadidae: zwei Gattungen und Arten; Pollicipedidae: eine Gattung und Art) und vier Familien von Eichel-Seepocken (Pachylasmatidae: eine Gattung und Art; Chthamalidae: fünf Gattungen und Arten; Tetraclitidae: fünf Gattungen und acht Arten; Balanidae: zwei Gattungen und sieben Arten). Unter Berücksichtigung früherer literarischer Aufzeichnungen sind insgesamt 97 Arten von den Molukkeninseln aus der Überordnung Thoracica (freilebend oder epizoisch) erfasst. Darunter fallen einundzwanzig neu erfasste Arten neben zwei derzeit unidentifizierten Arten *(Amphibalanus sp.* und *Microeuraphia sp.).*

Die von der Karubar-Expedition (1991) zusammengetragenen und im Muséum National d'Histoire Naturelle hinterlegten Tiefsee-Rankenfußkrebse werden im zweiten Abschnitt aufgearbeitet. Es werden vierzig Arten aus drei Familien von gestielten Seepocken (Heteralepadidae: zwei Gattungen und drei Arten; Poecilasmatidae: vier Gattungen und fünf Arten; Scalpellidae: zwölf Gattungen und einundzwanzig Arten) und fünf Familien von Eichelrassen (Verrucidae) identifiziert: Verrucidae: zwei Gattungen und Arten; Pachylasmatidae: eine Gattung und Art; Archaeobalanidae: drei Gattungen und sechs Arten; Pyrgomatidae: eine Gattung und Art; Balanidae: eine Gattung und Art. Durch die dreißig neu erfassten Arten erhöht sich die Gesamtzahl der Arten für die indonesischen Kei- und Tanimbar-Inseln auf vierzig.

Der dritte Abschnitt dieser Doktorarbeit befasst sich mit den schwammbewohnenden Seepocken der Molukken, die mit einer modernen zerstörungsfreien Bildgebungsmethode, der Röntgen-Mikro-Computertomographie (Mikro-CT-Scanning), untersucht werden. Die Ergebnisse deuten auf den Vorteil des Mikro-CT-Scannings bei der Untersuchung von Schwamm-Seepocken, da diese es ermöglicht die Seepocke aus ihrer tiefen Verankerung im Schwammgewebe zu befreien, ohne sie dabei zu zerbrechen. Obwohl bei kontrastverstärkenden Techniken diverse methodische Einschränkungen bekannt sind, erweist sich die Studie als nützlich für das Verständnis über Mikro-CT als zerstörungsfreie Technik für die integrative Taxonomie der schwammbewohnenden Seepocken.

Zielsetzung dieser Doktorarbeit ist das Darstellen der nun bekannten 126 Arten auf den Molukken-Inseln, worunter sich 46 neue Datensätze und 5 weitere bislang vorgeschlagene Arten befinden. Dadurch lässt sich nachweisen, dass die Region Indo-Malayan (inklusive der Molukken) fortwährend als Zentrum der benthischen Biodiversität bestehen geblieben ist und nicht von einem anderen Gebiet überholt wurde. Vergleicht man jedoch die in dieser Studie zusammengetragenen Daten mit der Anzahl der früher auf den Molukken nachgewiesenen Arten, offenbart sich eine starke Unterschätzung der Artenvielfalt der individuellen Inseln. Die molekularen Ergebnisse deuten ebenfalls auf eine schwache Erforschung der Seepockenfauna in jener Region. Nichtsdestotrotz konnte die Mikro-Röntgen-Computertomographie als eine effektive Technik zur Analyse der Morphologie und Taxonomie von Seepocken von den Molukken sichergestellt werden. In Assoziation mit der klassischen morphologischen Untersuchung besitzt diese Technik das Potenzial, um sich als vorteilhaftes Instrument zum Verständnis der integrativen Taxonomie von Seepocken herauszukristallisieren und zur zukünftigen Identifizierung weiterer Seepockenarten beizutragen.

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Chapter I

General introduction

1.1 Preface

Barnacles, belonging to subphylum Crustacea, are an ancient group that have endured and flourished; approximately 1,400 extant species are known, and although they are almost exclusively marine, a few species can tolerate the reduced salinity environments of bays, estuaries, and similar habitats (Newman and Abbot, 1980; Van Syoc, 2019). Barnacles often form a dense carpet-like layer, coating the surface of the sediment in the middle of the intertidal zone (Stephenson & Stephenson, 1972). An abundance of barnacles can be found, for example, on the Florida shelf, where 50% of carbonate sediments were built by barnacles (Milliman, 1974). According to Newman (1987), barnacles have an advantage compared with many other invertebrates in biogeographical studies because there is reasonable agreement on their phylogeny; the group has a well-preserved fossil record, beginning in the Palaeozoic, becoming stratigraphically useful in the Mesozoic, and being well represented in the Cenozoic.

The most diverse region in the world for marine species is the East Indies Triangle, a region including Indonesia, Philippines, Malay Peninsula, and New Guinea (Briggs, 1999). However, research on barnacles in this region remains very limited, particularly in the Moluccas, eastern Indonesia. The lack of studies on barnacles in this region is unfortunate, considering that the exceptionally high marine biodiversity of this region suggests that many barnacle species may have not yet been discovered. This area lies on the collision zone of the Asian and Australian continents, which have been separated for an extensive period (Turner et al., 2001). The region’s high diversity is believed to be partly due to the Indonesian Throughflow (ITF), the vast mass of seawater that flows from the Pacific Ocean to the Indian Ocean, as well as the counter-intake from the Indian Ocean to the South China Sea through Malacca Strait. The mixture of these two oceans, as well as the above-mentioned continental shelves, Australian (of Gondwanaland origin) and Eurasian (of Laurasian origin), contribute to making the East Indies Triangle a biodiversity hotspot (Hoeksema, 2013).

The absence of occurrence, distribution, and biogeographic data regarding barnacles in the Moluccas, a biodiversity hotspot area, has highly motivated me to study the topic.

1.2 Scientific background

1.2.1 The Moluccas, eastern Indonesia

The Indonesian archipelago of the Moluccas (also known as the Maluku Islands) is also known as the Spice Islands, as these islands were the only or best sources of spices such as cloves, nutmeg, and mace until the 1700s (Delaney, 2010). Geographically, the Moluccas lie between the island of Sulawesi to the west; New Guinea to the east; the Philippine Sea and the Pacific Ocean to the north; the Arafura Sea and the Timor Sea to the south; tectonically, they are located on the Halmahera Plate, within the Moluccas Sea Collision Zone (Kastanya, 2019).

The Moluccas (Figure 1.1) were administratively one province until 1999, when they were divided between Maluku Province and North Maluku Province. Maluku Province lies between 2°30' – 9° S latitude and 124° – 136° E longitude; it consists of 1,340 islands with an area of 712,479.65 km^2, including a land area of 54,185 km^2 (7.6%), a sea area of 658,294.69 km^2 (92.4%), and a coastline 10,622 km long. Its most prominent islands are Seram, Buru, and Ambon; other large islands include Banda, Kei, Aru, Tanimbar, and Wetar (https://maluku.bps.go.id/ProvinsiMalukudalamangka2019.html; Kastanya, 2019; Yushantarti and Rezky, 2020).

North Maluku Province lies between 3° N latitude and 3° S latitude, and from 124° – 129° E longitude. It consists of approximately 600 islands and covers an area of 140,255.36 km^2, which includes a land area of 33,278 km^2 (23.73%) and a sea area of 106,977.32 km^2 (76.27%). Its most prominent islands are Halmahera, Morotai, Taliabu, Mangole, Sulabesi, Ternate, and Tidore (https://malut.bps.go.id/ProvinsiMalukuUtaradalamangka2019.html; Kastanya, 2019; Yushantarti and Rezky, 2020).

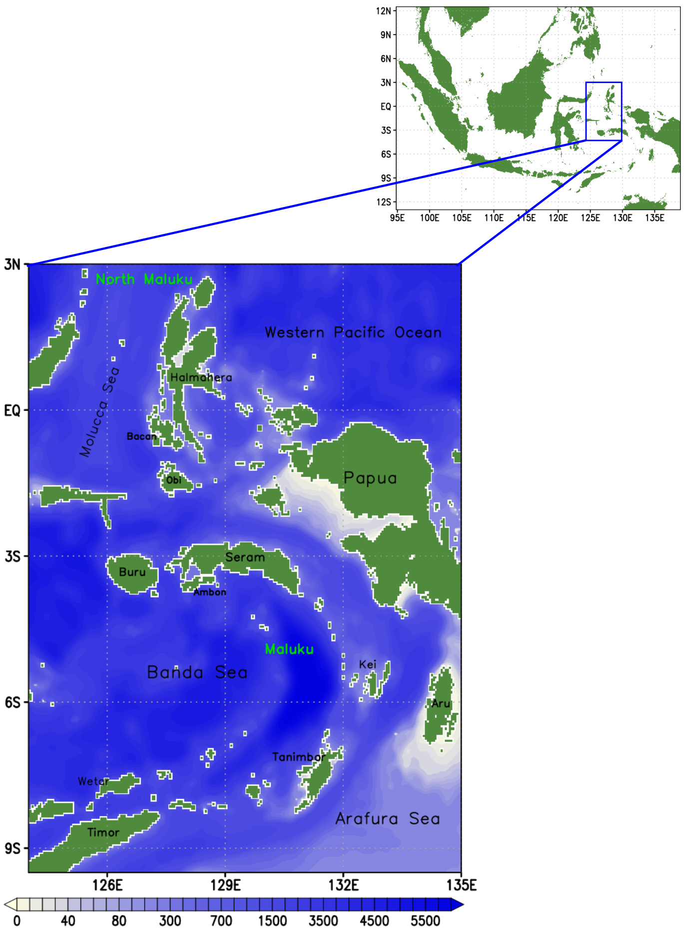

Figure 1.1. Map of the Moluccas showing Maluku Province and North Maluku Province. Map modified from Gebco Digital Atlas Team (2003). Map courtesy of Abdul Basit.

The geology of the Moluccas is complicated. In the general, these islands have been formed through the gradual impact of the Sunda Plate and the Australian Plate as well as through volcanic processes. Seven different island groups represent different elements of the Moluccas' complicated tectonic system. The first is Halmahera, which is a mixture of Plio-Pleistocene volcanic arcs and linked to an older impact complex that formed on the front edge of the Irian spur, moving westward from the Australian plate. The second group consists of the Banggai Islands, Sula Islands, and Bacan Islands, which represents small pieces of the Irian spur that have separated and collided with eastern Sulawesi after moving about 1,000 km westward; to the north and south, these islands are bound by crack lines and consist of a Palaeozoic granite base covered by Mesozoic metamorphic rocks. The third group of islands, which is dominated by Buru and Seram Island, represent Palaeozoic and old Mesozoic volcanic complexes on the front edge the Australian plate and resembles Halmahera. The fourth group is centred around Obi Island, which has geological features similar to Buru Island. The fifth spans from Wetar Island to the Banda Islands, which were formed from Quaternary volcanoes that have developed over the subduction zone of the Australian plate. The sixth group, which reaches from the Leti Islands to Tanimbar, Kai, Watubela and Gorong Island, consists of a mélange formed from the mixture of tertiary younger deposits and materials of an ancient continent that originated from the margins of the Australian plate. The last is the Aru Archipelago; these islands are the only ones that are not directly controlled by plate tectonic events, being composed of young sedimentary structures located on the shallow Arafura Seabed (Center for Data, Statistics and Information of the Secretariat General of the Ministry of Marine Affairs and Fisheries, Republic of Indonesia, 2013).

Although the Moluccas is far from the European centres where most of the formal work in natural science was occurring from the 15th through the mid-19th centuries, this archipelago and its surrounding seas have contributed importantly to the history of natural science (Lamoureux, 1990). Georg Everhard Rumpf (1627 or 1628–1702) and Alfred Russel Wallace (1823–1913) are probably the most renowned natural scientists whose ideas and publications reflect the contributions of the natural phenomena that they observed in the Moluccas (Strack, 1993; Glasby & al Hakim, 2017). After Rumphius's death in 1702, there was a vacuum in marine research activities in the Moluccas waters until the early 19th century, when many international research and scientific expeditions were conducted in the region. These included, for example, the Astrolobe expedition (1826–1829), research by Pieter Bleeker (1852–1874) which produced 90 scientific papers regarding fish in the Moluccas, and the Swiss expedition to Ambon Bay by M. Bedot and C. Pictet in 1890 (Tapilatu & Syahailatua, 2017; Strack, 1993).

The Moluccas have been a frequent destination for explorers, from the first circumnavigation voyages to modern scientific expeditions. There is recorded that the ships of Magellan (1521) and Francis Drake's *Golden Hind* (1579) landed in Ternate, one of the islands in the Moluccas (Lamoureux, 1990). Since then, at least fifty expeditions have visited the Moluccas, primarily for scientific exploration. Some important marine scientific expeditions in the Moluccas have included the famous British *Challenger* Expedition (1872–1876), which is considered the foundation of modern oceanography; the Dutch *Siboga* Expedition (1899–1900), which produced the first bathymetric map; the Danish *Mortensen* Expedition to the Kei Islands (1914–16), which suggested that the archipelago was an ideal place for a marine laboratory to study deep-sea fauna; the Dutch *Snellius* I Expedition (1929–1930), which was primarily a geological expedition; and the Danish *Galathea* Expedition to the Banda Sea (1950–1952). The most recent expedition, the French *Karubar* Expedition of 1991, focused on exploring deep-sea benthos in the Moluccas (Lamoureux, 1990; Strack, 1993; Nontji, 2009).

1.2.2 Barnacles (Crustacea, Cirripedia)

1.2.2.1 General description and taxonomy

Barnacles have been known since ancient times (Igić, 2007). In the Middle Ages, Europeans used Aristotle's mistaken observations to explain the arrival of barnacle geese each fall from their high Arctic breeding grounds as the transformation of the goose-neck barnacles commonly found on floating driftwood (Wilson, 2014). In 1758, Linnaeus described the order Thoracica of barnacle as "Vermes testacea", and Lamarck (1818) described barnacles as "Crustaces conchyliferes". Later barnacles were classified as molluscs, per Cuvier (1830), who argued that Thoracica are modified molluscs ("Cirrhopoda-Mollusca") due to their hard shells. However, based on their larval development, Strausse (1810), Thompson (1830), and Burmeister (1834) identified barnacles as crustaceans.

This past confusion can be attributed to the drastic adaptations that distinguish barnacles from all other crustaceans. Not only are barnacles the only sessile group of crustaceans, they also have significant morphological differences. Barnacles do not have an exoskeleton like other crustaceans, but rather possess a protective shell that consists of mineralised shell plates. These realities were observed by Charles Darwin, who comprehensively studied barnacles for eight years from 1846 to 1854 and produced four incomparable monographs on extant barnacles (Darwin 1851a; 1854a) and fossil barnacles (Darwin 1851b; 1854b). Through these four monographs, Darwin presented an understanding of barnacles that remains the foundation of studies today. Owing to his observations and taxonomic description of barnacles, Darwin has been recognised as history's greatest cirripedologist (Anderson, 1994).

Nonetheless, as knowledge has advanced, the classification of barnacles has continued to change. Newman (1987) placed barnacles under the superclass Maxillopoda and class Thecostraca. According to Anderson (1994), maxillopodan crustaceans are crustaceans with six head segments, six thoracic segments, and five abdominal segments; while Thecostraca includes all maxillopodans with a bivalve carapace and a reproductive system, usually hermaphroditic, which includes paired female openings on the first thoracic segment. The superclass Multicrustacea constitutes the largest superclass of crustaceans, containing approximately four-fifths of all described crustacean species, including barnacles (Regier et al., 2010). This classification, however, has changed based on recent work which indicates that Maxillopoda is not monophyletic (Regier et al. 2005), leading to the redefinition of Thecostraca's taxonomic placement within Arthropoda (Newman 1992; Regier et al. 2010; Oakley et al. 2013). Recent works using multiple lines of evidence have placed Thecostraca together with two other subclasses in the class Hexanauplia (Regier et al. 2010; Oakley et al. 2013).

Even though the higher classification of barnacles has changed, the majority of barnacles still fall under the classification of Cirripedia, as defined by Burmeister in 1834. Based on generally agreed recent advances, this study employs the following classification:

Kingdom	: Animalia
Phylum	: Arthropoda von Siebold, 1848
Subphylum	: Crustacea Brünnich, 1772
Superclass	: Multicrustacea Regier, Shultz, Zwick, Hussey, Ball, Wetzer, Martin & Cunningham, 2010
Class	: Hexanauplia Oakley, Wolfe, Lindgren & Zaharof, 2013
Subclass	: Thecostraca Gruvel, 1905
Infraclass	: Cirripedia Burmeister, 1834
Superorder	: Acrothoracica Gruvel, 1905
Superorder	: Rhizocephala Müller, 1862
Superorder	: Thoracica Darwin, 1854

The superorder Acrothoracica is a small group in Cirripedia with cirri bunched terminally at the end of the thorax; and the superorder Rhizocephala is a group of parasitic barnacles without cirri. The most abundant is the superorder Thoracica, which are characterised by six pairs of cirri spread along the length of a well-developed thorax (Anderson, 1994). All Thoracica are permanently attached as adults. Many form symbiotic associations with larger organisms such as whales, turtle, lobsters, corals, and sponges, and a few become dependent on their hosts for nutrition, support, and protection (Krüger, 1940; Newman, Zullo & Withers, 1969).

Thoracic barnacles, also called true barnacles, are considered the most ecologically important because of their abundance and conspicuousness (Newman and Abbott, 1980). There are two major morphological variants within Thoracica, i.e. acorn or sessile barnacles and stalked or pedunculata barnacles. According to Anderson (1994), pedunculata barnacles have an obvious peduncle between the basal attachment disc and plated apex, while in acorn barnacles the peduncle has been replaced by a broad basis. In stalked barnacles, the body is divided into two major parts: a capitulum (containing cirri, mouthparts, and most other organs) and a peduncle/stalk by which the animal is attached to the substratum. In sessile barnacles, meanwhile, the body lacks a peduncle; in the capitulum, certain plates become articulated to form a rigid wall, while others (anteriorly the scuta, posteriorly the terga) form a movable lid or operculum.

Buckeridge and Newman (2006) revised the Pedunculata barnacles into four orders: the Ibliformes, Cyprilepadiformes, Lepadiformes and Scalpelliformes. The bivalved Cyprilepadiformes, restricted to the Silurian (Wills, 1963), are certainly very distinct. Anderson (1994) recognized *Ibla* as distinct from Thoracica, and proposed a new superorder, the Prothoracica, to accommodate that sole genus. However, *Ibla* appears to be a thoracican cirripede, and related to *Eolepas* and separated from other living Thoracica by fossil forms such as *Praelepas* (Newman et al. 1969, Høeg et al., 1999). The genetic work of Pérez-Losada, et al., (2004), places *Ibla* as a sister group to other thoracicans. These results strengthen the assessment that *Ibla* is a part of Thoracica. Therefore, the superorder Thoracica Darwin, 1854 now consists of five orders, i.e. Cyprilepadiformes Buckeridge and Newman, 2006; Ibliformes Buckeridge and Newman, 2006; Lepadiformes Buckeridge and Newman, 2006; Scalpelliformes Buckeridge and Newman, 2006; and Sessilia Lamarck, 1818.

1.2.2.2 Distribution

Barnacles are abundant, with over 1000 species found in polar, tropical, and temperate waters worldwide, from the shore to the depths of the ocean (Fertl and Newman, 2009). They have adjusted to various lifestyles, from parasites of decapod crustaceans to free-living groups. Barnacles also have one of the best fossil records of the crustacea, extending from Middle Cambrian Burgess Shale to the Recent era (Newman, 1979; Schram, 1982). The most abundant number of thoracicans were found in the Mesozoic and Cenozoic and extends back to the Upper Silurian. Although it appears that cirripeds are an old group, extending well back in the Palaeozoic, the great radiation of calcareous forms may not have begun until the Triassic era (Whyte, 1976; Schram, 1982).

As burrowing barnacles, acrothoracicans are generally very small and show their greatest diversity in coral seas (Tomlinson, 1969). Their fossil record is known from the Late Devonian to the Recent era, but the only definitely identifiable acrothoracican is *Typetesa caveata*, in Late Palaeozoic myalinid clams (Rodriguez and Gutschick, 1977; Schram, 1982). On the other hand, the distribution of extant acrothoracican is cosmopolitan, with the largest number of species found in the Indo-West Pacific (Tomlinson 1969, 1973).

Rhizocephalan barnacles are a purely parasitic group that is found exclusively on crustaceans, primarily decapods. This order is probably the poorest known of the cirripeds, and has no fossil record (Schram, 1982; Abele, 1982).

As the most abundant Cirripedia, the Thoracica can be found in all marine environments, from the highest reaches of the tides to the depths of the oceans. Some Thoracica can be found in estuaries, but none completes its life cycle in freshwater. Their diversity is greatest in the tropical Indo-Pacific, less in the northeast Pacific, and far less in the North Atlantic (Cornwall, 1951, 1955; Henry, 1940, 1942; Ross, 1962; Zullo, 1966). There is a latitudinal pattern in these cirripeds, where the number of species of littoral thoracicans increases with decreasing latitude (Nilsson-Cantell 1938, 1978; Stubbings, 1967; Newman and Ross, 1971;

Spivey, 1981). There is also a longitudinal pattern, with the number of species increasing in the order Eastern Atlantic, Western Atlantic, Eastern Pacific, and Indo-West Pacific, as shown by the *Amphibalanus amphitrite* complex (Henry and McLaughlin, 1975).

1.3 Aims and objectives of the thesis

The main goal of this doctoral thesis is to provide an integrative taxonomic approach of barnacles from the Moluccas, including information on their morphology, distribution, and substrate. This thesis is divided into three major sections. The first seeks to establish a taxonomic checklist of barnacles from the Moluccas, eastern Indonesia, including molecular phylogeny and distribution data from recently collected material and previous records. The second examines deep-sea barnacle material collected from the Moluccas through the *Karubar* expedition (1991), which has been deposited at the Muséum National d'Histoire Naturelle (MNHN), Paris, but remained unstudied today. The third explores a new method for studying sponge-dwelling barnacles from the Moluccas, using X-ray micro-computed tomography (Micro-CT scanning), a modern non-destructive imaging method. This thesis seeks to answer the following key questions:

- How many species of Moluccan barnacles were recently collected?
  How many were already described? Are there new species or first records?
- How are the species from the checklist related? Are the morphologically characterized species supported by the molecular results?
- How many species of deep-sea barnacles were collected from the Moluccas Islands by the *Karubar* expedition (1991) and deposited in the Muséum National d'Histoire Naturelle (MNHN), Paris?
- Does an innovative imaging method like X-ray micro-computed tomography (Micro-CT scanning) allow a non-destructive study of the shell morphology of sponge-inhabiting barnacles? What are the differences compared to a conventional light microscopy approach?

This doctoral thesis consists of three research articles (three chapters and one additional data publication) that were written for and submitted to international peer-reviewed journals and the MfN Data Repository in Berlin. The first manuscript was published in *ZooKeys* and the second one was published in *Zoosystematics and Evolution*; the third manuscript has been submitted to *Treubia* and currently is under review. Chapter 1.4 below provides an overview of these three manuscripts and one published data repository of micro-CT scanning results.

1.4 Material and methods

1.4.1 Fieldwork

Fieldwork was undertaken during nineteen field trips to the intertidal zones of the Moluccan islands of Ambon, Saparua, Seram, Pombo, and Banda Neira, conducted between January 2016 and September 2017. Sampling was carried out at 24 localities in Ambon Island, 12 localities in Saparua Island, 7 localities in Seram Island, 4 localities in Pombo Island, and 2 localities in Banda Island. Additional material for molecular analysis and micro-CT scanning was collected from the island of Sulawesi between September and October 2017. Access to the deep-sea barnacle collection of the Muséum National d'Histoire Naturelle (MNHN), Paris, was undertaken between 1 and 14 September 2019.

Barnacles were collected by directly extracting them from their natural and artificial substrate in the sampling sites while snorkelling for underwater samples. Barnacle specimens firmly attached to a hard substrate (rocks, stone, concrete) were sampled using a chisel and hammer, whereas those attached to the softer substrate were sampled using a craft knife. The sample of barnacles was then put in a labelled plastic bag, with 96% ethanol added as a fixative, before being placed in a plastic container. After a day, the ethanol was replaced with the new ethanol solution. The ethanol replacement was repeated up to three times, before the specimen was transferred into 75% ethanol for long-term preservation.

1.4.2 Morphological analysis

The specimen of barnacle were determined at the Museum für Naturkunde Berlin using classical systematics by observing the morphology of its hard parts, such as the shell (parietes) and the cover shell (opercular plates); and soft body, such as the mouth part (trophy) and the filter legs (cirri). Observation of the hard parts was done using a stereomicroscope, whereas the anatomy of the soft body was observed using light microscopy. In this study, classical systematics was combined with biometric methodology using digital callipers (accurate to 0.1 mm), and many characters were utilised.

Characteristics measured through biometrics were basal length of shell, basal width, orifice length, orifice width, and carinal height (for acorn barnacles); total height, capitular height, diameter of the base of the capitulum, carina and scutum distance, scutal length, scutal width, tergal length and tergal width (for stalked barnacles); capitular height, capitular width, peduncular length, orifice height, number of crests, capitular thickness, and peduncular width (for deep-sea barnacles of *Heteralepas*); the number of teeth on upper lip (labrum), their average number on both sides of the labrum; the number of teeth or setae on the maxillule, the average number of spines between the upper and the lower pair; and the number of teeth on the mandible.

Species identification was conducted according to the classification and description of the species by Darwin (1852, 1854), Hoek (1883, 1907, 1913), Pilsbry (1890, 1907, 1916), Annandale (1905, 1906, 1908, 1909, 1910, 1913, 1916), Broch (1916, 1922, 1931), Calman (1918, 1919), Newman and Ross (1971, 1976), Foster (1974, 1978, 1980, 1981), Rosell (1981, 1989, 1991), Kolbasov (1993), Southward and Newman (2003), Chan et al. (2007), Pérez-Losada (2008, 2014), Chan et al. (2009, 2010), Shalaeva and Boxshall (2014), Tsang et al. (2015), and Chan et al. (2017).

1.4.3 Molecular phylogenetic analysis

Genomic DNA was extracted from the adductor muscle tissue using a CTab isolation buffer following the method of Doyle and Doyle (1987). This study used two gene fragments, cytochrome oxidase subunit I (COI) and 18S ribosomal RNA gene (18S). COI was sequenced using the primers LCO1490 (5'-GGT CAA CAA ATC ATA AAG ATA TTG G-3') and HCO2198 (5'-TAA ACT TCA GGG TGA CCA AAA AAT CA-3') (Folmer et al. 1994), and 18S using the primers ai (5'-CCT GAG AAA CGG CTA CCA CAT C-3') and 7R (5'-GCA TCA CAG ACC TGT TAT TGC-3') (Whiting 2002). PCR was conducted and the products were sent to Macrogen Europe for cycle sequencing of both strands of each gene. Chromatograms were edited using CodonCode Aligner version 5.1.5 (http://www.codoncode.com) for COI and Geneious 11 (http://www.geneious.com) for 18S. All new DNA sequences generated for this study were deposited in GenBank. For comparison, 84 COI sequences and 88 18S sequences of related barnacles were downloaded from GenBank. Sequences were aligned using Muscle (Edgar 2004), as implemented in Geneious and later exported as nexus or fasta files. Phylogenetic trees were reconstructed for each gene using both Maximum Likelihood (ML) and Bayesian Inference (BI). ML analyses were conducted using RAxML Black Box (Stamatakis et al. 2008), with 100 bootstrap replicates and under the GTR + I + G model of sequence evolution. Bayesian analyses were conducted in BEAST 2. Genetic distances (K2P) were calculated using MEGA version X (Kumar et al. 2018). All molecular work was done at the Museum für Naturkunde Berlin.

1.4.4 X-ray micro-computed tomography and 3D reconstruction

3D-data sets were obtained via µCT using an FF35 Scanner (Yxlon, Hamburg) at the Museum für Naturkunde Berlin. Scans were performed with the following parameters: e.g. 80 kV, 15 W, 16 µm voxel size, 2000 projections/turn helical CT. For all of the example data sets, raw files were produced with the help of the software VGStudio Max (Volume Graphics, Heidelberg, Germany).

For subsequent processing of the reconstructed 3D-data, the software Amira 6.0.0 was used. Segmentation was carried out with the magic wand tool to mark the barnacles inside the sponges. Each segmented barnacle was assigned a different "label", making it possible to differentiate between single barnacles by assigning different colours to individual labels. Switching back to project mode and using the "Volren" volume renderer, the opacity of the surrounding medium was adjusted so that the barnacles were clearly visible.

1. 5 Overview of the integrated manuscripts

This dissertation is written in a cumulative form and consists of three separate manuscripts and one published data repository (Chapters 2-4), which have been published in international peer-reviewed scientific journals (for Manuscript 1 and 2), submitted for publication in such a journal (for Manuscript 3) and published in the MfN Data Repository Berlin. Table 1.1 provides the title and authorship, selected scientific journal, and publication status of each manuscript.

Table 1.1: Overview of the three manuscripts presented in this thesis

Chapter	Title / *Authorship*	Journal / *Status*
2	**An annotated checklist and integrative biodiversity discovery of barnacles (Crustacea, Cirripedia) from the Moluccas, East Indonesia**	***ZooKeys*, Volume 945, pp. 17–83 doi: 10.3897/zookeys.945.39044**
	Pipit Pitriana, Luis Valente, Thomas von Rintelen, Diana S. Jones, Romanus E. Prabowo, Kristina von Rintelen	*published: 3 July 2020*
3	**New insights gained from museum collections: Deep-sea barnacles (Crustacea, Cirripedia, Thoracica) in the Muséum National d'Histoire Naturelle, Paris, collected during the *Karubar* expedition in 1991**	***Zoosystematics and Evolution*, Volume 96, Issue 2, pp.649–698 doi: 10.3897/zse.96.55733**
	Pipit Pitriana, Diana S. Jones, Laure Corbari, Kristina von Rintelen	*published: 28 September 2020*
4	**Exploring sponge-inhabiting barnacles of eastern Indonesia using Micro-CT scanning**	***Treubia***
	Pipit Pitriana, Andreas Wessel, Tina Aschenbach, Kristina von Rintelen	*submitted: 9 September 2020*
	Non-invasive 3D visualization of the sponge-inhabiting barnacle *Acasta sulcata* (Crustacea, Cirripedia, Balanomorpha) from the Moluccas, Indonesia. [Dataset]**.**	***Data Publisher: Museum für Naturkunde Berlin (MfN) - Leibniz Institute for Evolution and Biodiversity Science*. https://doi.org/10.7479/87tp-gr35.**
	Pipit Pitriana, Kristina von Rintelen, Andreas Wessel.	*published: 17 September 2020*

1.6 Contribution to the individual manuscripts

Pipit Pitriana is the main author of all manuscripts (chapters 2, 3 and 4) and predominantly planned, wrote and accomplished them. She collected all samples from the Maluku Islands, Indonesia and also conducted the research visit to the Muséum National d'Histoire Naturelle (MNHN), Paris, in order to study deep-sea barnacles collected by the Karubar expedition (1991). She treated all barnacle samples in the laboratory, identified the taxa, analysed the samples, took pictures of the specimens, and wrote, finalised, and published the manuscripts. Pipit Pitriana's contribution to each manuscript is given in Table 1.2.

Table 1.2: Overview of the author's contribution to each manuscript.

Chapter/ Manuscript	Contribution of Pipit Pitriana [%] conception	accomplishment	publication
2/ 1	90	80	85
3/ 2	90	80	90
4/ 3	90	90	90

CHAPTER 2

An annotated checklist and integrative biodiversity discovery of barnacles (Crustacea, Cirripedia) from the Moluccas, East Indonesia

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2.1 Abstract

To contribute to the taxonomic knowledge of barnacles in this understudied area, the first checklist of barnacles from the Moluccas Islands is presented, including additional information on morphology, distribution, and substrate as well as molecular data. The species of barnacles from the Moluccas have been determined using morphological analysis and DNA sequences. During 19 field trips conducted between January 2016 and September 2017, 1,513 specimens of 24 species of intertidal and one species of deep-sea barnacles were collected from 51 localities from the islands. Morphological and molecular analysis of the collected material detected members of three families of stalked barnacles and four families of acorn barnacles. In addition to sampling in the field, we also surveyed the literature on barnacles

from the Moluccas Islands. In total, our checklist comprises 97 species from the Moluccas including 23 new records, two of them yet to be described species. Results suggest that the Moluccas have a much higher diversity of barnacles than previously known, for example, from the reports of *Challenger* and *Siboga* expeditions. For further work, routine application of molecular systematics could aid the detection of cryptic species, while increased sampling of more islands and a taxonomic revision of several groups would likely lead to an even higher number of species than currently known.

2.2 Introduction

Barnacles (Crustacea: Cirripedia) are an ancient, species-rich and abundant group of crustaceans with about 1,400 extant species (Newman and Abbott 1980). They have a worldwide distribution in tropical and temperate marine environments and at different depths and are adjusted to various lifestyles, from parasites of decapod crustaceans to free-living groups. Most cirripeds usually have two free-swimming planktonic larval stages consisting of distinctive nauplii and a unique non-feeding cyprid (Darwin 1852, 1854; Pochai et al. 2017). In the most abundant group, the Thoracica, adult specimens are permanently attached to various types of substrates, other living organisms (e.g., mangroves, corals, molluscs, other barnacles, sponges), rocks, and man-made materials such as cargo ships and concrete walls (Newman and Abbott 1980; Power et al. 2010). The Thoracica comprise the orders Cyprilepadiformes, Ibliformes, Lepadiformes, Scalpelliformes, and Sessilia (Buckeridge and Newman 2006).

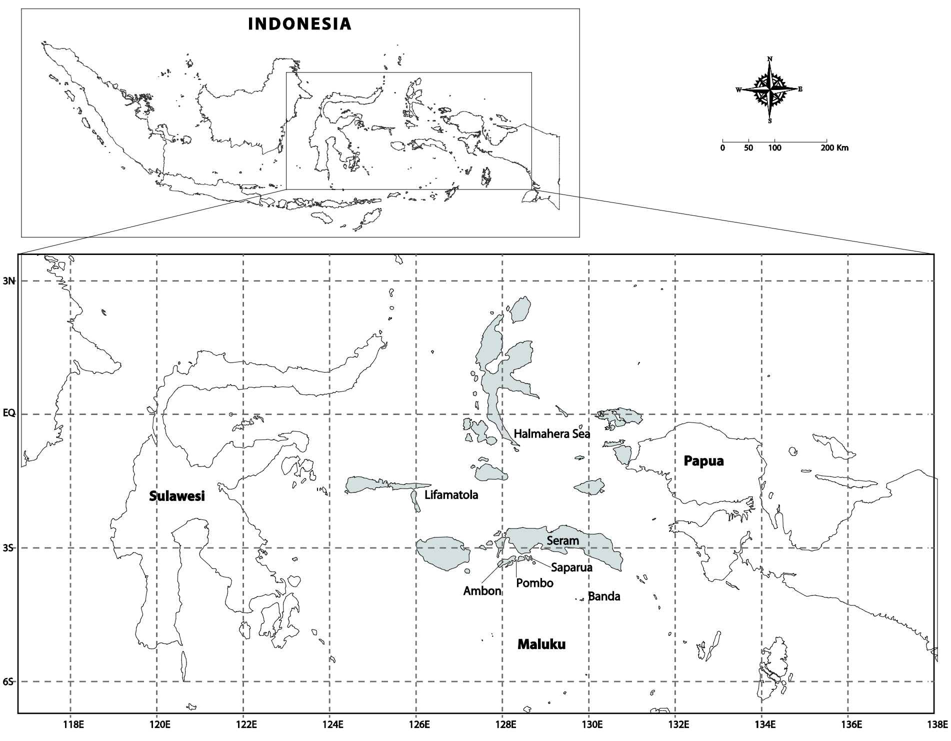

Figure 2.1. Map of the Moluccan Islands (Maluku in grey) in eastern Indonesia. Map modified from Shorthouse (2010).

The Indonesian Moluccas (or Spice Islands; Fig. 2.1) are part of the Coral Triangle, one of the most complex biogeographical and oceanographic areas on Earth. Although part of the global epicentre of marine biodiversity, knowledge of the barnacle fauna of the Moluccas Islands is relatively sparse. The exploration of the natural history of the Moluccas Islands dates back to the 17th century, starting with Georg Everhard Rumphius, and later, for example, Alfred Russel Wallace (Strack 1993; Lamoureux 1990). In the 19th and 20th centuries, there were approximately fifty scientific expeditions passing through or specifically targeting the area, such as the British *Challenger* (1872-1876), the Dutch *Siboga* (1899-1900) and the *Snellius* (1929-1930) expeditions (Lamoureux 1990). The most recent being the French *Karubar* expedition in 1991 (Crosnier et al. 1997).

Rumphius provided the first record of a barnacle (the stalked *Mitella* Oken, 1815 (= *Capitulum*, Gray, 1825) found on a rock near the beach at Ambon Island) in his posthumously published 'Amboinsche Rariteitkamer' (Rumphius 1705). Indonesian and Moluccan barnacles were also studied by Darwin (1854), who assigned them to one of four geographical 'provinces', the third being the East Indian Archipelago. Moluccan barnacles have not been studied since Buckeridge (1994) examined some material from the *Karubar* expedition.

To contribute to the taxonomic knowledge of this understudied area, we herein present the first checklist of barnacles from the Moluccas Islands, including additional information on morphology and molecular data, as well as distribution and substrate.

2.3 Material and methods

2.3.1 Sampling

Specimens examined in this study were collected by the first author during 19 field trips between January 2016 and September 2017 to the intertidal zones of the Moluccan islands of Ambon, Saparua, Seram, Pombo, and Banda Neira (Fig. 2.1, Table 2.1, Supplementary Table 7.1). Deep-water barnacles (Table 2.1) from the Lifamatola Passage (250 m) and Halmahera Sea (250 m) were provided by Nurul Fitriya. Additional material used for the molecular analyses was collected from the island of Sulawesi in September to October 2017 (Supplementary Table 7.1). In total, 159 lots containing 1,513 specimens were collected from 51 Moluccan localities.

Barnacle specimens firmly attached to hard substrate (rocks, stone, concrete) were sampled using a chisel and hammer whereas those attached to softer substrate using a craft knife. Specimens were fixed and stored in 96% ethanol and transferred into 75% ethanol for long-term preservation.

2.3.2 Morphological analyses

For detailed morphological analyses, all samples were studied at the Museum für Naturkunde in Berlin (**ZMB**), Germany. All specimens are deposited at the Museum Zoologicum Bogoriense (**MZB**; Supplementary Table 7.1), Research Center for Biology, Indonesian Institute of Sciences – **LIPI**, Indonesia. Barnacle species attached to other barnacle species were not separated (except for specimens dissected and measured) but were kept within the same glass container, enabling further morphological studies of different species attached to each other, e.g., with MicroCT scans.

Specimens were studied by the first author. All species were determined based on external shell morphology, including the pattern of the parietes, opercular plates, mouth parts, and arthropodal characters, as described by Darwin (1852, 1854), Hoek (1907, 1913), Southward and Newman (2003), Chan et al. (2007), Pérez-Losada (2008, 2014), Chan et al. (2009a), Tsang et al. (2015), and Chan et al. (2017).

Hard body parts (parietes and opercular plates) were separated from soft body parts using a scalpel. Shell plates were separated and cleaned with a bleach solution to remove any organic material, rinsed with fresh water, dried and observed under a stereo microscope (Leica M125) and photographed with a digital camera (Leica Microsystems M205C and Leica Z16 APo-A) (Fig. 2.2).

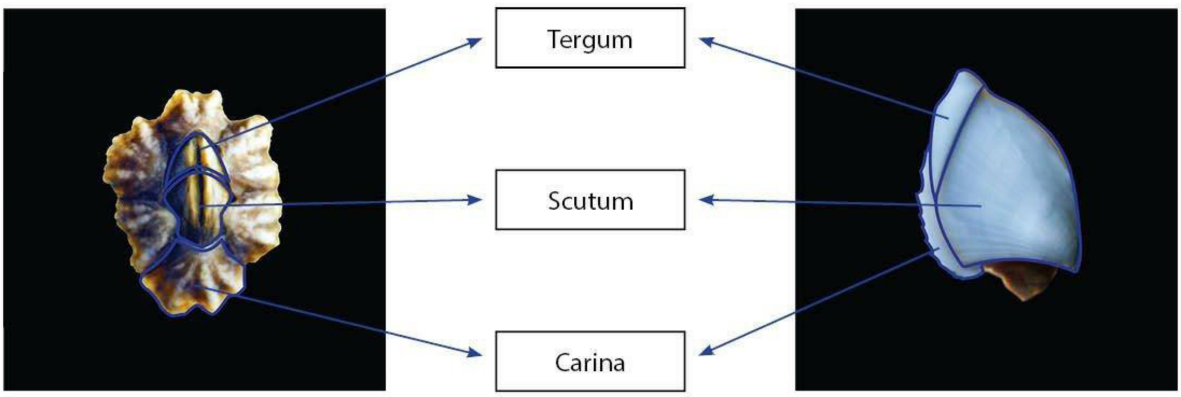

Figure 2.2 External morphology of barnacles showing the two parts of the operculum (tergum and scutum) and carina (without scale).

The mouthparts (labrum, palps, maxilla, maxillule, and mandible) were dissected using a scalpel, each was mounted on a glass slide and examined under a light microscope (Axioskop 20). The cirri were separated into couples of cirri I-VI and the penis, before being mounted on glass slides. The anatomy of these soft body parts was studied using a light microscope.

All measurements were made using digital callipers (accurate to 0.1 mm; Supplementary Tables 2-26) generally following the method described in Beşir and Çınar (2012): basal length of shell, basal width, orifice length, orifice width, and carinal height. For stalked cirripeds, measurement of total height, capitular height, diameter of the base of the capitulum, carina and scutum distance, scutal length, scutal width, tergal length and tergal width were taken following the method described by Igić (2007). For deep-water barnacles, capitular height, capitular width, peduncular length, orifice height, number of crests, capitular thickness, and peduncular width were taken following the method described by Chan et al. (2009b).

2.3.3 Molecular phylogenetic analyses

We performed molecular phylogenetic analyses including new DNA sequences from our new samples from the Moluccas in combination with sequences of multiple barnacle specimens retrieved from GenBank. Our aim with the molecular analyses was not to provide a robust phylogeny of barnacles or to develop DNA barcodes for Moluccan barnacle taxa. Instead, our goal was to confirm the molecular taxonomic identity of the barnacles from the Moluccas with the published sequences in the GenBank, to examine whether they cluster near to congeneric or conspecific accessions. With this exercise we aimed to gain insights into the taxonomic positions of Moluccan barnacles in addition to those we may gain from morphology.

Genomic DNA was extracted from the adductor muscle tissue using CTAB isolation buffer following the method of Doyle & Doyle (1987), as described at http://www.geocities.com/CapeCanaveral/8431/CTAB.html. Tissue was ground and placed in 200 µl CTAB buffer and 5 µl Proteinase K, homogenized by shaking, and incubated at 56°C overnight. DNA was extracted from the lysate using a Qiagen BioSprint 96 using the manufacturer's protocol. The purified DNA was stored at −20°C until required, and dilutions of 1 to 10 were used for the polymerase chain reaction (PCR).

We sequenced two gene fragments: cytochrome oxidase subunit I (COI), a rapidly evolving gene from the mitochondrial genome; and the 18S ribosomal RNA gene (18S), a slowly evolving and generally highly conserved gene from the ribosome. We chose these markers because of their contrasting evolutionary rates, but also because they have been widely used in barnacle phylogenetic analyses (Pérez-Losada et al., 2008, 2014; Tsang et al., 2014, 2015).

COI was sequenced using primers LCO1490 (5'-GGT CAA CAA ATC ATA AAG ATA TTG G-3') and HCO2198 (5'-TAA ACT TCA GGG TGA CCA AAA AAT CA-3') (Folmer et al. 1994), and 18S using primers ai (5'-CCT GAG AAA CGG CTA CCA CAT C-3') and 7R (5'-GCA TCA CAG ACC TGT TAT TGC-3') (Whiting 2002). PCR was performed in 25 µl volumes containing 17.8 µl ddH2O, 2.5 µl 10 x Puffer, 1 µl Mg (25mM), 0.5 µl dNTP Mix, 0.5 µl of each primer, and 0.2 µl Taq Polymerase (2.00 units/25 µl PCR) with 2 µl DNA. The reaction conditions of PCR were 94º C for 3 minutes before 35 cycles of amplification, with 94º C for 30 sec, 55º C for 1 minute and 72º C for 60 sec, followed by a final extension at 72º C for 5 minutes. PCR products were sent to Macrogen Europe for cycle sequencing of both strands of each gene.

Chromatograms were edited using CodonCode Aligner version 5.1.5 (http://www.codoncode.com) for COI and Geneious 11 (http://www.geneious.com) for 18S. All new DNA sequences generated for this study are deposited in GenBank under the accession numbers provided in Supplementary Table 7.1.

For comparison, 84 COI sequences and 88 18S sequences of related barnacles were downloaded from GenBank (accession numbers are provided in Figs 2.28-2.29). Sequences were aligned using Muscle (Edgar 2004) as implemented in Geneious and later exported as nexus or fasta files.

Phylogenetic trees were reconstructed for each gene using both Maximum Likelihood (ML) and Bayesian Inference (BI). ML analyses were conducted with RAxML Black Box (Stamatakis et al. 2008) with 100 bootstrap replicates and under the GTR + I + G model of sequence evolution. Bayesian analyses were conducted in BEAST 2. As our goal was to obtain a topology and not dates for the branching events, we used a Bayesian relaxed lognormal clock with a rate of 1. Therefore, the ages obtained in the ultrametric trees emerging from this analysis are relative not absolute. Substitution model selection was performed in jModeltest (Posada 2008) using the Akaike information criterion, and GTR + I + G was identified as the best model for both genes. For each analysis, we ran two independent chains of between 10 and 40 million generations, with a birth-death tree prior. Convergence of chains and burn-ins were assessed with Tracer, runs combined using LogCombiner, and maximum clade credibility trees produced in Tree Annotator.

Genetic distances (K2P) were calculated by MEGA version X (Kumar et al. 2018).

2.4 Results

2.4.1 Checklist tabulation

This study provides the most comprehensive overview of barnacle species from the Moluccan islands (Table 2.1). The morphological analyses of the collected material revealed 24 intertidal species and one deep-water species from three families of stalked barnacles (Heteralepadidae: one genus and species; Lepadidae: two genera and species; Pollicipedidae: one genus and species) and four families of acorn barnacles (Pachylasmatidae: one genus and species; Chthamalidae: five genera and species; Tetraclitidae: five genera and eight species; Balanidae: two genera and seven species).

Including previous records from the literature, we found a total of 97 species from the Moluccan islands (Table 2.1) from the superorder Thoracica (free living or epizoic). Of these, 21 are new records and two (*Amphibalanus* sp. and *Microeuraphia* sp.) are currently unidentified species.

All specimens obtained from field work, except for one floating specimen, were attached to types of natural and artificial substrates (Table 2.1), and several smaller species, e.g., *Chthamalus moro*, were also attached to other larger barnacle species, e.g., *Megabalanus tintinnabulum*. In general, the smallest species was *C. moro* (basal length: 2.4-5.1 mm; basal width: 1.4-4.1; height 0.8-1.7 mm), and the largest *M. tintinnabulum* (basal length: 26.0-49.3 mm; basal width 29.0-43.1 mm; height 20.1-49.4 mm).

Table 2.1. Annotated checklist tabulation of barnacle species from the Moluccas, Eastern Indonesia

ORDER Suborder	Family Subfamily	Genus / Species No.	Genus / Species Name	Locality	Substrate	References
LEPADIFORMES Heteralepadomorpha	Heteralepadidae	1	*Heteralepas japonica* (Aurivillius, 1892)	Lifamatola Sea and Halmahera Sea	Deep-water cable to mooring	This study
		2	*Heteralepas ovalis* (Hoek, 1907)	West from Kei Islands		Hoek (1913)
		3	*Heteralepas tenuis* (Hoek, 1907)	South of Seram		Hoek (1913)
Lepadomorpha	Oxynaspididae	4	*Oxynaspis connectens* Broch, 1931	Kei Islands		Jones and Hosie (2016)
	Poecilasmatidae	5	*Glyptelasma carinatum* (Hoek, 1883)	Seram Sea		Hoek (1913)
		6	*Megalasma striatum* (Hoek, 1883)	East of Kei Islands		Hoek (1913)
		7	*Octolasmis orthogonia* Darwin, 1852	Tual anchorage		Hoek (1913)
		8	*Octolasmis weberi* (Hoek, 1907)	Kei Islands, Banda Sea		Hoek (1913), Jones and Hosie (2016)
		9	*Poecilasma kaempferi* Darwin, 1852	Banda Sea		Jones and Hosie (2016)
		10	*Temnaspis fissum* (Darwin, 1852)	Ternate anchorage		Hoek (1913)
	Lepadidae	11	*Conchoderma virgatum* Spengler, 1789	Banda Sea		Jones et al. (2001)
		12	*Dosima fascicularis* (Ellis & Solander, 1786)	Ambon	Floating in water at the beach	This study
		13	*Lepas anserifera* Linnaeus, 1767	Ambon, Saparua, Seram, Pombo	Mangrove, stone ship chart and ship wall, port pole, shell of *Megabalanus zebra*	This study
		14	*Lepas pectinata* Spengler, 1793	Banda Sea		Jones and Hosie (2016)
SCALPELLIFORMES	Calanticidae	15	*Calantica pollicipedoides* (Hoek, 1907)	East of Kei Islands		Hoek (1913)
		16	*Euscalpellum rostratum* (Darwin, 1852)	Kei Islands		Jones and Hosie (2016)
	Pollicipedidae	17	*Capitulum mitella* (Linnaeus, 1758)	Ambon, Saparua	Rocks, stone, wall of fortress, port pole and concrete wall	Rumphius (1705), this study
	Scalpellidae Scalpellinae	18	*Compressoscalpellum inflatum* (Hoek, 1907)	West of Aru Island		Hoek (1913)

ORDER Suborder	Family Subfamily	Genus / Species No.	Name	Locality	Substrate	References
		19	*Scalpellum fissum* Hoek, 1913	West of Halmahera		Hoek (1913)
		20	*Scalpellum stearnsi* Pilsbry, 1890	Near Kei Islands		Hoek (1913)
	Arcoscalpellinae	21	*Amigdoscalpellum vitreum* (Hoek, 1883)	South of Seram, South of Ambon		Hoek (1913)
		22	*Anguloscalpellum pedunculatum* (Hoek, 1883)	Kei Islands		Hoek (1913)
		23	*Arcoscalpellum cilliatum* (Hoek, 1907)	South of Ambon		Hoek (1913)
		24	*Arcoscalpellum discolor* (Hoek, 1907)	Banda Sea		Hoek (1913)
		25	*Arcoscalpellum sculptum* (Hoek, 1907)	Banda Sea		Hoek (1913)
		26	*Arcoscalpellum sociabile* (Annandale, 1905)	Banda Sea		Jones et al. (2001)
		27	*Planoscalpellum hexagonum* (Hoek, 1907)	Banda Sea		Hoek (1913)
		28	*Teloscalpellum imbricatum* (Hoek, 1907)	Near Kei Islands		Hoek (1913)
		29	*Trianguloscalpellum balanoides* (Hoek, 1883)	Banda Sea		Hoek (1913), Shalaeva and Boxshall (2014)
		30	*Trianguloscalpellum diota* (Hoek, 1907)	Near Kei Islands		Hoek (1913)
		31	*Trianguloscalpellum hamulus* (Hoek, 1907)	Kei Islands		Hoek (1913)
		32	*Trianguloscalpellum hirsutum* (Hoek, 1883)	Moluccan Sea		Hoek (1913), Shalaeva and Boxshall (2014)
		33	*Trianguloscalpellum indicum* (Hoek, 1883)	Banda Sea		Hoek (1913), Shalaeva and Boxshall (2014)
		34	*Trianguloscalpellum moluccanum* (Hoek, 1883)	Banda Sea; West of Aru Island		Hoek (1913), Shalaeva and Boxshall (2014)
		35	*Trianguloscalpellum sessile* (Hoek, 1907)	Seram Sea		Hoek (1913)
		36	*Verum candidum* (Hoek, 1907)	Near Kei Islands		Hoek (1913), Jones and Hosie (2016)

ORDER Suborder	Family Subfamily	Genus / Species No.	Name	Locality	Substrate	References
	Meroscalpellinae	37	*Annandaleum japonicum* (Hoek, 1883)	Aru Island		Hoek (1913)
		38	*Annandaleum laccadivicum* (Annandale, 1906)	Kei Islands		Hoek (1913)
SESSILIA Verrucomorpha	Verrucidae	39	*Altiverruca navicula* (Hoek, 1913)	Between Seram and New Guinea, Kei Islands, Tanimbar Island		Hoek (1913), Buckeridge (1994)
		40	*Brochiverruca dens* (Broch, 1932)	Tanimbar Island		Buckeridge (1994)
		41	*Cristallinaverruca cristallina* (Gruvel, 1907)	Banda Sea		Jones and Hosie (2016)
		42	*Metaverruca recta* (Aurivillius, 1898)	Kei Islands		Hoek (1913)
		43	*Newmaniverruca albatrossiana* (Pilsbry, 1912)	East of Kei Islands, Tanimbar Island		Hoek (1913), Buckeridge (1994)
		44	*Rostratoverruca intexta* (Pilsbry, 1912)	Kei Islands, Tanimbar Island		Hoek (1913), Buckeridge (1994)
		45	*Rostratoverruca kruegeri* (Broch, 1922)	Kei Islands, Tanimbar Island		Jones et al. (2001), Buckeridge (1994)
		46	*Verruca capsula* Hoek, 1913	Between Seram and New Guinea		Hoek (1913)
Balanomorpha	Pachylasmatidae Hexelasmatinae	47	*Hexelasma arafurae* Hoek, 1913	Kei Islands, Arafura Sea		Hoek (1913), Jones and Hosie (2016)
		48	*Hexelasma velutinum* Hoek, 1913	Kei Islands		Jones et al. (2001)
	Pachylasmatinae	49	*Pachylasma integrirostrum* Broch, 1931	Ambon		Jones et al. (2001)
		50	*Pseudoctomeris sulcata* (Nilsson-Cantell, 1932)	Ambon	Rocks, shell of *Tetraclita squamosa*	This study
	Chthamalidae Notochthamalinae	51	*Hexechamaesipho pilsbryi* (Hiro, 1936)	Ambon	Rocks	This study
		52	*Nesochthamalus intertextus* (Darwin, 1854)	Ambon	Stone	This study
	Euraphiinae	53	*Europhia hembeli* Conrad, 1837	Ambon	Rocks	This study

ORDER Suborder	Family Subfamily	Genus / Species No.	Name	Locality	Substrate	References
		54	*Microeuraphia withersi* (Pilsbry, 1916)	Kei Islands		Jones and Hosie (2016)
		55	*Microeuraphia* sp.	Seram Island	Stone, concrete wall at port	This study
	Chthamalinae	56	*Chthamalus malayensis* Pilsbry, 1916	Arafura Sea		Jones et al. (2001)
		57	*Chthamalus moro* Pilsbry, 1916	Ambon, Saparua, Seram, Pombo	Mangrove, stone, port pole, mol-lusk shell, shells of *Tetraclita squamosa*, *Tesseropora rosea,* and *Capitulum mitella*	This study
	Tetraclitidae Tetraclitellinae	58	*Tetraclitella (Eotetraclitella) costata* (Darwin, 1854)	Banda		Hoek (1913)
		59	*Tetraclitella divisa* (Nilsson-Cantell, 1921)	Ambon	Concrete wall at port	This study
		60	*Tetraclitella karandei* Ross, 1971	Ambon	Stone, shells of *Capitulum mitella* and *Euraphia hembeli*	This study
	Tetraclitinae	61	*Tesseropora rosea* (Krauss, 1848)	Ambon, Saparua	Stone, mollusc shell	This study
		62	*Tetraclita kuroshioensis* Chan, Tsang & Chu, 2007	Ambon, Saparua	Rocks, concrete wall at port	This study
		63	*Tetraclita squamosa* (Bruguière, 1789)	Ambon, Saparua	Stone, rocks, concrete bridge and wall at port, shipyard.	This study
	Newmanellinae	64	*Yamaguchiella coerulescens* (Spengler, 1790)	Banda, Kei Islands, Ambon, Saparua	Stone	Hoek (1913), Jones and Hosie (2016), This study
		65	*Neonrosella vitiata* (Darwin, 1854)	Ambon, Banda Neira, Saparua	Port pole, reef, stone	This study
		66	*Newmanella spinosus* Chan & Cheang, 2016	Ambon	Stone, reef surface	This study
	Archaeobalanidae Archaeobalaninae	67	*Armatobalanus allium* (Darwin, 1854)	Banda Sea		Jones and Hosie (2016)
		68	*Armatobalanus cepa* (Darwin, 1854)	Aru Island		Jones and Hosie (2016)

ORDER Suborder	Family Subfamily	Genus / Species No.	Name	Locality	Substrate	References
		69	*Armatobalanus quadrivittatus* (Darwin, 1854)	Banda Sea		Jones and Hosie (2016)
		70	*Conopea dentifer* (Broch, 1922)	Kei Islands		Jones et al. (2001)
		71	*Conopea navicula* (Darwin, 1854)	Near Damar Island (South of Halmahera)		Hoek (1913)
		72	*Membranobalanus cuneiformis* (Hiro, 1936)	Arafura Sea		Jones and Hosie (2016)
		73	*Solidobalanus auricoma* (Hoek, 1913)	Banda Sea, Ternate, Kei Islads		Hoek (1913) Jones et al. (2001)
		74	*Solidobalanus socialis* (Hoek, 1883)	Arafura Sea		Hoek (1913)
		75	*Striatobalanus amaryllis* (Darwin, 1854)	Arafura Sea		Jones and Hosie (2016)
		76	*Striatobalanus kruegeri* (Pilsbry, 1916)	Moluccas		Jones and Hosie (2016)
		77	*Striatobalanus tenuis* (Hoek, 1883)	Kei Islands, Arafura Sea		Hoek (1913), Jones and Hosie (2016)
	Bryozobiinae	78	*Multatria terebratus* (Darwin, 1854)	Kei Islands		Hoek (1913), Jones and Hosie (2016)
		79	*Eoatria quinquevittatus* (Hoek, 1913)	Banda Sea, Ambon Island		Jones and Hosie (2016)
	Pyrgomatidae Pyrgomatinae	80	*Cantellius euspinulosum* (Broch, 1931)	Ambon		Jones and Hosie (2016)
		81	*Cantellius gregarious* (Sowerby, 1823)	Banda Sea		Jones et al. (2001)
		82	*Cantellius pallidus* (Broch, 1931)	Banda Sea		Jones et al. (2001)
		83	*Galkinius indica* (Annandale, 1924)	Kei Islands		Jones and Hosie (2016)
		84	*Hoekia fornix* Ross & Newman, 1995	Moluccas		Jones and Hosie (2016)
		85	*Nobia grandis* Sowerby, 1839	Kei Islands		Jones et al. (2001)
		86	*Pyrgoma kuri* Hoek, 1913	Kei Islands		Hoek (1913)
	Balanidae Amphibalaninae	87	*Amphibalanus amphitrite* (Darwin, 1854)	Ambon, Saparua	Stone, mollusc shell, capitulum of *Lepas anserifera*	This study

ORDER Suborder	Family Subfamily	Genus / Species No.	Genus / Species Name	Locality	Substrate	References
		88	*Amphibalanus reticulatus* (Utinomi, 1967)	Ambon	Stone, concrete wall at port	This study
		89	*Amphibalanus variegatus* (Darwin, 1854)	Ambon, Saparua	Stone, plastic	This study
		90	*Amphibalanus zhujiangensis* (Ren, 1989)	Ambon, Saparua, Seram	Stone, capitulum of *Lepas anserifera*	This study
		91	*Amphibalanus* sp.	Ambon, Seram	Stone, concrete wall at port	This study
	Balaninae	92	*Balanus arcuatus* Hoek, 1913	Banda		Hoek (1913)
		93	*Balanus hystrix* Hoek, 1913	Ambon		Hoek (1913)
		94	*Balanus longirostrum* Hoek, 1913	Bacan		Hoek (1913)
	Megabalaninae	95	*Megabalanus occator* (Darwin, 1854)	Near Obilatu Island	Coral	Kolosváry (1950)
		96	*Megabalanus tintinnabulum* (Linnaeus, 1758)	Ambon, Saparua	Conrete bridge at port, stone, reef surface	This study
		97	*Megabalanus zebra* (Darwin, 1854)	Ambon	Stone, capitulum of *Lepas anserifera*	This study

Systematic account of the 25 species morphologically examined for this study

Class Hexanauplia Oakley, Wolfe, Lindgren & Zaharoff, 2013
Subclass Thecostraca Gruvel, 1905
Infraclass Cirripedia Burmeister, 1834 (= Cirrhipèdes Lamarck, 1806)
Superorder Thoracica Darwin, 1854

Order Lepadiformes Buckeridge & Newman, 2006
Suborder Heteralepadomorpha Newman, 1987
Family Heteralepadidae Nilsson-Cantell, 1921
Genus *Heteralepas* Pilsbry, 1907

Heteralepas japonica (Aurivillius, 1892)

Figure 2.3a-g, Table 2.1: species no. 1

Alepas japonica Aurivillius, 1892: 125: Aurivillius 1894: 28, pl. II figs 14, 15, pl. VIII figs 3, 7, pl. IX fig. 3.

Alepas indica Gruvel, 1901: 259: Gruvel 1905a: 162, fig. 179.

Heteralepas (*Heteralepas*) *japonica*: Pilsbry 1907a: 101.

Heteralepas (*Heteralepas*) *japonica var*. *alba* Krüger, 1911a: 34, pl. 1 fig. 2b.
Heteralepas (*Heteralepas*) *dubia* Broch, 1922: 288, fig. 38.
Heteralepas japonica: Pilsbry 1911a: 71, fig. 4; Zevina et al. 1992: 31, fig. 19; Chan et al. 2009a: 61; Chan et al. 2009b: 88-91, figs 2A-D, 3A-D, 4, 5.

Material examined:

Deep-Sea: 32 specimens, MZB Cru Cir 050, Stn.23 Mooring Lifamatola, 250 m, coll. N. Fitriya, 9 Nov 2016; 13 specimens, MZB Cru Cir 051, Stn.39 Mooring Halmahera Seas, 250 m, coll. N. Fitriya, 13 Nov 2016; 27 specimens, MZB Cru Cir 052, Stn.56 MO2, 200 m, coll. N. Fitriya, 23 Nov 2016; 42 specimens, MZB Cru Cir 053, Stn.58 MO3, 250 m, coll. N. Fitriya, 25 Nov 2016.

GenBank accession numbers: COI gene (MK995372), 18S (MK981386).

Diagnosis:

Capitulum rounded without hard valves and opercular plates, wall of capitulum tick with crest not more than two on the carinal region; cirrus I with filamentary appendage at the basal region; anterior rami shorter than posterior rami in cirri V-VI; caudal appendage present; maxillule strongly notched.

Description:

Orifice slightly protuberant, crenulated, occupying one half to one third capitular length, parallel to or at oblique angle to capitulum; integument thick, chitinous; carinal margin sometimes with warty protuberances on slight keel; peduncle naked; colour of capitulum and peduncle yellowish (Fig. 2.3a-c). Cirrus I with anterior rami (19-segmented) shorter than posterior rami (25-segmented) and a filamentary appendage present at the basal region (Fig. 2.3d); cirri II - IV long, slender, anterior rami of cirri V and VI shorter than posterior rami; cirrus VI has a caudal appendage with 20-segmented and one fourth length of anterior ramus (Fig. 2.3e). Mandible with four large teeth excluding inferior angle (Fig. 2.3f); maxillule strongly notched with two big teeth on upper angle and blade-shaped setae on cutting margin (Fig. 2.3g); labrum concave, teeth numerous. Ranges of height of capitulum 11.9-18.6 mm, width 8.7-15.3 mm, thickness 7.0-13.3 mm; length of peduncle 7.7-27.6 mm and width 5.1-10.4 mm (measurements for 25 specimens are presented in Supplementary Table 7.2).

Distribution:

Heteralepas japonica is widely distributed in Indo-west Pacific: Indian Ocean; Australia; Singapore, Malacca Str., Indonesia; Malay Archipelago; Vietnam; Condor Island; S China Sea; E China Sea; Taiwan, Philippines; S Japan; NE New Zealand; fouling hard rock substrata, crabs, gorgonians, antipatharians, deep-sea cables; 48–500 m (Jones and Hosie 2016). In this study, *Heteralepas japonica* was found attached to cable moorings in Lifamatola Sea and Halmahera Sea (a map with the occurrence of *Heteralepas japonica* in the Moluccas is shown in Supplementary Fig. 7.1).

Remarks:

The external appearance of this species is extremely variable (Nilsson-Cantell 1927). After an extensive study of *H. japonica,* Nilsson-Cantell could not distinguish *H. japonica* and *H. indica* (Gruvel, 1901) and placed the latter in synonymy with *H. japonica,* and later authors have followed this suggestion (e.g., Broch 1931, Utinomi 1958). At the same time, Nilsson-Cantell (1927) also suggested that *H. nicobarica* Annandale, 1909, *H. gigas* Annandale, 1905 and *H. cygnus* Pilsbry, 1907 could be invalid species and future revision may synonymize some or all of them. Zullo & Newman (1964) pointed out the uncertainty surrounding the status of several of the species assigned to *Heteralepas* due to a lack of zoogeographic and morphological data, since extensive collections are unavailable. Furthermore, Foster (1978) suggested that a revision of the genus was called for since the variability of *H. japonica,* as noted by Foster and tabulated by Nilsson-Cantell (1927), encompasses characters which have been used to distinguish several different species by other authors (e.g., *H. dubia* Broch, 1922, *H. cornuta* Darwin, 1852 , *H. indica* Gruvel, 1901, *H. lankestri* Gruvel, 1900).

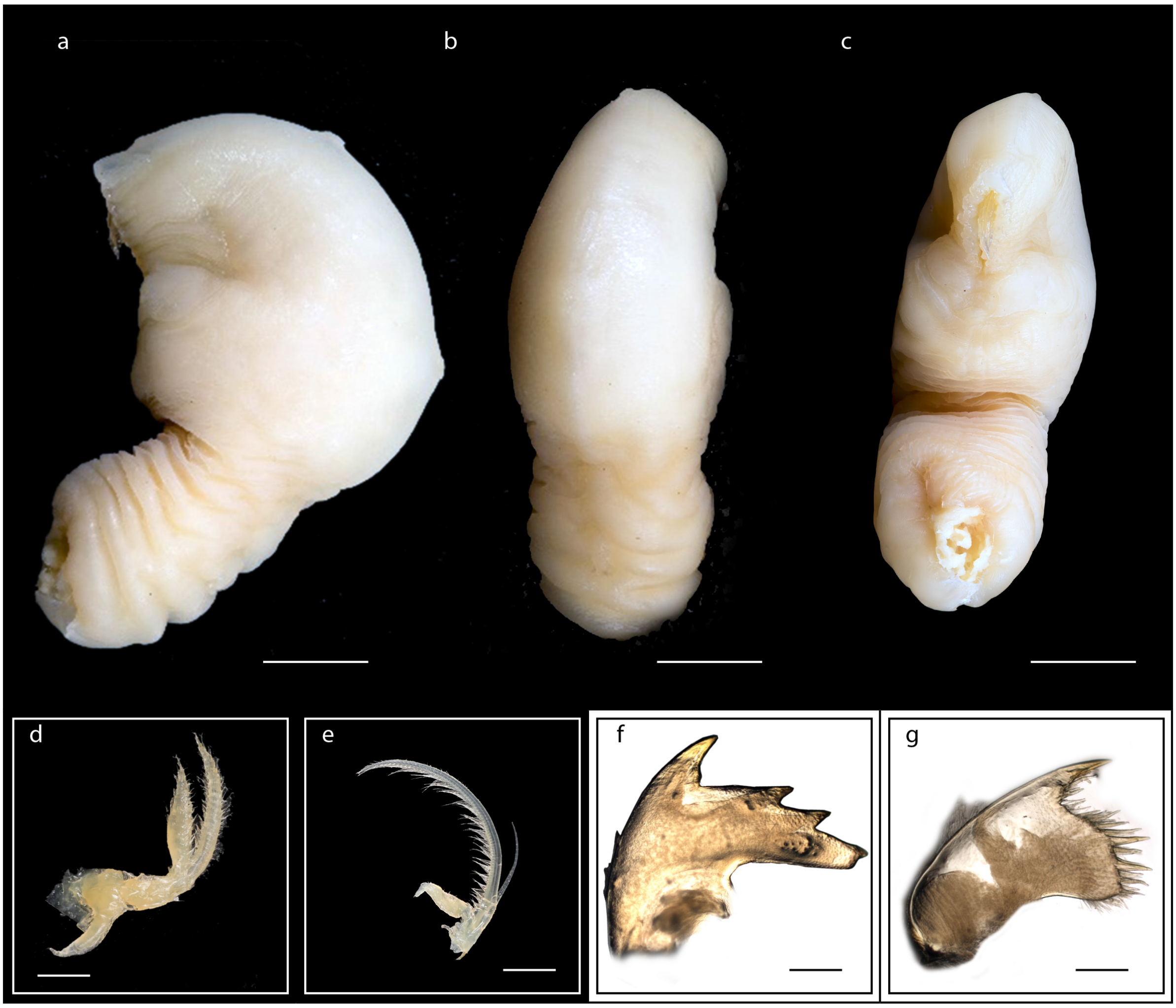

Figure 2.3. *Heteralepas japonica* (Aurivillius, 1892) (MZB Cru Cir 050-2). (a) Side view showing the capitulum and peduncle, (b) upper view showing the capitulum and peduncle, (c) side view showing the opening of operculum, (d) cirrus I showing the filamentary appendage at the basal region, (e) cirrus VI showing the caudal appendage, (f) mandible, (g) maxillule. Scale bars: a-c) 5 mm, d) 2 mm, e) 3 mm, f-g) 0.5 mm.

Suborder Lepadomorpha Pilsbry, 1916

Family Lepadidae Darwin, 1852

Genus *Dosima* Gray, 1825

Dosima fascicularis (Ellis and Solander, 1786)

Figure 2.4a-c, Table 2.1: species no. 12

Lepas fascicularis Ellis and Solander, 1786: 197, tab. 15 fig. 6; Darwin 1852: 92, pl. 1 fig. 6.
Lepas fascicularis aurivillii Nilsson-Cantell, 1921: 238, fig. 40b.
Lepas cygnea Spengler, 1790: pl. 6 fig. 8.
Pentalasmis spirulicola, P. donovani Leach, 1818: 413.
Pentalasmis fascicularis: Brown 1844: pl. 51 fig. 2.
Lepas fasciculatus: Pilsbry 1907: 81, pl. IX fig.6.
Lepas (*Dosima*) *fascicularis*: Weisbord 1979: 28, pl. 2 figs 10-11; Jones et al. 1990: 8.
Dosima fascicularis: Gray 1825: 100; Zevina 1982: 21, fig. 11.

Material examined:

Ambon Island: 19 specimens, MZB Cru Cir 048, Tial, 3°38’10.2”S 128°20’46.9”E, coll. Adin, 19 Sep 2017.

GenBank accession numbers: COI gene (MK995371), 18S (MK981385).

Diagnosis:

The only pelagic barnacle with its own gas-filled float; plates very thin and paper-like; carina angle bent with a prominent umbo and expanded basal disk; cirri acanthopod.

Description:

Five capitular plates, white, thin, delicate, wide interspaces between dark purple; base of carina almost round, not imbedded in membrane, distinct angle formed at sub-central carinal umbo peduncle short, naked (Fig. 2.4a); five filamentary appendages located at base of cirri on each side of body; caudal appendages small, smooth, summits rounded; mandible with five teeth (Fig. 2.4c); penis hirsute. Ranges of diameter of capitulum base 4.0-6.8 mm; capitular height 10.5-17.1 mm; total height 11.7-19.5 mm; scutal width 5.4-7.3 mm; scutal length 8.1-11.1 mm; tergal width 2.7-4.4 mm; tergal length 6.2-11.1 mm (measurements for six specimens are presented in Supplementary Table 7.3).

Distribution:

Dosima fascicularis is cosmopolitan in tropical and temperate seas (Jones and Hosie 2016). While it has been reported found at New Zealand, South Africa and South America (Newman and Ross 1971). In the present study, *D. fascicularis* was found at Ambon Island at Tial (floating in water at the beach) (a map with the occurrence of *Dosima fascicularis* in the Moluccas is shown in Supplementary Fig. 7.2).

Remarks:

Dosima fascicularis is the only pelagic barnacle that produces its own gas-filled float enabling it to sustain itself on the sea surface (Weisbord 1979). *Dosima* can also be distinguished from members of the genus *Lepas* by the distinct angle formed at the sub-central umbo of the carina, and by very thin and brittle plates (Hinojosa et al. 2006).

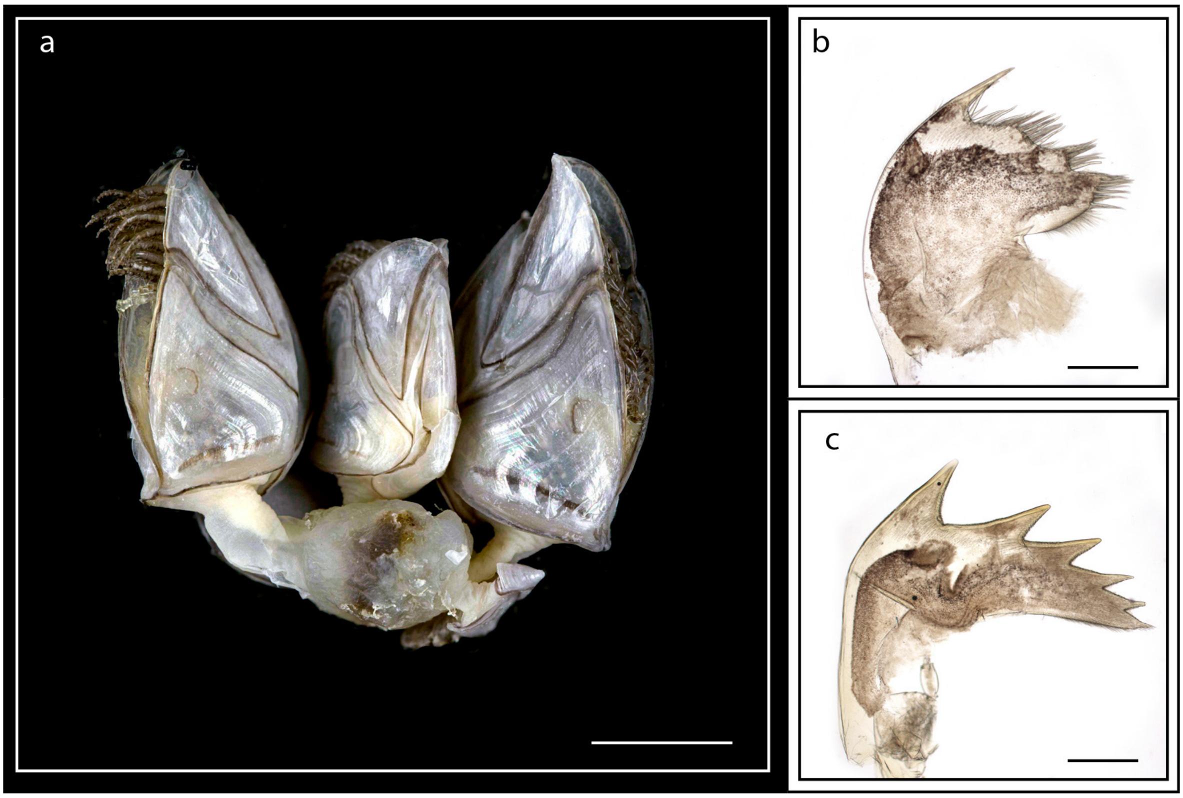

Figure 2.4. *Dosima fascicularis* (Ellis and Solander, 1786) (MZB Cru Cir 048-19). (**a**) Side view showing the capitulum and peduncle, (**b**) maxillule, (**c**) mandible. Scale bars: a) 5 mm, b-c) 0.5 mm.

Genus *Lepas* Linnaeus, 1758

Subgenus *Anatifa* Bruguière, 1789

Lepas anserifera Linnaeus, 1767

Figure 2.5a-n, Table 2.1: species no.13

Anatifa striata Bruguière, 1789: pl. 166 fig. 3.

Pentalasmis anseriferus: Brown 1844: pl. 51 fig. 1.

Lepas anserifera Linnaeus, 1767: 1109; Darwin 1852: 81, pl. 1 fig. 4; Hoek 1907: 2; Hiro 1937a: 57, fig. 48; Utinomi 1949: 20; Stubbings 1967: 237; Newman 1971: 32, fig. 1; Dong et al. 1982: 73; Zevina et al. 1992: 14, fig. 6; Igic 2007: 37, fig. 10; Chan et al. 2009a: 45, fig. 34; Keable and Reid 2015: 266.

Material examined:

- Ambon Island: 5 specimens, MZB Cru Cir 056, Galala, 3°41’22.2”S 128°10’52.6”E, coll. P. Pitriana & D. Tala, 6 Sep 2016; 8 specimens, MZB Cru Cir 057, Laha, 3°43’22.5”S 128°05’02.5”E, coll. P. Pitriana & D. Tala, 5 Sep 2016; 74 specimens, MZB Cru Cir 058, Suli, 3°37’02.0”S 128°16’31.6”E, coll. Adin, 19 Sep 2017; 93 specimens, MZB Cru Cir 059, Tial, 3°38’10.2”S 128°20’46.9”E, coll. Adin, 19 Sep 2017.
- Pombo Island: 5 specimens, MZB Cru Cir 060, Pombo, 3°31’55.5”S 128°22’28.8”E, coll. P. Pitriana & D. Tala, 8 Sep 2016.

- Seram Island: 13 specimens, MZB Cru Cir 061, Lepas Pantai Kawa, 2°57'32.5"S 128°05'33.4"E, coll. P. Pitriana & D. Tala, 19 Sep 2017; 10 specimens, MZB Cru Cir 062, Desa Murnaten, 2°51'48.8"S 128°20'32.3"E, coll. P. Pitriana & D. Tala, 20 Sep 2017; 10 specimens, MZB Cru Cir 063, Desa Kasie, 2°51'05.5"S 128°32'54.1"E, coll. P. Pitriana & D. Tala, 20 Sep 2017; 10 specimens, MZB Cru Cir 064, Dermaga Pelita Jaya, 3°00›13.5»S 128°07›09.2»E, coll. P. Pitriana & D. Tala, 21 Sep 2017.
- Saparua Island: 19 specimens, MZB Cru Cir 065, Negeri Mahu, 3°31'52.9"S 128°41'12.4"E, coll. P. Pitriana & D. Tala, 11 Apr 2016.

  GenBank accession numbers: COI gene (MK995373 - MK995375), 18S (MK981387 - MK981388).

Diagnosis:

Capitulum with five completely calcified plates; surfaces striated with radiating lines; scuta with conspicuous growth lines; scutal margin of terga without notch, occluding margin of scutum strongly convex and swollen; carina apex extending to tergum, base of carina forked; filamentary appendages and caudal appendage present.

Description:

Five capitular plates, closely approximate, white, slightly furrowed, terga sometimes strongly pectinated, occluding margin arched, protuberant (Fig. 2.5a, b). Scutum with well developed, strong internal umbonal tooth, left internal umbonal tooth small, or mere ridge; carina produced below base of scutum as fork, apex pointed (Fig. 2.5c-f); 5-6 filamentary appendages on each side, one on side of prosoma below base of pedicel of cirrus I, four others placed in pairs beneath basal segment of pedicel of cirrus I, lowest posterior filament of the four generally larges (Fig. 2.5g); caudal appendages small, smooth, curved, claw-like, tip pointed; mandible with five teeth excluding inferior angle, lower angle pectinate (Fig. 2.5j), labrum concave, toothed (Fig. 2.5l-m). Basal diameter of capitulum 2.0-7.2 mm; capitular height 8.1-14.8 mm; total height 14.2-31.9 mm. Scutal width 4.7-11.3 mm; scutal length 6.3-12.5 mm. Tergal width 4.7-11.3 mm; tergal length 4.3-9.6 mm (measurements for 25 specimens are presented in Supplementary Table 7.4).

Distribution:

Lepas anserifera is a cosmopolitan, pelagic species occurring in tropical and temperate oceans (Jones et al. 2001). In this study, *Lepas anserifera* was found on the islands of Ambon (at Suli, Tial, Galala, Laha), Pombo, Seram (at Lepas Pantai Kawa, Desa Murnaten, Desa Kasie, Dermaga Pelita Jaya), and Saparua (at Negeri Mahu). *Lepas anserifera* was found attached to mangroves, stone ship charts and ship walls, port poles, and shells of *Megabalanus zebra* (a map with the occurrence of *Lepas anserifera* in the Moluccas is shown in Supplementary Fig. 7.3).

Remarks:

Lepas anserifera can be easily recognized by the presence and positions of the 5-6 filamentary appendages and the curved caudal appendages (Igić 2007).

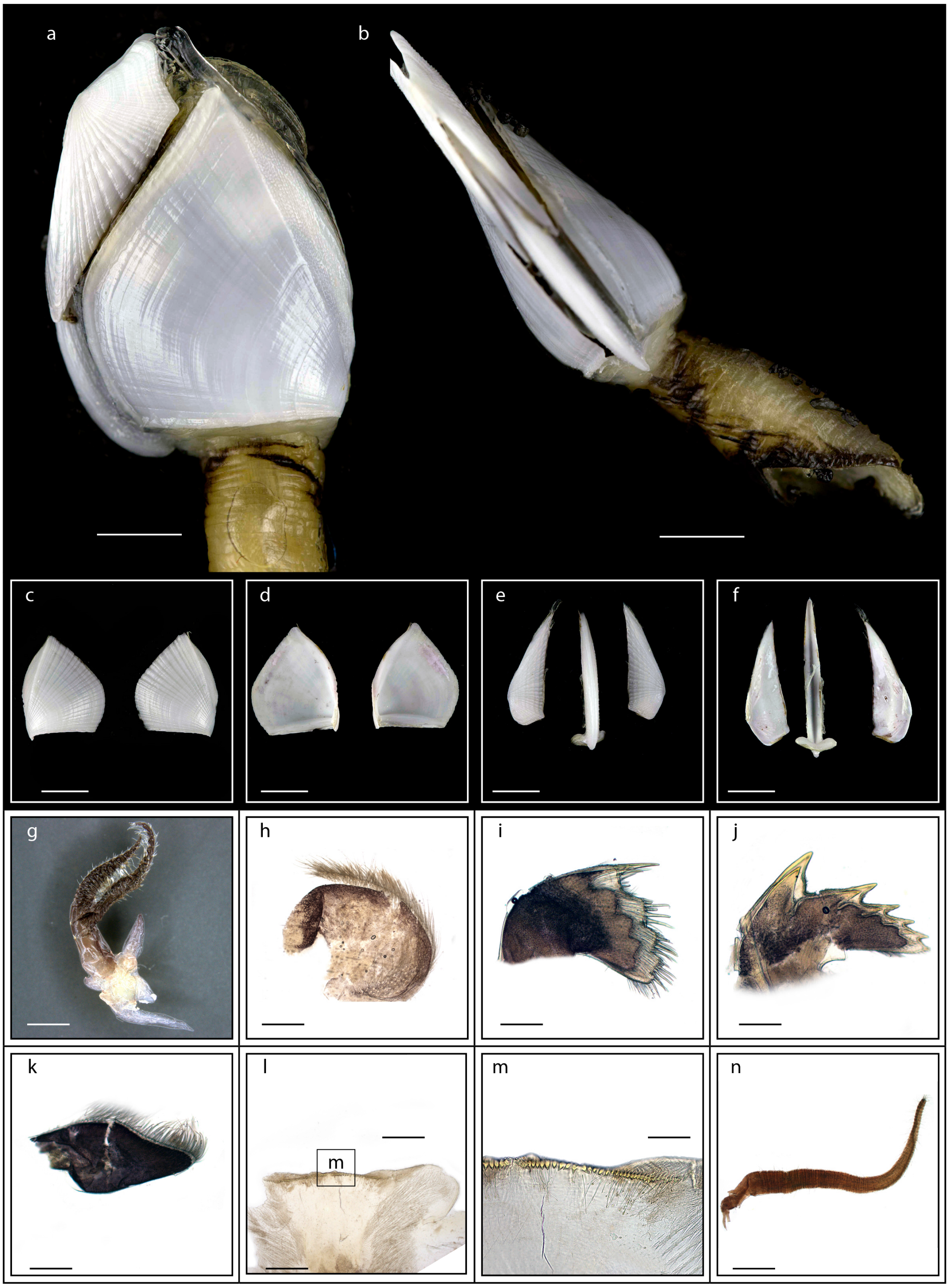

Figure 2.5. *Lepas anserifera* Linnaeus, 1767 (MZB Cru Cir 058-2). (**a**) Side view showing the capitulum and peduncle, (**b**) side view showing the carina, (**c**) external view of scutum, (**d**) internal view of scutum, (**e**) external view of tergum and carina, (**f**) internal view of tergum and carina, (**g**) cirrus I, (**h**) maxilla, (**i**) maxillule, (**j**) mandible, (**k**) mandibular palp, (**l**) labrum, (**m**) close up view on the teeth of labrum, (**n**) penis. Scale bars: a-b) 4 mm, c-f) 3 mm, g, n) 1 mm, h-m) 0.5 mm.

Order Scalpelliformes Buckeridge & Newman, 2006

Suborder Scalpellomorpha Newman, 1987

Family Pollicipedidae Leach, 1817

Genus *Capitulum* Gray, 1825

Capitulum mitella (Linnaeus, 1758)

Figure 2.6a-l, Table 2.1: species no.17

Lepas mitella Linnaeus, 1758: 668.

Pollicipes mitella: Sowerby 1833: fig. 2; Darwin 1852: 316, pl. VII fig. 3; Utinomi 1970: 339; Dong et al. 1982: 69; Zevina et al. 1992: 37, fig. 23.

Polylepas mitella: Blainville 1824: pl. 1 fig. 5.

Mitella mitella: Pilsbry 1907: 6; Annandale 1916: 128, pl. 12 fig. 1.

Capitulum mitella: Gray 1825: 101; Foster 1980: 209; Chan et al. 2009a: 85, fig. 70; Williamson 2014: 758, fig. 1D.

Material examined:

- Ambon Island: 10 specimens, MZB Cru Cir 023, Liang, 3°30’13.3”S 128°20’34.1”E, coll. P. Pitriana & D. Tala, 30 Aug 2016; 2 specimens, MZB Cru Cir 024, Liang, 3°30’13.3”S 128°20’34.1”E, coll. P. Pitriana & D. Tala, 7 Sep 2016; 2 specimens, MZB Cru Cir 025, Alang, 3°45’11.0”S 128°01’23.1”E, coll. Adin, 20 Sep 2017; 4 specimens, MZB Cru Cir 026, Asilulu, 3°40’50.4”S 127°55’27.6”E, coll. Adin, 20 Sep 2017; 3 specimens, MZB Cru Cir 027, Dermaga Tulehu, 3°35’21.8”S 128°20’02.8”E, coll. P. Pitriana & D. Tala, 7 Sep 2017; 15 specimens, MZB Cru Cir 028, Tawiri, 3°42’10.1”S 128°06’13.4”E, coll. P. Pitriana & D. Tala, 29 Mar 2016; 5 specimens, MZB Cru Cir 029, Tawiri, 3°42’10.1”S 128°06’13.4”E, coll. P. Pitriana & D. Tala, 5 Sep 2016; 2 specimens, MZB Cru Cir 030, Laha, 3°43’22.5”S 128°05’02.5”E, coll. P. Pitriana & D. Tala, 5 Sep 2017; 6 specimens, MZB Cru Cir 031, Morella, 3°31’06.5”S 128°13’18.0”E, coll. Adin, 20 Sep 2017; 5 specimens, MZB Cru Cir 032, Ureng, 3°40’14.0”S 127°56’47.6”E, coll. Adin, 20 Sep 2017; 5 specimens, MZB Cru Cir 033, Wakasihu, 3°46’27.6”S 127°56’36.6”E, coll. Adin, 20 Sep 2017.
- Saparua Island: 10 specimens, MZB Cru Cir 034, Teluk Saparua, 3°34’25.7”S 128°39’25.8”E, coll. P. Pitriana & D. Tala, 8 Apr 2016; 11 specimens, MZB Cru Cir 035, Benteng Durstede, 3°34’32.8”S 128°39’34.7”E, coll. P. Pitriana & D. Tala, 8 Apr 2016.

  Genbank accession number: 18S (MK981390).

Diagnosis:

Capitulum with more than 18 plates, all with apical umbones; lateral plates numerous and only one big plate under the rostrum; scales of the peduncle symmetrically arranged in close whorls.

Description:

Capitulum fan-shaped, with eight large plates, basal ring of 18-25 smaller plates, all plates yellowish, umbos apical; peduncle covered by numerous yellowish, fine scales (Fig. 2.6a, b); mandible with five teeth (Fig. 2.6j); labrum concave, teeth lacking (Fig. 2.6l). Capitular diameter base ranges 4.5-20.4 mm; total height 10.7-47.1 mm; capitular height 7.0-24.6 mm. Ranges of distance from rostrum to carina 5.8-27.3 mm and rostral height 5.5-24.2 mm (measurements for 25 are presented in Supplementary Table 7.5).

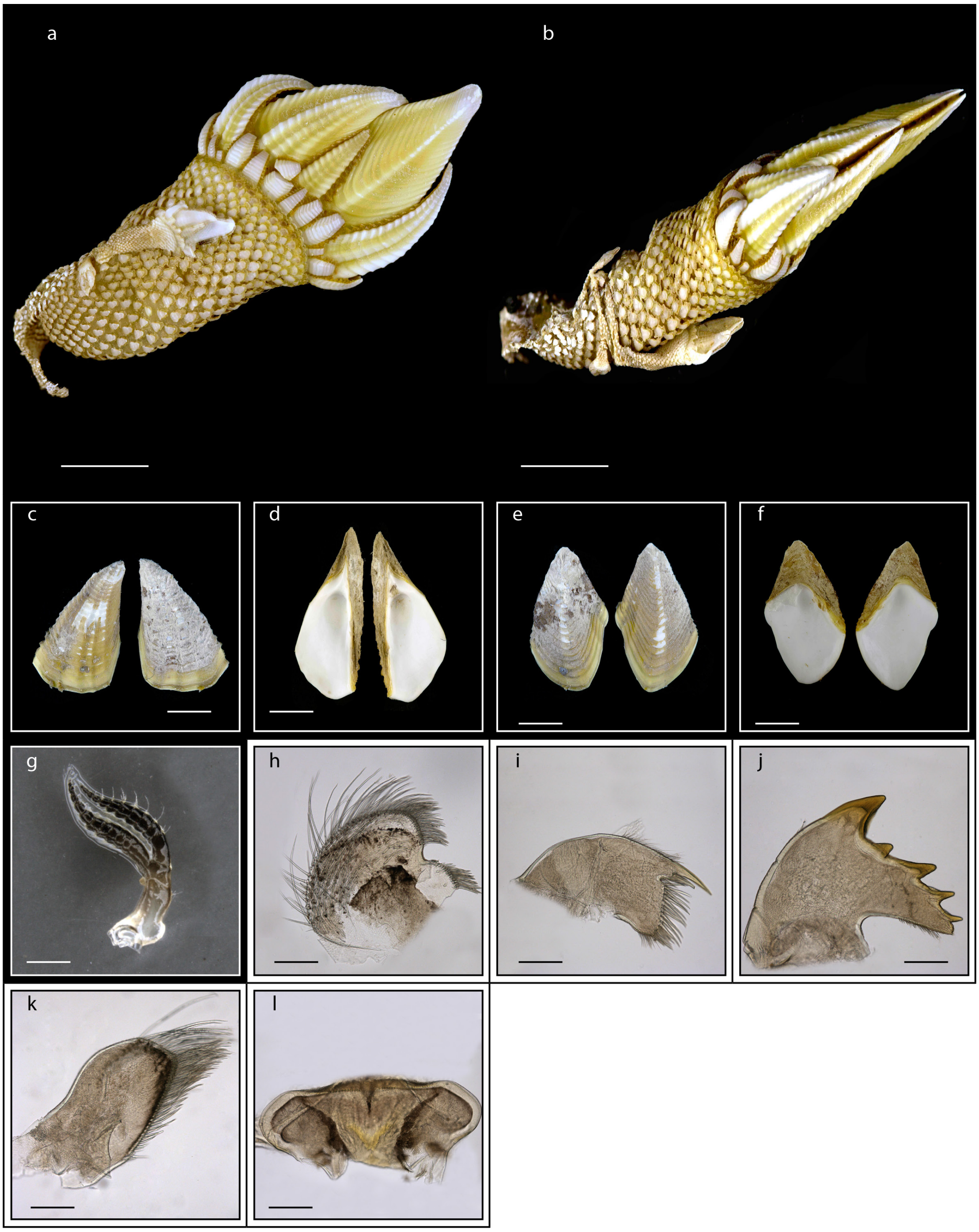

Figure 2.6. *Capitulum mitella* (Linnaeus, 1758) (MZB Cru Cir 026-4). (**a**) Side view showing the capitulum and peduncle, (**b**) side view showing the rostrum, (**c**) external view of scutum, (**d**) internal view of scutum, (**e**) external view of tergum, (**f**) internal view of tergum, (**g**) cirrus I, (**h**) maxilla, (**i**) maxillule, (**j**) mandible, (**k**) mandibular palp, (**l**) labrum. Scale bars: a-b) 6 mm, c-f) 2 mm, g) 1 mm, h-l) 0.5 mm.

Distribution:

Darwin (1852) reported *Capitulum mitella* from the Philippine Archipelago, Ambon, East Indian Archipelago and Madagascar. Chan et al. (2009) and Jones & Hosie (2016) reported the species as widely distributed in warmer parts of the Indo-Pacific region, from Madagascar to southern Japan. In this study, *C. mitella* was found on the islands of Ambon (at Ureng, Alang, Dermaga

Liang, Asilulu, Doc. Tawiri, Morella, Wakasihu, Laha, and Tulehu) and Saparua (at Benteng Duurstede and Teluk Saparua). *Capitulum mitella* attach on rocks, stone, wall of fortress, port pole and concrete wall (a map with the occurrence of *Capitulum mitella* in the Moluccas is shown in Supplementary Fig. 7.4).

Remarks:

Capitulum mitella is the famous Japanese goose barnacle or 'kame-no-te' (meaning the hand of the turtle, referring to its shape). This barnacle is edible and sold as an expensive seafood in Japan, China, Taiwan, and Korea, as well as in Portugal and Spain, where it is known as 'percebes'.

Order Sessilia Lamarck, 1818

Suborder Balanomorpha Pilsbry, 1916

Family Pachylasmatidae Utinomi, 1968

Subfamily Pachylasmatinae Utinomi, 1968

Genus *Pseudoctomeris* Poltarukha, 1996

Pseudoctomeris sulcata (Nilsson-Cantell, 1932)

Figure 2.7a-h, Table 2.1: species no. 50

Octomeris sulcata Nillson-Cantell, 1932: 8; Newman & Ross 1976: 40.
Pseudoctomeris sulcata: Poltarukha 1996: 988; Chan et al. 2009a: 156, fig. 131.

Material examined:

Ambon Island: 4 specimens, MZB Cru Cir 073, Leahari, 3°42'45.3"S 128°16'16.5"E, coll. P. Pitriana, 14 Jan 2016; 2 specimens, MZB Cru Cir 074, Hatu, 3°43'52.7"S 128°02'51.4"E, coll. Adin, 20 Sep 2017.

Diagnosis:

Shell with eight plates; compound rostrum; scutum and tergum fused; mandible tridentate; multi-jointed caudal appendage present.

Description:

Shell externally white, internally black; eight plated, rostrum partially fused with rostrolaterals giving external appearance of six plates (Fig. 2.7a-b); basis membranous, calcareous; orifice *rhomboidal*; scutum and tergum thick (Fig. 2.7c, d); maxilla triangular, maxillule not notched (Fig. 2.7g), mandible with three teeth (Fig. 2.7h), labrum concave, with blunt teeth; cirrus VI with long, multi-segmented caudal appendages. *Ranges of basal length* 16.2-16.7 *mm, basal width* 11.5-15.0 *mm, height* 7.4-7.7 *mm. Orifice* length 5.5-7.9 mm, orifice width 4.3-6.1 mm *(measurements* for two specimens are presented in Supplementary Table 7.6).

Distribution:

Pseudoctomeris sulcata was previously recorded from southern Japan, China, and Taiwan (Jones et al. 2001; Poltarukha and Zevina 2006). In this study, *P. sulcata* was found on Ambon Island at Leahari and Hatu on rocks and shells of *Tetraclita squamosa* (a map with the occurrence of *Pseudoctomeris sulcata* in the Moluccas is shown in Supplementary Fig. 7.2).

Figure 2.7. *Pseudoctomeris sulcata* (Nilsson-Cantell, 1932) (MZB Cru Cir 073-4). (**a**) upper view, (**b**) side view, (**c**) external view of scutum and tergum, (**d**) internal view of scutum and tergum, (**e**) cirrus I, (**f**) cirrus III, (**g**) maxillule, (**h**) mandible. Scale bars: a-b) 4 mm, c-d) 2 mm, e) 1 mm, f) 2 mm, g-h) 0.5 mm.

Remarks:

Externally, the fused rostrum and rostrolaterals are six-plated, but the sutures are visible internally (Poltarukha 1996). Morphologically, *Pseudoctomeris sulcata* shows features of the scutum and tergum similar to those of representatives of the family Pachylasmatida. However, the species can be distinguished by its tridentate mandible and the presence of multi-jointed caudal appendages (Poltarukha 2006). A previous molecular study showed that *P. sulcata* clustered together with members of the family Pachylasmatidae, not with members of the Chthamalidae (Chan et al. 2017). According to Chan et al. (2017), *P. sulcata* is an intertidal species of the Pachylasmatidae, previously believed to be an exclusive deep-sea taxon.

Superfamily Chthamaloidea Darwin, 1854

Family Chthamalidae Darwin, 1854

Subfamily Notochthamalinae Foster & Newman, 1987

Genus *Hexechamaesipho* Poltarukha, 1996

Hexechamaesipho pilsbryi (Hiro, 1936)

Figure 2.8a-f, Table 2.1: species no. 51

Chthamalus pilsbryi Hiro, 1936: 227, fig. 3.
Euraphia pilsbryi: Newman & Ross, 1976: 41.
Hexechamaesipho pilsbryi: Poltarukha 1996: 989; Poltarukha 2006: 73-74; Chan et al. 2008: 320, fig. 3; Chan et al. 2009a: 149, fig. 125; Tsang et al. 2013: 188.

Material examined:

Ambon Island: 20 specimens, MZB Cru Cir 054, Hila, 3°34’57.5”S 128°05’31.9”E, coll. Adin, 20 Sep 2017; 1 specimen, MZB Cru Cir 055, Hatu, 3°43’52.7”S 128°02’51.4”E, coll. Adin, 20 Sep 2017.

Diagnosis:

Shell with six plates; surface grey with black spots scattered; scutum and tergum deeply interlock forming a sinuous line; cirri I and II with multi-cuspid setae.

Description:

Surface of parietes grey or light brown in colour and spotted with black; orifice rhomboidal (Fig. 2.8a); basis calcareous; scutum and tergum strongly articulated, forming sinuous line; scutum elongated, triangular, tergal margin strongly articulated tergum narrow, basi-scutal angle almost 90˚ (Fig. 2.8b-c); cirrus II with multi-cuspid setae; mandible with three large teeth (Fig. 2.8f), labrum with row of large teeth. Basal *length* 8.9-17.0 *mm, basal width* 10.3-16.4 *mm, height* 1.0-3.7 *mm. Orifice* length 4.2-6.9 mm, orifice width 3.6-5.6 mm *(measurements for ten specimens* are presented in Supplementary Table 7.7).

Distribution:

Previously, *Hexechamaesipho pilsbryi* was reported from Japan (Honshu, Shimoda, Wakayama, Okinawa); Taiwan (Turtle Island, Da Xiang Lang, Shi Ti Ping, Kenting); Philippines (Puerto Galera, Tiwi-Bicol, Boracay); Malaysia (Nexus Beach, Kota Kinnabalu, Sabah) (Tsang et al. 2013). In the present study, *H. pilsbryi* was collected from Hatu and Hila on Ambon Island (a map with the occurrence of *Hexechamaesipho pilsbryi* in the Moluccas is shown in Supplementary Fig. 7.2).

A previous study of *H. pilsbryi* indicated that the distribution of this species bridges the junction of the Japan region and the Indo-Polynesian province of Briggs (Briggs 1974). Molecular results of *H. pilsbryi* analysed by Tsang et al. (2013) suggested that this species can be divided into two highly diverged lineages: (1) a northern lineage, predominantly distributed in Japan and Okinawa, and (2) a southern lineage, primarily distributed in Taiwan and Southeast Asia. Assuming that we have molecular data of *H. pilsbryi* in our samples, there is a probability that our samples from the Moluccas include members of the southern lineage.

Remarks:

Hexechamaesipho pilsbryi was first identified from Japan as *Chthamalus pilsbryi* Hiro, 1936. However, due to the presence of three large teeth on the mandible, a characteristic of the subfamily Euraphiinae, the species was placed in the genus *Euraphia* (Nilsson-Cantell 1921). Later, due to the presence of multicuspidate setae on cirrus II, Poltarukha (1996) moved *E. pilsbryi* to the sub-family Notochthamalinae and determined a new genus, *Hexechamaesipho*, which had six parietes and a deeply interlocking scutum and tergum. Currently, *H. pilsbryi* is the only species in the genus.

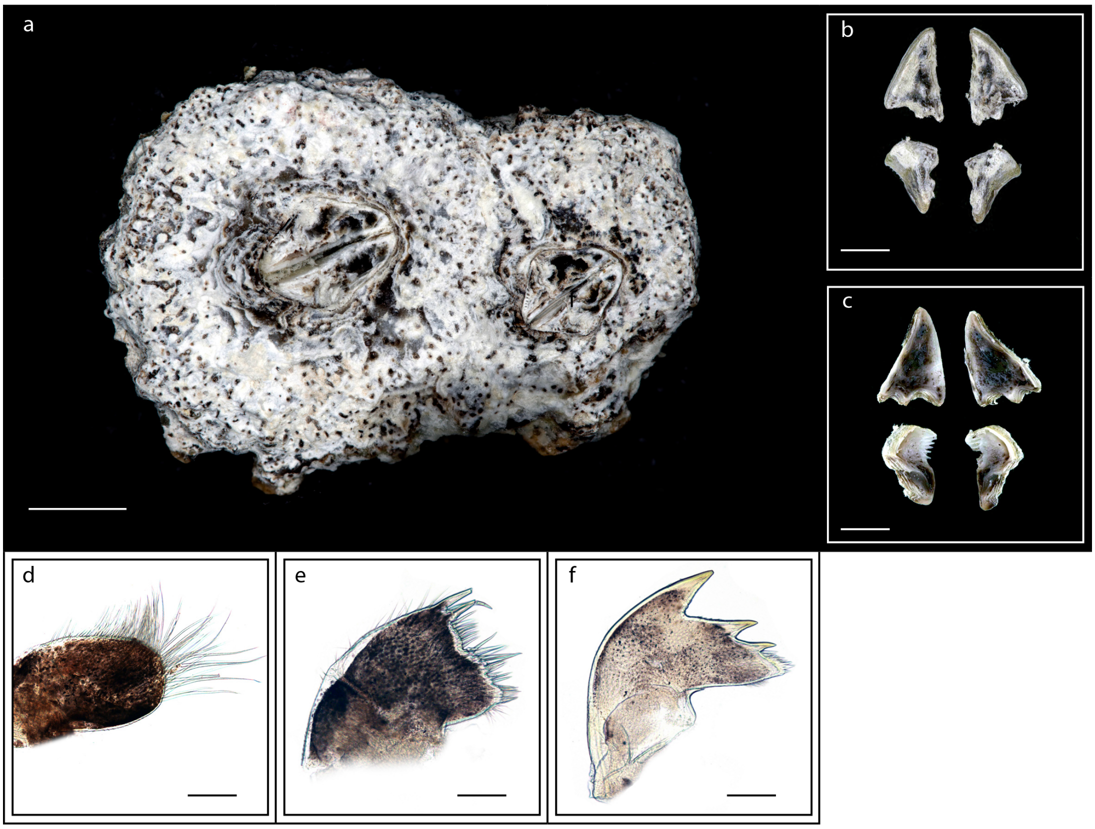

Figure 2.8. *Hexechamaesipho pilsbryi* (Hiro, 1936) (MZB Cru Cir 055). (**a**) Upper view, (**b**) external view of scutum and tergum, (**c**) internal view of scutum and tergum, (**d**) maxilla, (**e**) maxillule, (**f**) mandible. Scale bars: a) 4 mm, b-c) 2 mm, d-f) 0.5 mm.

Genus *Nesochthamalus* Foster & Newman, 1987

Nesochthamalus intertextus (Darwin, 1854)

Figure 2.9a-h, Table 2.1: species no. 52

Chthamalus intertextus Darwin, 1854: 467, pl. 19 figs 1a, b; Dong et al. 1982: 82; Pope 1965: 29, pl. I figs 1f, 3a-d.

Euraphia intertextus: Newman & Ross 1976: 41; Zevina et al. 1992: 79, fig. 53.

Nesochthamalus intertextus: Foster & Newman 1987: 326, fig. 3; Southward et al. 1998: 120, fig. 1D, 1H; Chan et al. 2009a: 147, fig. 124.

Material examined:

Ambon Island: 5 specimens, MZB Cru Cir 070, Laha, 3°43’22.5”S 128°05’02.5”E, coll. P. Pitriana & D. Tala, 7 Sep 2016; 5 specimens, MZB Cru Cir 071, Hila, 3°34’57.5”S 128°05’31.9”E, coll. Adin, 20 Sep 2017.

GenBank accession numbers: COI gene (MK995376), 18S (MK981389).

Diagnosis:

Shell depressed with large diamond-shaped orifice; scutum and tergum fused; external radii consist of oblique laminae arising on both sides of the sutures, standing nearly parallel to the parietes, interfolding with each other; cirri II and III with multi-cuspid setae.

Description:

Shell with six plates, oval, flattened, colour of external shell white to pale grey, interior of shell violet; orifice rhomboidal; parietal sutures with conspicuous interlocking pattern (Fig. 2.9a, b); basis membranous with partial secondary calcification with age; opercular plates fused but separable (Fig. 2.9c, d); cirrus I with rami unequal; mandible with three large teeth (Fig. 2.9e), mandibular palp with long setae on exterior basal margin (Fig. 2.9f); labrum strongly dentate (Fig. 2.9g). *Basal length* 8.9-12.1 *mm, basal width* 6.9-10.3 *mm, height* 1.3-3.1 *mm. Orifice* length 3.0-4.9 mm, orifice width 2.6-3.9 mm (measurements for ten specimens are presented in Supplementary Table 7.8).

Distribution:

Nesochthamalus intertextus is known from islands in the West and Central Pacific Ocean - Indonesia, New Guinea, Malaysia to Vietnam; China; Taiwan; Philippines; Japan; Hawaii; Pitcairn I (Pope 1965; Newman and Ross 1976; Chan et al. 2009; Jones and Hosie 2016). In this study, *N. intertextus* was found on Ambon Island at Laha and Hila on stone (a map with the occurrence of *Nesochthamalus intertextus* in the Moluccas is shown in Supplementary Fig. 7.2).

Remarks:

Nesochthamalus intertextus can be distinguished by the conspicuous interlocking pattern exhibited by the parietal sutures and features of the basis, which is membranous in young specimens but becomes secondarily calcified with age, leaving a membranous centre only (Poltarukha 2008; Pope 1965).

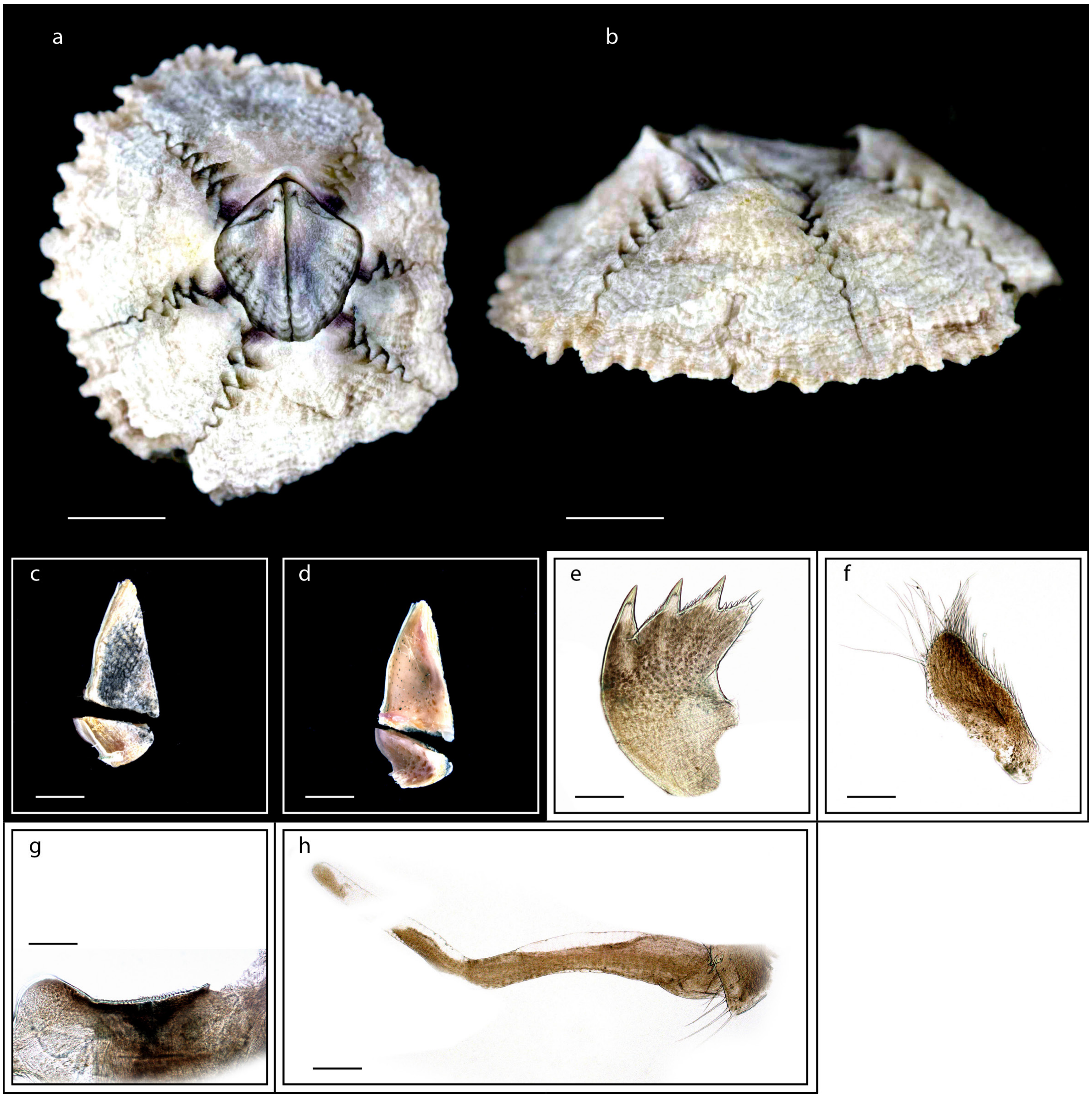

Figure 2.9. *Nesochthamalus intertextus* (Darwin, 1854) (MZB Cru Cir 070-5). (**a**) Upper view, (**b**) side view, (**c**) external view of scutum and tergum, (**d**) internal view of scutum and tergum, (**e**) mandible, (**f**) mandibular palp, (**g**) labrum, (**h**) penis. Scale bars: a,) 3 mm, c-d) 0.75 mm, e-g) 0.25 mm, h) 1 mm.

FAMILY CHTHAMALIDAE Darwin, 1854

SUBFAMILY EURAPHIINAE Newman & Ross, 1976

Genus *Euraphia* Conrad, 1837

Euraphia hembeli Conrad, 1837

Figure 2.10a-c, Table 2.1: species no. 53

Chthamalus hembeli Darwin, 1854: 465, fig. 5a-5d; Pilsbry 1916: 324.

Euraphia hembeli Conrad, 1837: 261, pl.20 fig.6; Newman and Ross 1976: 41; Foster and Newman 1987: 330; Southward et al. 1998: 120, fig. 1E; Paulay and Ross 2003: 307; Jones 2012: 372; Pochai et al. 2017: 17.

Material examined:

Ambon Island: 1 specimen, MZB Cru Cir 049, Asilulu, 3°40’50.4”S 127°55’27.6”E, coll. Adin, 20 Sep 2017.

Diagnosis:

Shell with interlocking teeth between plates; base with a true calcareous and complete secondary calcification; scutum higher than wide and interlocked but not concrescent with tergum.

Description:

Shell with six plates, parietes symmetrical, calcareous, solid, separable, due to coarsely serrate sutures with interlocking toothed structure (Fig. 2.10a-c); colour yellowish or brownish grey, inner surface of parietes smooth, white with dark brown and pale violet horizontal striations around aperture; external surface of shell irregularly ribbed around basal margin, basis calcareous; orifice rhomboidal; tergum and scutum separable; scutum triangular, occluding margin with strong teeth; tergum strongly marked with 10-12 lateral depressor crests, scutal margin strongly articulated. Measurements for one specimen are presented in Supplementary Table 7.9.

Distribution:

Euraphia hembeli has been recorded from the Mediterranean, West Africa, Indian Ocean: Ceylon; Andaman Sea, Cocos-Keeling Islands; Malay Archipelago (Sunda Islands); Pacific Ocean (Japan; Caroline Islands; Hawaiian Islands, California (Newman and Ross 1976; Jones 2012; Barrett and Freeman 2016; Pochai et al. 2017). In this study, *Euraphia hembeli* was found on Ambon Island at Asilulu on rocks (a map with the occurrence of *Euraphia hembeli* in the Moluccas is shown in Supplementary Fig. 7.2).

Remarks:

Euraphia hembeli has a true calcareous basis and complete secondary calcification on its parietal wall and basis (Southward et al. 1998). It can be also distinguished from other species of the genus *Euraphia* by its size (up to 30 mm) and the presence of strong marked lateral depressor crests (between 10-12 in number) (Pochai et al. 2017).

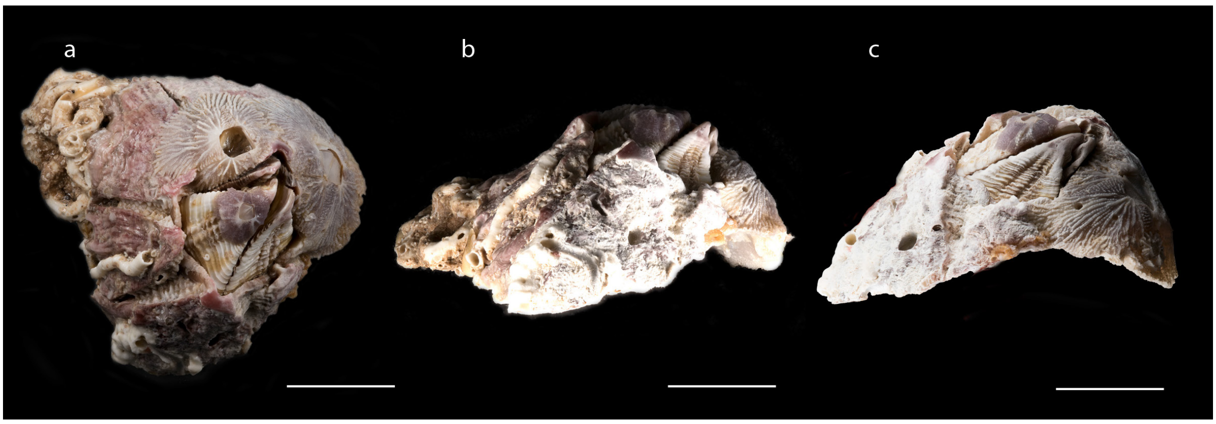

Figure 2.10. *Euraphia hembeli* Conrad, 1837 (MZB Cru Cir 049). (**a**) Upper view of *E. hembeli* which is overgrown with other species of barnacles in its operculum, (**b**) right side view, (**c**) left side view. Scale bar: 16 mm.

Genus *Microeuraphia* Poltarukha, 1997

Microeuraphia sp.

Figure 2.11a-o, Table 2.1: species no. 55

Material examined:

Seram Island: 2 specimens, MZB Cru Cir 138, Pantai Waimeteng-Piru, 3°04’15.3”S 128°11’45.8”E, coll. P. Pitriana & D. Tala, 21 Sep 2017.

GenBank accession numbers: COI gene (MK995389, MK995390), 18S (MK981401, MK981402).

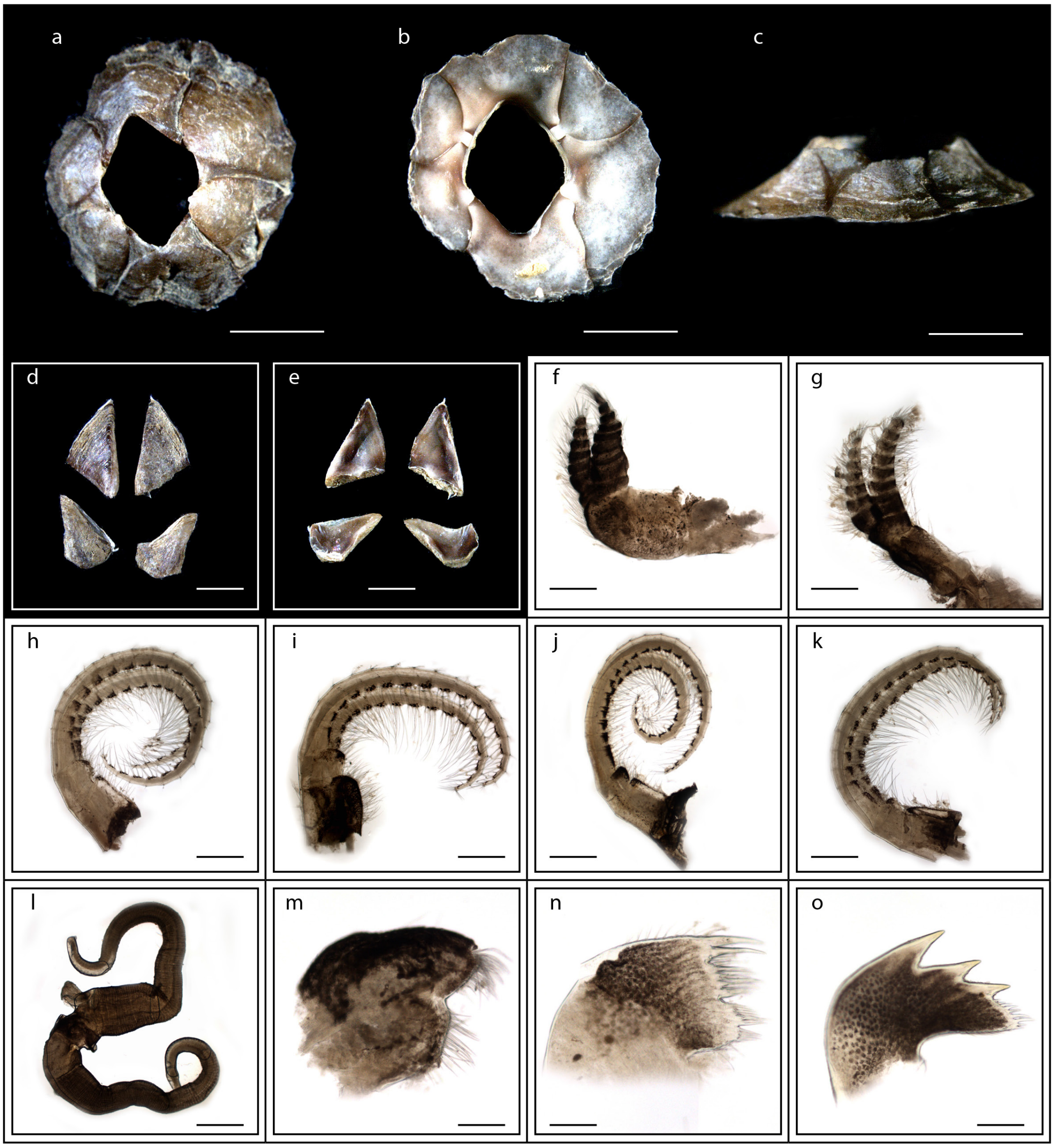

Figure 2.11. *Microeuraphia* sp. (MZB Cru Cir 136-1). (**a**) Upper view, (**b**) lower view, (**c**) side view, (**d**) external view of scutum and tergum, (**e**) internal view of scutum and tergum, (**f**) cirrus I, (**g**) cirrus II, (**h**) cirrus III, (**i**) cirrus IV, (**j**) cirrus V, (**k**) cirrus VI, (**l**) penis, (**m**) maxilla, (**n**) maxillule, (**o**) mandible. Scale bars: a-c) 3 mm, d-l) 0.5 mm, m-o) 0.25 mm.

Diagnosis:
Shell small with six thin plates; basis membranous; scutum and tergum remain articulated, scutum higher than wide; mandible tridentate; caudal appendage absent; one individual with two penises.

Description:
Shell brownish (Fig. 2.11a, b), depressed (Fig. 2.11c); orifice diamond shaped (Fig. 2.11a, b); overlap of 'rostrolateral' forming T junction (Fig. 2.11b); scutum and tergum triangular, tergal margins straight (Fig 2.11d, e); cirrus I with anterior ramus longer than posterior (Fig 2.11f); mandible with smooth tridentate teeth (2.11o). R*anges of basal length* 3.6-9.9 *mm, basal width* 3.0-9.1 *mm, height* 1.2-2.2 *mm.* Orifice of diamond shape with orifice length 1.5-4.5 mm, orifice width 0.7-3.6 mm (measurements for two specimens are presented in Supplementary Table 7.10).

Distribution:
In this study, *Microeuraphia* sp. was found on Seram Island (at Pantai Waimeteng, Piru) (a map with the occurrence of Microeuraphia sp. in the Moluccas is shown in Supplementary Fig. 7.5).

Remarks:
Microeuraphia sp. clustered as a unit, forming a well-supported clade in the COI tree (Fig. 2.29). Morphologically, one individual of this species exhibited two penises.

Family Chthamalidae Darwin, 1854
Subfamily Chthamalinae Darwin, 1854
Genus *Chthamalus* Ranzani, 1817
Chthamalus moro Pilsbry, 1916
Figure 2.12a-b, Table 2.1: species no. 57

Chthamalus malayensis: Utinomi 1954: 18–21 (part.); Karande & Palekar 1963 (part.); Pope 1965 (part.); Newman & Ross 1976 (part.).

Chthamalus moro Pilsbry, 1916: 311; Nilsson-Cantell 1921: 277; Broch 1922: 307 (part.); Hiro 1937b: 49; Rosell 1972: 178; Dong et al. 1980: 125; Ren 1984: 153; Southward & Newman 2003: 798, fig. 2B; Chan et al. 2009a: 165, fig.141.

non *Chthamalus moro* Broch, 1922: 307 (part.); Broch 1931: 56 (includes a euraphiid).

non *Chthamalus moro* Nilsson-Cantell, 1934: 50 (a euraphiid).

non *Chthamalus moro* Poltarukha, 2001b: 160 (= *C. malayensis*).

Material examined:
- Ambon Island: 2 specimens, MZB Cru Cir 036, Alang, 3°45'11.0"S 128°01'23.1"E, coll. Adin, 20 Sep 2017; 2 specimens, MZB Cru Cir 037, Asilulu, 3°40'50.4"S 127°55'27.6"E, coll. Adin, 20 Sep 2017; 10 specimens, MZB Cru Cir 038, Hila, 3°34'57.5"S 128°05'31.9"E, coll. Adin, 20 Sep 2017; 7 specimens, MZB Cru Cir 039, Hatu, 3°43'52.7"S 128°02'51.4"E,

coll. Adin, 20 Sep 2017; 44 specimens, MZB Cru Cir 040, Mamala, 3°33›20.5»S 128°11›32.8»E, coll. Adin, 20 Sep 2017; 38 specimens, MZB Cru Cir 041, Morella, 3°31’06.5”S 128°13’18.0”E, coll. Adin, 20 Sep 2017; 25 specimens, MZB Cru Cir 042, Wakasihu, 3°46’27.6”S 127°56’36.6”E, coll. Adin, 20 Sep 2017.

- Pombo Island: 4 specimens, MZB Cru Cir 043, Pombo, 3°31’55.5”S 128°22’28.8”E, coll. P. Pitriana & D. Tala, 8 Sep 2016.
- Saparua Island: 32 specimens, MZB Cru Cir 044, Dermaga Ihamahu, 3°31’13.0”S 128°41’14.9”E, coll. P. Pitriana & D. Tala, 11 Apr 2016; 31 specimens, MZB Cru Cir 045, Kulur, 3°29’48.5”S 128°36’10.7”E, coll. P. Pitriana & D. Tala, 20 Sep 2016; 40 specimens, MZB Cru Cir 046, Waisisil, 3°34’48.6”S 128°39’04.8”E, coll. P. Pitriana & D. Tala, 8 Apr 2016.
- Seram Island: 15 specimens, MZB Cru Cir 047, Desa Murnaten, 2°51’48.8”S 128°20’32.3”E, coll. P. Pitriana & D. Tala, 19 Sep 2017.

GenBank accession numbers: COI gene (MK995377 - MK995388), 18S (MK981391 - MK981400).

Diagnosis:

Shell with six plates; rostrum and carina with radii; rostral lateral lacking radii; carinal lateral absent; base membranous; conical spines on cirrus I absent; basal guard on apex setae of cirrus II absent.

Description:

Shell white to grey, surface with strong, radiating lines, orifice elliptical (Fig. 2.12a); parietes solid (Fig. 2.12b); scutum triangular, tergal margin straight; tergum triangular, scutal margin curved; conical spines on dorsal side of cirrus I absent, cirrus II with multi-cuspidate setae without basal guard. Basal length 2.4-5.1 mm, basal width 1.4-4.1 mm and height 0.8-1.7 mm. Orifice length 1.0-3.4 mm and orifice width 0.7-1.7 mm (measurements for 25 specimens are presented in Supplementary Table 7.11).

Distribution:

Chthamalus moro is widely distributed in the Indo-Pacific-Indonesia, Philippines, Taiwan, Xisha Islands, Ryukyu Islands, Palau, Mariana Islands, Caroline Islands, Fiji, and Samoa (Southward and Newman 2003). In this study, *C. moro* was found on the islands of Ambon (at Hatu, Mamala, Alang, Asilulu, Hila, Morella, Wakasihu), Pombo, Seram (at Murnaten), and Saparua (at Ihamahu, Kulur, and Waisisil) on mangroves, stone, port pole, mollusd shell, shells of *Tetraclita squamosa*, *Tesseropora rosea* and *Capitulum mitella* (a map with the occurrence of *Chthamalus moro* in the Moluccas is shown in Supplementary Fig. 7.3).

Remarks:

Species of the genus *Chthamalus* are very difficult to distinguish in the field. *Chthamalus moro* has a stellate appearance and is smaller than *C. malayensis* (Southward and Newman 2003). In addition, conical spines on the dorsal side of cirrus I are absent and setae on cirrus II are without basal guards in *C. moro*.

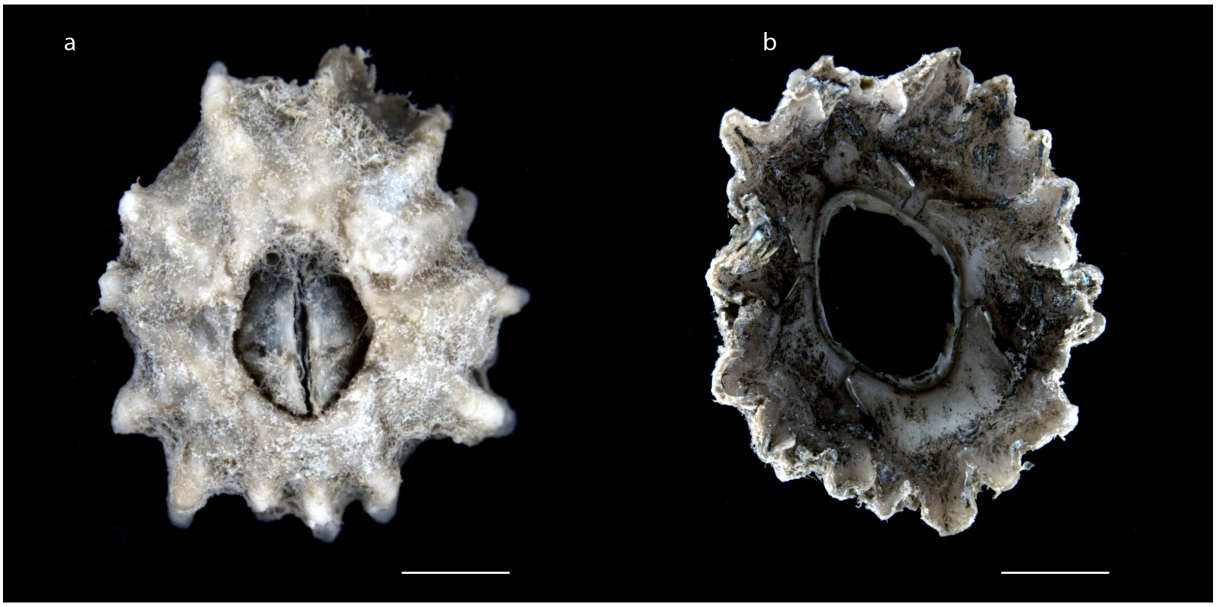

Figure 2.12. *Chthamalus moro* Pilsbry, 1916 (MZB Cru Cir 042-1). (**a**) Upper view, (**b**) lower view. Scale bar: 1 mm.

Superfamily Tetraclitoidea Gruvel, 1905

Family Tetraclitidae Gruvel, 1903

Subfamily Tetraclitellinae Newman & Ross, 1976

Genus *Tetraclitella* Hiro, 1939

Subgenus *Tetraclitella* Hiro, 1939

Tetraclitella divisa (Nilsson-Cantell, 1921)

Figure 2.13a-b, Table 2.1: species no. 59

Tetraclita divisa Nilsson-Cantell, 1921: 362, fig. 83, pl. 3 fig. 11.

Tetraclitella (*Tetraclitella*) *divisa*: Ross & Perreault 1999: 6.

Tetraclitella divisa: Ross 1968: 13; Dong et al. 1982: 111; Foster 1974: 45, figs 6E-F, 7E-F; Bacon et al. 1984: 86; Paulay and Ross 2003: 308; Chan et al. 2009a: 208, fig. 178.

Material examined:

Ambon Island: 1 specimen, MZB Cru Cir 120, Laha, 3°43’22.5”S 128°05’02.5”E, coll. P. Pitriana & D. Tala, 7 Sep 2016.

Diagnosis:

Shell with four plates, flattened, not strongly articulated; radii tubiferous; summit of radii horizontal; tergal spur well separated from scutal margin.

Description:

Shell depressed, covered by furry chitinous integument; shell plates with prominent radiating ribs; radii wide, porose, tubes running parallel to base of shell; colour of shell pale purplish; orifice diamond shaped (Fig. 2.13a–b); scutum triangular, tergal margin straight; tergum higher than wide, scutal margin straight, spur short; mandible with four teeth, second and third teeth bidentate; labrum with smooth cutting edge (measurements for one specimen are presented in Supplementary Table 7.12).

Distribution:

Tetraclitella divisa was previously recorded from Western Africa, Java, Malaysia, Sumatra, Northern Australia, Singapore, South China Sea, China, Taiwan, Japan, the Pacific Ocean to Hawaii and Pitcairn (Jones and Hosie 2016). In this study, *T. divisa* was found on Ambon Island at Laha on a concrete wall at the port (a map with the occurrence of *Tetraclitella divisa* in the Moluccas is shown in Supplementary Fig. 7.2).

Remarks:

Tetraclita divisa exhibits a brooded phase to the cypris larval stage in the mantle cavity, whereas most other species release the first stage nauplius (Nilsson-Cantell 1921; Hiro 1939).

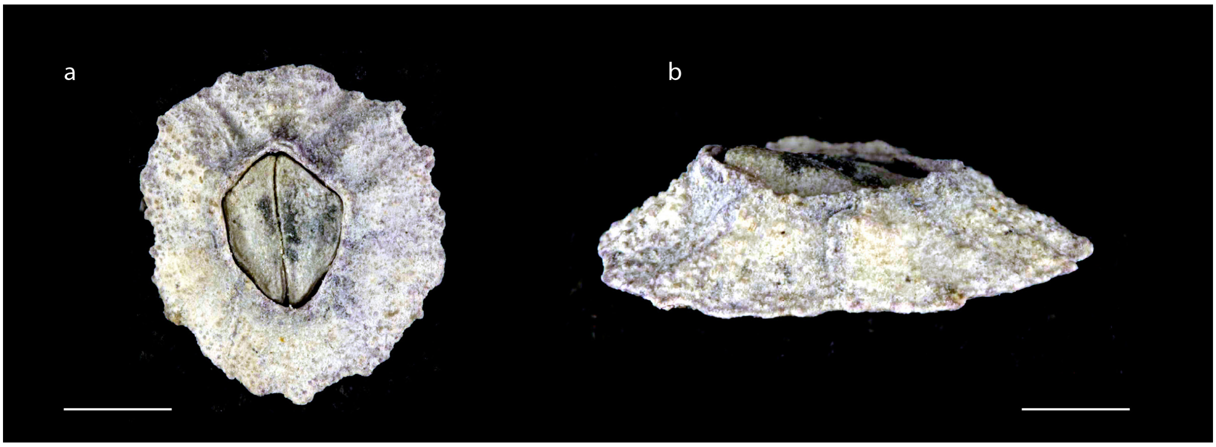

Figure 2.13. *Tetraclitella divisa* (Nilsson-Cantell, 1921) (MZB Cru Cir 120098). (**a**) Upper view, (**b**) side view. Scale bar: 4 mm.

Tetraclitella karandei Ross, 1971

Figure 2.14a-g, Table 2.1: species no. 60

Tetraclitella (*Tetraclitella*) *karandei*: Ross & Perreault 1999: 6.

Tetraclitella karandei Ross, 1971: 217, figs 2-3, 4A-J; Newmann & Ross 1979: 47; Chan et al. 2009a: 214, fig.184.

Material examined:

Ambon Island: 10 specimens, MZB Cru Cir 121, Waitatiri, 3°37’04.0”S 128°16’20.3”E, coll. P. Pitriana & D. Tala, 21 Sep 2017; 2 specimens, MZB Cru Cir 122, Asilulu, 3°40’50.4”S 127°55’27.6”E, coll. Adin, 20 Sep 2017.

Diagnosis:

Shell with four plates, tubiferous, not strongly articulated; radii tubiferous; summit of radii horizontal and elevated above the surface of the parietes; parietes with longitudinal ribs; scutum with nodose ornamentation.

Description:

Shell with orifice diamond shaped, colour greyish (Fig. 2.14a); surface of parietes with chitinous coating and fine hairs, *p*arietes with longitudinal ribs intercalated with lower secondary and tertiary ribs; radii broad, horizontally ridged from base to apex; scutum triangular, occluding and basal margins almost perpendicular, tergal margin straight, surface ornamentation nodose; tergum higher than wide, scutal margin straight, spur small; mandible with four teeth (Fig. 2.14g), labrum slightly notched, two small teeth on each cutting edge. B*asal length* 10.1-17.4 *mm, basal width* 8.2-18.2 *mm, height* 0.4-0.7 *mm.* Orifice length 3.8-5.6 mm, orifice width 2.7-5.2 mm (measurements for three specimens are presented in Supplementary Table 7.13).

Distribution:

Tetraclitella karandei was previously recorded from India, Taiwan, the Philippine (Chan et al. 2009a). In this study, *T. karandei* was found on Ambon Island at Waitairi and Asilulu on stone, on the shells of *Capitulum mitella* and *Euraphia hembeli* (a map with the occurrence of *Tetraclitella karandei* in the Moluccas is shown in Supplementary Fig. 7.2).

Remarks:

Tetraclitella karandei can be distinguished by its radii, which are broad and have extended out and over the adjoining plates. The scutum is also unique because it has nodose ornamentation (Ross 1971).

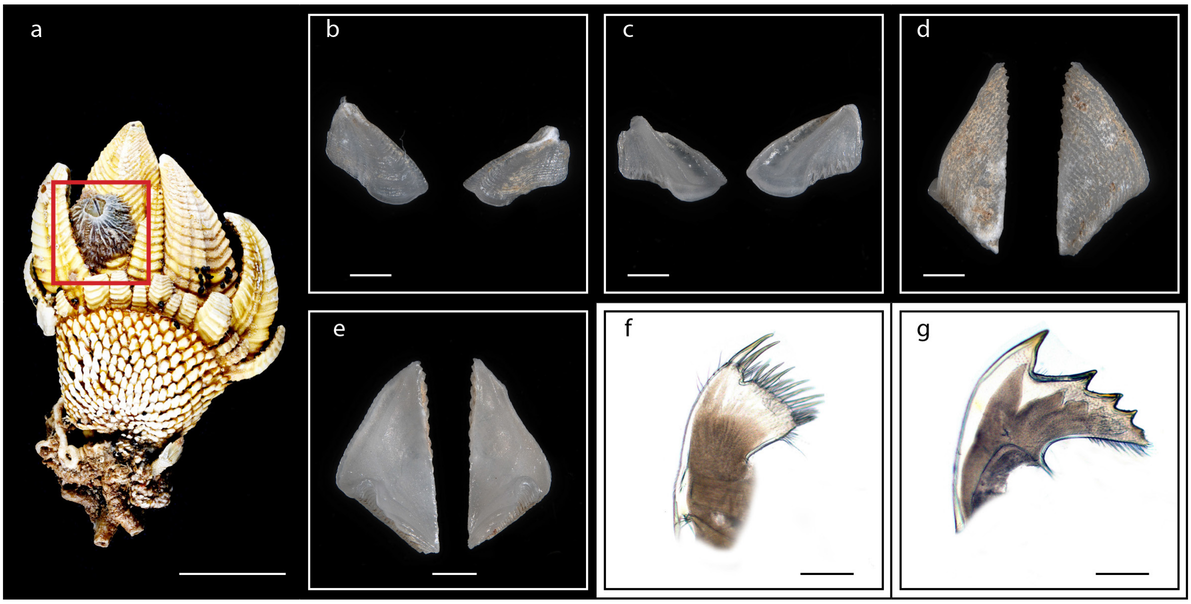

Figure 2.14. *Tetraclitella karandei* Ross, 1971 (MZB Cru Cir 122-2) on tergum of *Capitulum mitella*. (**a**) Upper view of *Tetraclitella karandei* on *Capitulum mitella*, (**b**) external view of scutum, (**c**) internal view of scutum, (**d**) external view of tergum, (**e**) internal view of tergum, (**f**) maxillule, (**g**) mandible. Scale bars: a) 15 mm, b-e) 1 mm, f-g) 0.25 mm.

Subfamily Tetraclitinae Gruvel, 1903

Genus *Tesseropora* Pilsbry, 1916

Tesseropora rosea (Krauss, 1848)

Figure 2.15a-e, Table 2.1: species no. 61

Conia rosea Krauss, 1848: 136.

Tetraclita rosea Darwin, 1854: 335, pl.10 fig. 3a-3d; Pilsbry 1916: 260, pl. 58 fig. 4.

Tesseropora rosea Newman & Ross, 1976: 47; Anderson & Anderson 1985: 89, figs 1-10; Jones & Anderson 1990: 13.

Material examined:

- Ambon Island: 6 specimens, MZB Cru Cir 075, Rutong, 3°42›23.7»S 128°16›08.9»E, coll. P. Pitriana, 14 Jan 2016; 1 specimen, MZB Cru Cir 076, Leahari, 3°42'45.3"S 128°16'16.5"E, coll. P. Pitriana, 14 Jan 2016; 25 specimens, MZB Cru Cir 077, Liang, 3°30'13.3"S 128°20'34.1"E, coll. P. Pitriana & D. Tala, 7 Sept 2016.
- Saparua Island: 25 specimens, MZB Cru Cir 078, Dermaga Ihamahu, 3°31'13.0"S 128°41'14.9"E, coll. P. Pitriana & D. Tala, 11 Apr 2016; 4 specimens, MZB Cru Cir 079, Kulur, 3°29'48.5"S 128°36'10.7"E, coll. P. Pitriana & D. Tala, 20 Sep 2016; 10 specimens, MZB Cru Cir 080, Porto, 3°34›58.2»S 128°36›58.2»E, coll. P. Pitriana & D. Tala, 20 Sep 2016.

  GenBank accession number: COI gene (MK995370).

Diagnosis:

Shell with four plates; wall of the parietes with a single row of parietal pore; orifice with traces of pink in colour; oral cone relatively broad; mouthparts relatively large.

Description:

Shell steeply conical, whitish tinged pink, with longitudinal purple pinkish striations (Fig. 2.15a); four parietal plates with single row of large, square tubes, often eroded in upper areas giving pillared appearance (Fig. 2.15b, c); radii solid, well developed; orifice pentagonal in uneroded specimens, triangular in eroded specimens; basis mostly calcareous; scutum thick, articular furrow short, deep, articular ridge long, adductor ridge prominent, crests for lateral depressor faint; tergum with short, broad spur set close to basiscutal angle, wide articular furrow, carinal depressor crests prominent (Fig.2.15d, e); maxillule with two large setae at the lateral angle; mandible with four teeth, labrum shallowly concave in shape, teeth on each side. B*asal length* 9.7-25.6 *mm, basal width* 9.7-24.5 *mm, height* 4.4-13.0 *mm. Orifice* length 2.9-7.8 mm, orifice width 2.3-6.9 mm (measurements for 15 specimens are presented in Supplementary Table 7.14).

Distribution:

Tesseropora rosea was originally described from a specimen collected at Algoa Bay, South Africa (Krauss 1848; Darwin 1854) and has since been recorded from Australia (SW and SE); Lord Howe Island and the Kermadec Islands (Jones 1990). In this study, *T. rosea* was found on Ambon Island (at Rutong, Leahari, and Liang) and Saparua Island (at Ihamahu, Kulur, and Porto) on stone and mollusc shells (a map with the occurrence of *Tesseroppora rosea* in the Moluccas is shown in Supplementary Fig. 7.4).

Remarks:

According to Anderson and Anderson (1985), *T. rosea* feeds in different ways, extending the cirral fan only in response to the fast water currents. Thus, *T. rosea* cannot survive in areas with a low current velocity. *Tesseropora rosea* exhibits a wide distribution although the species is represented by relatively few specimens.

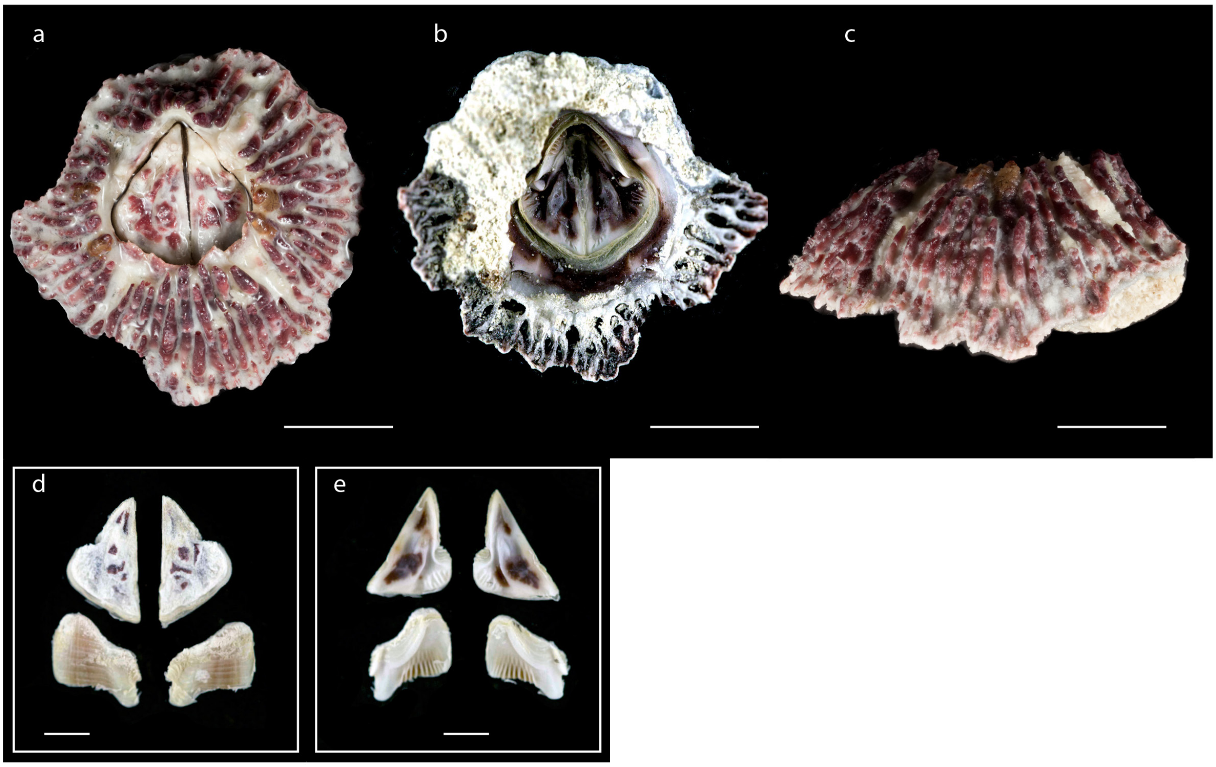

Figure 2.15. *Tesseropora rosea* (Krauss, 1848) (MZB Cru Cir 077-1). (**a**) Upper view, (**b**) lower view, (**c**) side view, (**d**) external view of scutum and tergum, (**e**) internal view of scutum and tergum. Scale bars: a-c) 6 mm, d, e) 2 mm.

Genus *Tetraclita* Schumacher, 1817

Tetraclita kuroshioensis Chan, Tsang & Chu, 2007

Figure 2.16a-g, Table 2.1: species no. 62

Tetraclita squamosa viridis: Hiro 1936b: 635.
Tetraclita squamosa squamosa: Utinomi 1968a: 178.
Tetraclita pacifica Chan et al., 2007a: 88, figs 4-6.
Tetraclita kuroshioensis Chan et al., 2007: 56; Chan et al. 2009a: 192, fig. 164; Pochai et al. 2017: 21, fig. 6.

Material examined:

- Ambon Island: 1 specimen, MZB Cru Cir 097, Hatu, 3°43’52.7”S 128°02’51.4”E, coll. Adin, 20 Sep 2017; 6 specimens, MZB Cru Cir 098, Ureng, 3°40’14.0”S 127°56’47.6”E, coll. Adin, 20 Sep 2017.

- Saparua Island: 1 specimen, MZB Cru Cir 100, Dermaga Ihamahu, 3°31’13.0”S 128°41’14.9”E, coll. P. Pitriana & D. Tala, 11 Apr 2016.
  GenBank accession numbers: COI gene (MK995363, MK995364, MK995367), 18S (MK981375, MK9876, MK981379).

Diagnosis:

Shell conical with four plates, tubiferous; radii solid; tergum broad, apex not beaked.

Description:

Shell with four inseparable, multi-tubiferous plates, greyish black to purplish-grey or deep green to green, surfaces with mosaic scales pattern radiating randomly from base to apex, internal surface of parietes smooth, white with dark grey striations around aperture; radii solid (Fig. 2.16a-c); basis membranous; scutum larger than tergum, triangular, external surface with horizontal striations, occluding margin with fine teeth; tergum broad, higher than wide, apex not produced as beak, spur sharp, basi-scutal angle smaller than that of *Tetraclita squamosa* (Fig. 2.16d, e); external surface of operculum grey and yellowish-light brown, internal surface greyish-dusky green; mandible with four large teeth; maxillule not notched with eleven setae; labrum with five small teeth on each side; cirrus I possessing serrulate setae. *Basal length* 12.1-21.6 *mm, basal width* 18.1-21.8 *mm, height* 7.3-10.4 *mm. Orifice* length 3.2-5.3 mm, orifice width 2.4-4.2 mm (measurements for five specimens are presented in Supplementary Table 7.15).

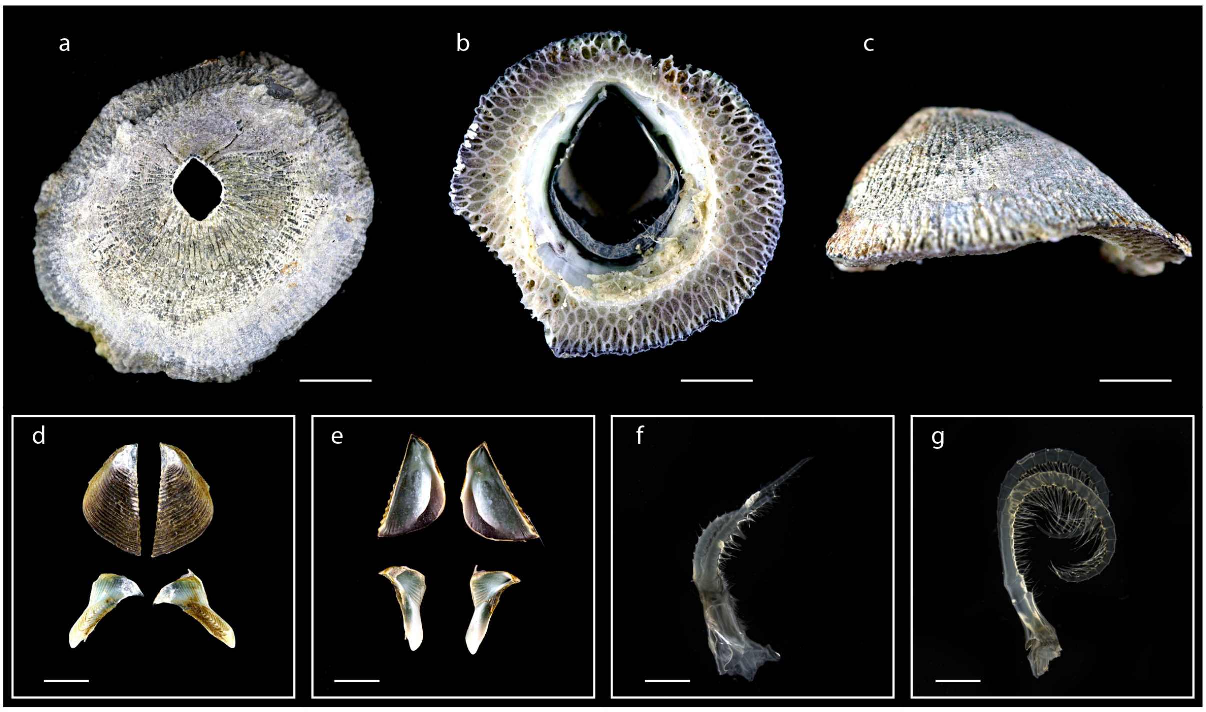

Figure 2.16. *Tetraclita kuroshioensis* Chan, Tsang & Chu, 2007 (MZB Cru Cir 097). (**a**) Upper view, (**b**) lower view, (**c**) side view, (**d**) external view of scutum and tergum, (**e**) internal view of scutum and tergum, (**f**) cirrus I, (**g**) cirrus VI. Scale bars: a-c) 7 mm, d-e) 2 mm, f, g) 1 mm.

Distribution:

Tetraclita kuroshioensis was previously recorded from Japan, Taiwan, Palau, and Thailand (Chan et al. 2009a; Pochai et al. 2017). In this study, *T. kuroshioensis* was found on Ambon Island (at Hatu and Ureng) and Saparua Island (at Dermaga Ihamahu) on rocks and concrete wall of a port (a map with the occurrence of *Tetraclita kuroshioensis* in the Moluccas is shown in Supplementary Fig. 7.4).

Remarks:

Tetraclita kuroshioensis and *T. squamosa* share great morphological similarity. However, DNA sequences separate the two species (Chan et al. 2007), which was confirmed in this study (Fig. 2.29). Morphologically, the shape of the tergum is definitive; that of *T. kuroshioensis* is broader and the apex blunter compared to *T. squamosa* (Chan et al. 2007).

Tetraclita squamosa **(Bruguiére, 1789)**

Figure 2.17 a-k, Table 2.1: species no. 63

Balanus squamosus Bruguière, 1789: 170, pl. 165 figs 9, 10.
Lepas fungites Spengler, 1790: 189.
Lepas porosa Gmelin, 1791: 3212; Wood 1815: pl. 9 fig. 4.
Tetraclita squamulosa Schumacher, 1817: 91.
Asemus porosus: Ranzani 1820: pl. 3 figs 32–35.
Conia porosa: Sowerby 1823: pl. 1.
Tetraclita porosa var. (3) *viridis* Darwin, 1854a: 329.
Tetraclita porosa viridis: Nilsson-Cantell 1921: 364.
Tetraclita squamosa squamosa: Pilsbry 1916: 251; Dong et al. 1982: 110, fig.
Tetraclita squamosa forma *viridis*: Broch 1922: 337.
Tetraclita squamosa viridis: Hiro 1936b: 635.
Tetraclita porosa perfecta Nilsson-Cantell, 1931a: 133, pl. II fig. 8a-e.
Tetraclita squamosa: Stebbing 1910: 570; Ren & Liu 1979: 339, pl. 1 figs 1–11; Yamaguchi 1987: 344; Zevina et al. 1992: 45, fig. 30; Chan 2001: 625, fig. 8; Chan et al. 2007a: 82, fig. 4; Chan et al. 2009a: 195, fig. 167; Pochai et al. 2017: 25, fig.8.

Material examined:

- Ambon Island: 17 specimens, MZB Cru Cir 081, Alang, 3°45’11.0”S 128°01’23.1”E, coll. Adin, 20 Sep 2017; 15 specimens, MZB Cru Cir 082, Dermaga Liang, 3°30’13.3”S 128°20’34.1”E, coll. P. Pitriana & D. Tala, 30 Aug 2016; 2 specimens, MZB Cru Cir 083, Dermaga Tulehu, 3°35’21.8”S 128°20’02.8”E, coll. P. Pitriana & D. Tala, 7 Sep 2016; 15 specimens, MZB Cru Cir 084, Doc Tawiri, 3°42’10.1”S 128°06’13.4”E, coll. P. Pitriana & D. Tala, 29 Mar 2016; 2 specimens, MZB Cru Cir 085, Gudang Arang, 3°42’07.2”S 128°09’43.7”E, coll. P. Pitriana & D. Tala, 5 Sep 2016; 5 specimens, MZB Cru Cir 086, Hila, 3°34’57.5”S 128°05’31.9”E, coll. Adin, 20 Sep 2017; 17 specimens, MZB Cru Cir 087, Hutumuri, 3°41’47.6”S 128°17’44.1”E, coll. P. Pitriana, 14 Jan 2016; 5 specimens, MZB Cru Cir 088, Leahari, 3°42’45.3”S 128°16’16.5”E, coll. P. Pitriana, 14 Jan 2016; 6 specimens, MZB Cru Cir 089, Tawiri, 3°42’10.1”S 128°06’13.4”E, coll. P. Pitriana & D. Tala, 5 Sep 2016; 3 specimens, MZB Cru Cir 090, Tulehu, 3°35’21.8”S 128°20’02.8”E, coll. P. Pitriana & D. Tala, 7 Sep 2016; 7 specimens, MZB Cru Cir 091, Waai, 3°33’23.5”S 128°19’33.9”E, coll. P. Pitriana & D. Tala, 7 Sep 2016; 2 specimens, MZB Cru Cir 092, Waai, 3°33’23.5”S 128°19’33.9”E, coll. P. Pitriana & D. Tala, 31 Mar 2017; 45 specimens, MZB Cru Cir 096, Asilulu, 3°40’50.4”S 127°55’27.6”E, coll. Adin, 20 Sep 2017; 40 specimens, MZB Cru Cir 099, Wakasihu, 3°46’27.6”S 127°56’36.6”E, coll. Adin, 20 Sep 2017.

- Saparua Island: 5 specimens, MZB Cru Cir 093, Benteng Durstede, 3°34’32.8”S 128°39’34.7”E, coll. P. Pitriana & D. Tala, 8 Apr 2016; 6 specimens, MZB Cru Cir 094, Teluk Saparua, 3°34’25.7”S 128°39’25.8”E, coll. P. Pitriana & D. Tala, 8 Apr 2016; 5 specimens, MZB Cru Cir 095, Teluk Saparua, 3°34’25.7”S 128°39’25.8”E, coll. P. Pitriana & D. Tala, 22 Sept 2016.

GenBank accession numbers: COI gene (MK995360 - MK995362), 18S (MK981368 - MK981373).

Diagnosis:

Shell conical with four plates, tubiferous; radii solid; tergum narrow, concaved, apex beaked.

Description:

Shell consisting of four fused, inseparable plates (Fig. 2.17a), parietes with eight rows of multi-tubiferous parietal tubes (Fig. 2.17b), external surface with longitudinal lines from base to apex, internal surface smooth, white with purplish grey striations close to aperture; *orifice rhomboidal;* basis membranous; shell greenish with brownish grey (Fig. 2.17a), external surface of operculum brownish grey, internal surface purplish grey; scutum triangular, larger than tergum, external surface with horizontal striations, occluding margin with very shallow teeth; tergum narrow, apex beaked, spur long, sharp (Fig. 2.17c, d); mandible with four large teeth, first tooth with three small spines, lower margin pectinate (Fig. 2.17k); maxillule notched with two large setae above notch, elevan small setae below notch (Fig. 2.17j); labrum with four large teeth on each side of notch; cirrus I with bidentate serrulate setae (Fig. 2.17e). B*asal length* 20.1-30.2 *mm, basal width* 19.3-28.3 *mm, height* 11.9-14.2 *mm. Orifice* length 4.4-7.9 mm, orifice width 3.4-7.2 mm (measurements for five specimens are presented in Supplementary Table 7.16).

Distribution:

Tetraclita squamosa is widespread in the Indo-Pacific region, Australia, South China coast, and Taiwan (Newman 1978; Jones et al. 2001; Chan et al. 2009a). In this study, *T. squamosa* was found on Ambon Island (at Alang, Dermaga Liang, Dermaga Tulehu, Doc Tawiri, Gudang Arang, Hila, Hutumuri, Leahari, Tawiri, Tulehu, Waai, Asilulu, Wakasihu) and Saparua Island (at Benteng Duurstede and Teluk Saparua) on stone, rocks, shipyards, concrete bridges and walls of the port (a map with the occurrence of *Tetraclita squamosa* in the Moluccas is shown in Supplementary Fig. 7.4).

Remarks:

Tetraclita squamosa has characteristic green parietes (Yamaguchi 1987) and a wide distribution throughout the Indo-Pacific (Newman and Ross 1976). However, the taxonomy of *Tetraclita squamosa* has been confusing due to a high degree of morphological variation, and it is now considered a species complex. *Tetraclita squamosa* and *Tetraclita japonica* can be separated using characters such as the shape of the parietes, scutum geometry, and mandible structures (Darwin 1854; Pilsbry 1916). In addition, a key character for *T. squamosa* is the tergum with a beak on its apex (Chan et al. 2009a).

Figure 2.17. *Tetraclita squamosa* (Bruguiére, 1789) (MZB Cru Cir 081-3). (**a**) Upper view, (**b**) lower view, (**c**) external view of scutum and tergum, (**d**) internal view of scutum and tergum, (**e**) cirrus I, (**f**) cirrus II, (**g**) cirrus III, (**h**) cirrus IV, (**i**) cirrus VI, (**k**) maxillule, (**l**) mandible. Scale bars: a, b) 8 mm, c, d) 2 mm, e, f) 1 mm, g-i) 2 mm, j, k) 0.5 mm.

Subfamily Newmanellinae Ross & Perreault, 1999

Genus *Yamaguchiella* Ross & Perreault, 1999

Yamaguchiella coerulescens (Spengler, 1790)

Figure 2.18a-g, Table 2.1: species no. 64

Lepas coerulescens Spengler, 1790: 191.

Tetraclita coerulescens: Darwin 1854: 342, pl. 11 figs 4a-d; Hoek 1883: 161, pl. 13 fig. 34; Pilsbry 1916: 259; Nilsson-Cantell 1938: 77; Newman & Ross 1976: 47; Dong et al. 1982: 111; Zevina et al. 1992: 48, fig. 31.

Yamaguchiella (*Yamaguchiella*) *coerulescens*: Ross & Perreault 1999: 5; Jones & Hosie 2016: 271; Chan et al. 2009a: 202, fig. 173.

Material examined:

- Ambon Island: 13 specimens, MZB Cru Cir 123, Gudang Arang, 3°42’07.2”S 128°09’43.7”E, coll. P. Pitriana & D. Tala, 5 Sep 2016; 4 specimens, MZB Cru Cir 124, Dermaga Tulehu, 3°35’05.4”S 128°19’43.3”E, coll. P. Pitriana & D. Tala, 7 Sep 2016; 5 specimens, MZB Cru Cir 125, Tulehu, 3°35’21.8”S 128°20’02.8”E, coll. Adin, 19 Sep 2017; 14 specimens, MZB Cru Cir 126, Doc Tawiri, 3°42’10.1”S 128°06’13.4”E, coll. P. Pitriana & D. Tala, 29 Mar 2016; 8 specimens, MZB Cru Cir 127, Tawiri, 3°42’10.1”S 128°06’13.4”E, coll. P. Pitriana & D. Tala, 5 Sep 2016; 2 specimens, MZB Cru Cir 128, Galala, 3°41’22.2”S 128°10’52.6”E, coll. P. Pitriana & D. Tala, 6 Sep 2016; 11 specimens, MZB Cru Cir 129, Waai, 3°33’23.5”S 128°19’33.9”E, coll. P. Pitriana & D. Tala, 7 Sep 2016; 4 specimens, MZB Cru Cir 130, Pelabuhan Yos Sudarso, 3°41’36.5”S 128°10’35.6”E, coll. P. Pitriana & D. Tala, 6 Sep 2016.
- Saparua Island: 1 specimen, MZB Cru Cir 131, Kulur, 3°29’48.5”S 128°36’10.7”E, coll. P. Pitriana & D. Tala, 20 Sep 2016.
  GenBank accession number: 18S (MK981381).

Diagnosis:

Shell with the upper part tinged greenish-blue, longitudinally ribbed; radii moderately wide, with their summits oblique; scutum with a small adductor and extremely prominent articular ridge, united together and forms a small sub-cylindrical cavity; tergum with the spur not joined to the basi-scutal angle.

Description:

Shell low conical to cylindro-conic (Fig. 2.18c) with four multi-tubiferous plates (Fig. 2.18b), parieties greenish or greyish with radiating lines (Fig. 2.18a); radii wide, summits oblique; basis calcareous, radii wide, tubiferous, summits oblique; orifice occluded wholly by scutum (Fig. 2.18a); scutum and tergum strongly articulated (Figs 2.18d, e); mandible with four teeth, the third teeth is tridentate (Fig. 2.18g); labrum with three large teeth on each side of cutting edge; penis with basidorsal point. Basal length 8.3-29.0 mm, basal width 8.5-27.8 mm, height 5.7-17.7 mm. Orifice length 4.2-11.5 mm, orifice width 3.2-11.8 mm (measurements for 25 specimens are presented in Supplementary Table 7.17).

Distribution:

Yamaguchiella coerulescens was previously recorded from the Indo-west Pacific: the Indian Ocean, Bay of Bengal, Mergui Archipelago, Kei Islands, Banda Island, Malay Archipelago, Sulu Archipelago, Vietnam, China, Philippines, Goram Island, Palao Island, and Taiwan (Jones and Hosie 2016). In this study, *Y. coerulescens* was found on Ambon Island (at Tulehu, Dermaga Gudang Arang, Waai, Doc. Tawiri, Liang, Galala, Dermaga Yos Sudarso) and Saparua Island (at Kulur) on stone (a map with the occurrence of *Yamaguchiella coerulescens* in the Moluccas is shown in Supplementary Fig. 7.6).

Remarks:

The subgenus *Yamaguchiella* was proposed by Ross and Perreault (1999) in honour of Toshiyuki Yamaguchi (Chiba University Japan), in appreciation of his contributions to the knowledge of recent and fossil barnacles.

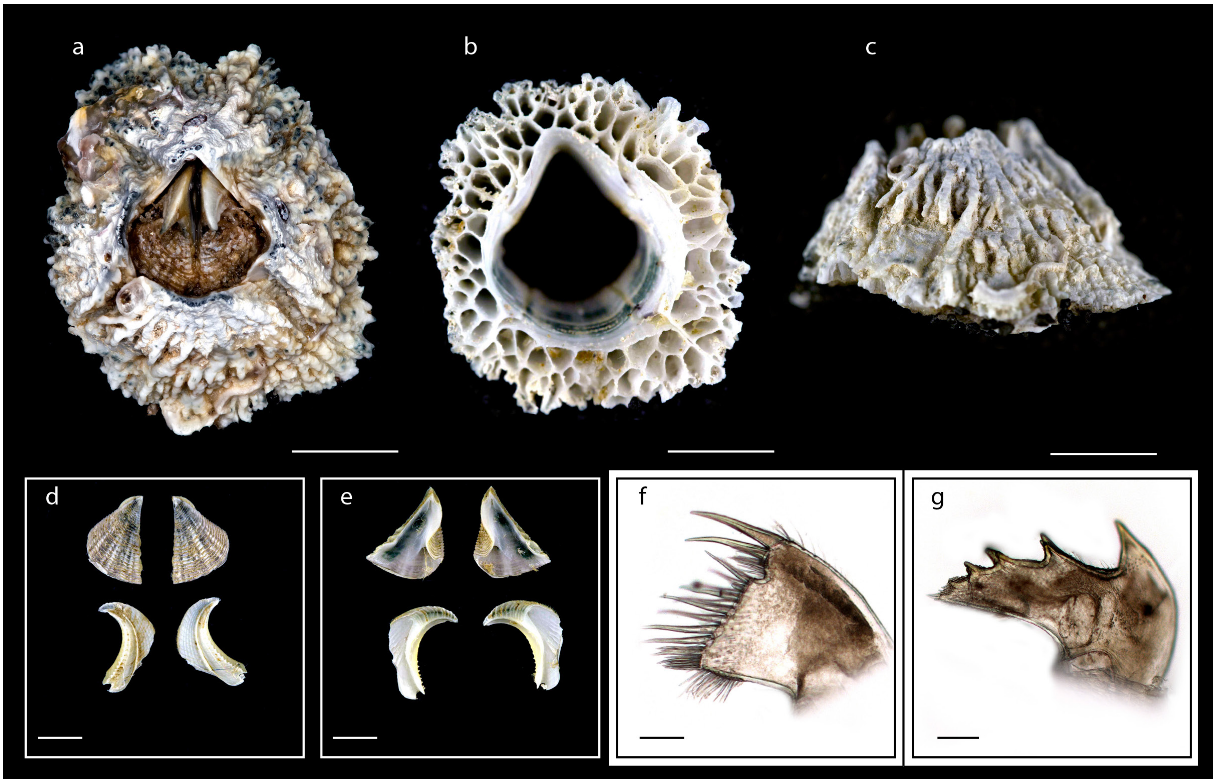

Figure 2.18. *Yamaguchiella coerulescens* (Spengler, 1790) (MZB Cru Cir 123-2). (**a**) Top view, (**b**) bottom view, (**c**) side view, (**d**) external view of scutum and tergum, (**e**) internal view of scutum and tergum, (**f**) maxillule, (**g**) mandible. Scale bars: a-c) 7 mm. d, e) 1 mm, f, g) 0.5 mm.

Genus *Yamaguchiella* Ross & Perreault, 1999

Subgenus *Neonrosella* Jones, 2010

Neonrosella vitiata (Darwin, 1854)

Figure 2.19a-f, Table 2.1: species no. 65

Tetraclita vitiata Darwin, 1854: 340, pl. 11 fig. 3a-e.
Tetraclita (*Tetraclita*) *vitiata*: Rosell 1972: 214.
Newmanella vitiata: Ikeya & Yamaguchi 1993: 93; Jones et al. 1990: 14.
Yamaguchiella (*Rosella*) *vitiata*: Ross & Perreault 1999: 5.
Yamaguchiella (*Neonrosella*) *vitiata*: Jones 2010: 214.
Neonrosella vitiata: Sukparangsi et al. 2019:4, figs 1-4.

Material examined:

- Ambon Island: 3 specimens, MZB Cru Cir 132, Liang, 3°30'13.3"S 128°20'34.1"E, coll. P. Pitriana & D. Tala, 7 Sep 2016.
- Banda Neira Island: 1 specimen, MZB Cru Cir 133, Banda Neira, 4°31'22.8"S 129°53'52.5"E, coll. P. Pitriana, 25 May 2016.
- Saparua Island: 4 specimens, MZB Cru Cir 134, Tuhaha, 3°32'38.1"S 128°40'58.0"E, coll. P. Pitriana & D. Tala, 21 Sep 2016.

  GenBank accession number: 18S (MK981384).

Diagnosis:

Parietes low with wall spreading; peritreme slightly toothed; base calcareous with two rows of irregular shape and size of parietal tubes; tergum with broad spur; lateral scutal depressor crests numerous and deep; five toothed mandibles; segments of posterior cirri with four pairs spines.

Description:

Shell four plated, conical, whitish with spots of purple in upper part (Fig. 2.19a); parietal tubes irregular shape, size unequal (Fig. 2.19b); radii moderately wide, summits oblique, interior of irregularly branching ridges with solid interspaces (Fig. 2.19c); orifice trigonal; scutum and tergum coalesced, strongly articulated (Fig. 2.19d, e); tergum with broad spur, lateral tergal depressor crests on basal margin long, with numerous, deep crests, lateral scutal depressor crests numerous, deep; mandible with five teeth (Fig. 2.19f). *Basal length* 15.4-22.8 *mm, basal width* 13.8-22.8 *mm, height* 5.3-6.9 *mm.* Orifice length 5.2-6.9 mm, orifice width 4.6-5.4 mm (measurements for four specimens are presented in Supplementary Table 7.18).

Distribution:

Neonrosella vitiata was previously recorded from the Indo-west Pacific, Indian Ocean, Nicobar Island to Australia, Indonesia, Malay Archipelago, Sulu Archipelago, Philippines, and the Pacific Ocean (Jones and Hosie 2016). Recently, *Neonrosella vitiata* also was discovered in the Andaman Sea of Thailand (Sukparangsi et al. 2019). In this study, *N. vitiata* was found on Ambon Island (at Liang), Banda Island and Saparua Island (at Tuhaha) on port poles, reef and stones (a map with the occurrence of *Neonrosella vitiata* in the Moluccas is shown in Supplementary Fig. 7.7).

Remarks:

Neonrosella vitiata can be distinguished by its irregular parietal tubes, the shape of the terga, the five toothed mandibles and four pairs of spines on the segments of the posterior cirri (Darwin 1854).

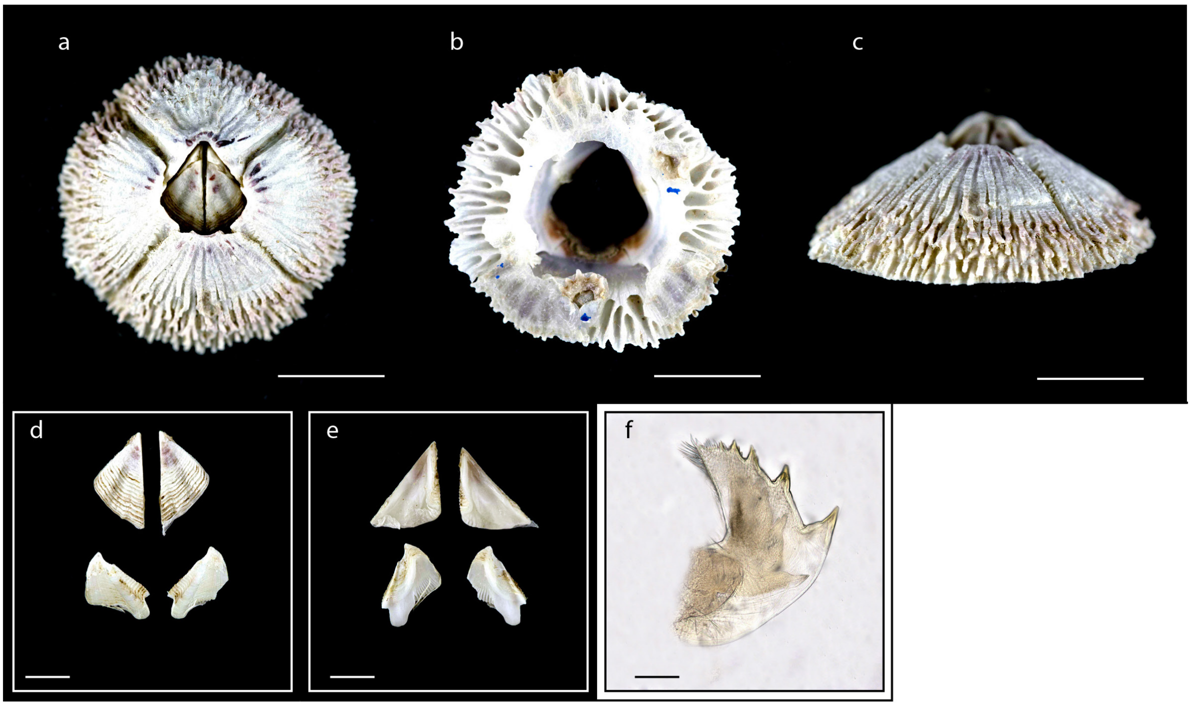

Figure 2.19. *Neonrosella vitiata* (Darwin, 1854) (MZB Cru Cir 132-3). (**a**) Upper view, (**b**) lower view, (**c**) side view, (**d**) external view of scutum and tergum, (**e**) internal view of scutum and tergum, (**f**) mandible. Scale bars: a-c) 8 mm, d, e) 1 mm, f) 0.5 mm.

Genus *Newmanella* Ross, 1969

Newmanella spinosus Chan & Cheang, 2016

Figure 2.20a-e, Table 2.1: species no. 66

Newmanella radiata: Chan et al. 2009: 199, fig. 170.
Newmanella sp. Tsang et al., 2015: 325, fig. 1A; 327 fig. 2.
Newmanella spinosus Chan & Cheang, 2016: 212, figs 9-15; Pochai et al. 2017: 20, fig. 5; Sukparangsi et al. 2019: 10, figs 5-8.

Material examined:

- Ambon Island: 5 specimens, MZB Cru Cir 072, Rutong, 3°42’23.7”S 128°16’08.9”E, coll. P. Pitriana, 14 Jan 2016.

Diagnosis:

Shell low conical to cylindro-conical; parietes discrete; base calcareous; radii broad; scutum with very deep depressor muscle crests; cirrus II and cirrus IV having numerous triangular spines; fourth and fifth teeth of mandible separated; cutting edge of maxillule below notch protruding; intromittent organ of penis lacking basi-dorsal point.

Description:

Shell low conical, four plates externally greyish in colour, parietes with deep longitudinal, radiating lines from base to apex, internally with multiple rows of irregular parietal tubes (Fig. 2.20a, b); radii wide with horizontal striations, summits oblique (Fig. 2.20c); scutum triangular, external surface with horizontal striations, adductor ridge conspicuous; tergum high, narrow, basal margin with well-developed depressor muscle crests projecting beyond border; orifice pentagonal (Fig. 2.20d, e); basis calcareous, tubiferous, tubes in single layer; mandible with five teeth, the first tooth is the largest and separated from the rest, while the fifth tooth is the smallest and located at the middle of lower margin; labrum with V-shaped notch, two large teeth on the right side, five teeth on the left side of cutting margin; penis without basidorsal point, with few bundles of setae distally. Basal length 17.4-20.9 mm, basal width 15.9-20.5 mm, height 6.8-8.9 mm. Orifice length 5.3-7.3 mm, orifice width 5.0-6.7 mm (measurements for five specimens are presented in Supplementary Table 7.19).

Distribution:

Newmanella spinosus was previously recorded from Japan, Taiwan, Philippines, and Thailand (Chan and Cheang 2016; Pochai et al. 2017). In the current study, this range is extended to Rutong (on stones and reef surface), Ambon Island (a map with the occurrence of *Newmanella spinosus* in the Moluccas is shown in Supplementary Fig. 7.2).

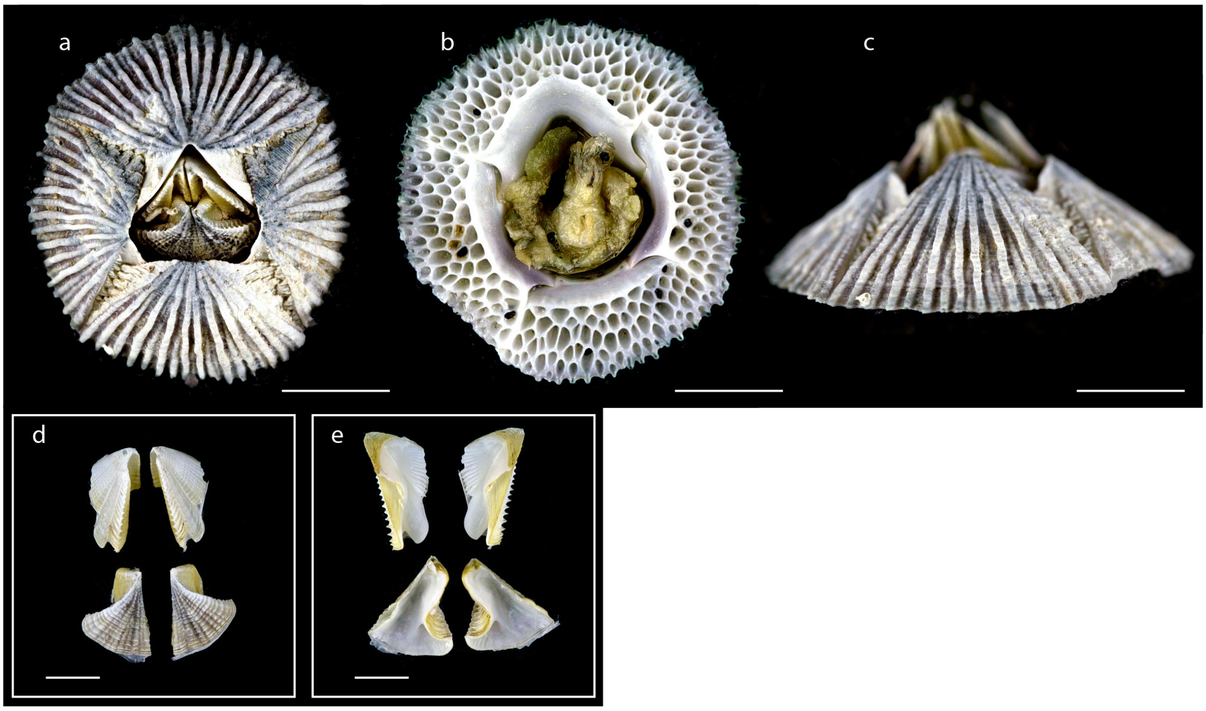

Figure 2.20. *Newmanella spinosus* Chan & Cheang, 2016 (MZB Cru Cir 072-1). (**a**) Upper view, (**b**) lower view, (**c**) side view, (**d**) external view of scutum and tergum, (**e**) internal view of scutum and tergum. Scale bars: a-c) 7 mm, d, e) 2 mm.

Remarks:

Newmanella spinosus is morphologically close to *Newmanella radiata* but it can be distinguished by the morphology of the scutum, tergum, cirrus II, mandible and maxillule. *N. spinosus* also has numerous spines on its cirri, especially on cirrus II, which is different from *N. radiata* (Chan and Cheang 2016).

Family Balanidae Leach, 1817

Subfamily Amphibalaninae Pitombo, 2004

Genus *Amphibalanus* Pitombo, 2004

Amphibalanus amphitrite (Darwin, 1854)

Figure 2.21a-h, Table 2.1: species no. 87

Balanus amphitrite Darwin, 1854: 240 (part.), pl. 5. figs 2a-d, i-k, m-o; Weltner 1897:264; Hoek 1913: 167; Pilsbry 1916: 89; Zevina et al. 1992: 89, fig. 61; Puspasari et al. 2001b: 7.

Balanus amphitrite var. (1) *communis* Darwin, 1854: 240, pl. 5 fig. 2e, h, l.

Balanus amphitrite communis: Nilsson-Cantell 1921: 311, fig. 64.

Balanus amphitrite forma *hawaiiensis* Broch, 1922: 314, fig. 56 (part.).

Balanus amphitrite forma *denticulata* Broch, 1927b: 133, fig. 14 (part.).

Balanus amphitrite hawaiiensis: Hiro 1937c: 432, figs 20, 21.

Balanus amphitrite cochinensis Nilsson-Cantell, 1938b: 43, fig. 11a-e.

Balanus amphitrite var. *fluminensis* Oliveira, 1941: 21, pl. 4 fig. 4, pl. 5 figs 1, 2, pl. 8 figs 1-5.

Balanus amphitrite var. *aeratus* Oliveira, 1941: 22, pl. 4 fig. 5, pl. 9 figs 1-4.

Balanus amphitrite herzi Rogers, 1949: 8, pl. 1 figs 6, 12-15.

Balanus amphitrite franciscanus Rogers, 1949: 9, pl. 1 figs 5, 7, 16-19.

Balanus amphitrite var. *columnarius* Tarasov & Zevina, 1957: 179, 184, fig. 68 a-e.

Balanus amphitrite denticulata Henry, 1959: 192, pl. 1 fig. 5, pl. 3 fig. 7, upper row right.

Balanus amphitrite amphitrite: Harding 1962: 274, pl. 1a-g, pl. 2a-k; Dong et al. 1982: 90, fig. A-E; Rosell 1981: 302.

Balanus amphitrite var. *hawaiiensis*: Stubbings 1963b: 15.

Amphibalanus amphitrite: Pitombo 2004: 263, 274, figs 2A, B, 7A, B, 8C; Chan et al. 2009a: 241; Chen et al. 2014: 1071; Shahdadi et al. 2014: 213; Pochai et al. 2017: 27, fig. 9; Xu 2017: 48.

Material examined:

- Ambon Island: 4 specimens, MZB Cru Cir 005, Galala, 3°41’22.2”S 128°10’52.6”E, coll. P. Pitriana & D. Tala, 6 Sep 2016.
- Saparua Island: 4 specimens, MZB Cru Cir 007, Desa Mahu, 3°32’19.6”S 128°41’17.3”E, coll. P. Pitriana & D. Tala, 11 Apr 2016; 5 specimens, MZB Cru Cir 008, Negeri Mahu, 3°31’52.9”S 128°41’12.4”E, coll. P. Pitriana & D. Tala, 11 Apr 2016; 2 specimens, MZB Cru Cir 009, Tuhaha, 3°32’38.1”S 128°40’58.0”E, coll. P. Pitriana & D. Tala, 21 Sep 2016.

Diagnosis:

Primary parietal tubes with transverse septa; exterior of shell with longitudinal purple striations, horizontal striations absent; tergum short with wide spur; cirri III-VI with erect teeth below posterior angles of distal; cirrus III without complex setae.

Description:

Shell six plated, conical, round;, externally smooth, white with groups of well-spaced, dark purple vertical stripes, horizontal striations on shell surface absent (Fig. 2.21a, b), interior of parietes with single row of tubes (Fig. 2.21c); radii solid, wide; alae with summits moderately oblique (Fig. 2.21a, b); basis porous, calcareous; scutum externally striped, internally with prominent articular ridge 3/5 length of tergal margin, well separated from straight adductor ridge, occluding margin toothed, lateral depressor muscle pit small (Fig. 2.21d, e); tergum with spur wider than long, less than its own width from basi-scutal angle (Fig. 2.21d, e); mandible with four teeth (Fig. 2.21g); labrum multi-denticulate (Fig. 2.21h). Basal length 3.1-17.8 mm; basal width 2.8-17.6 mm; height 2.1-10.8 mm; orifice length 1.5-8.1 mm; orifice width 1.5-5.4 mm (measurements for 15 specimens are presented in Supplementary Table 7.20).

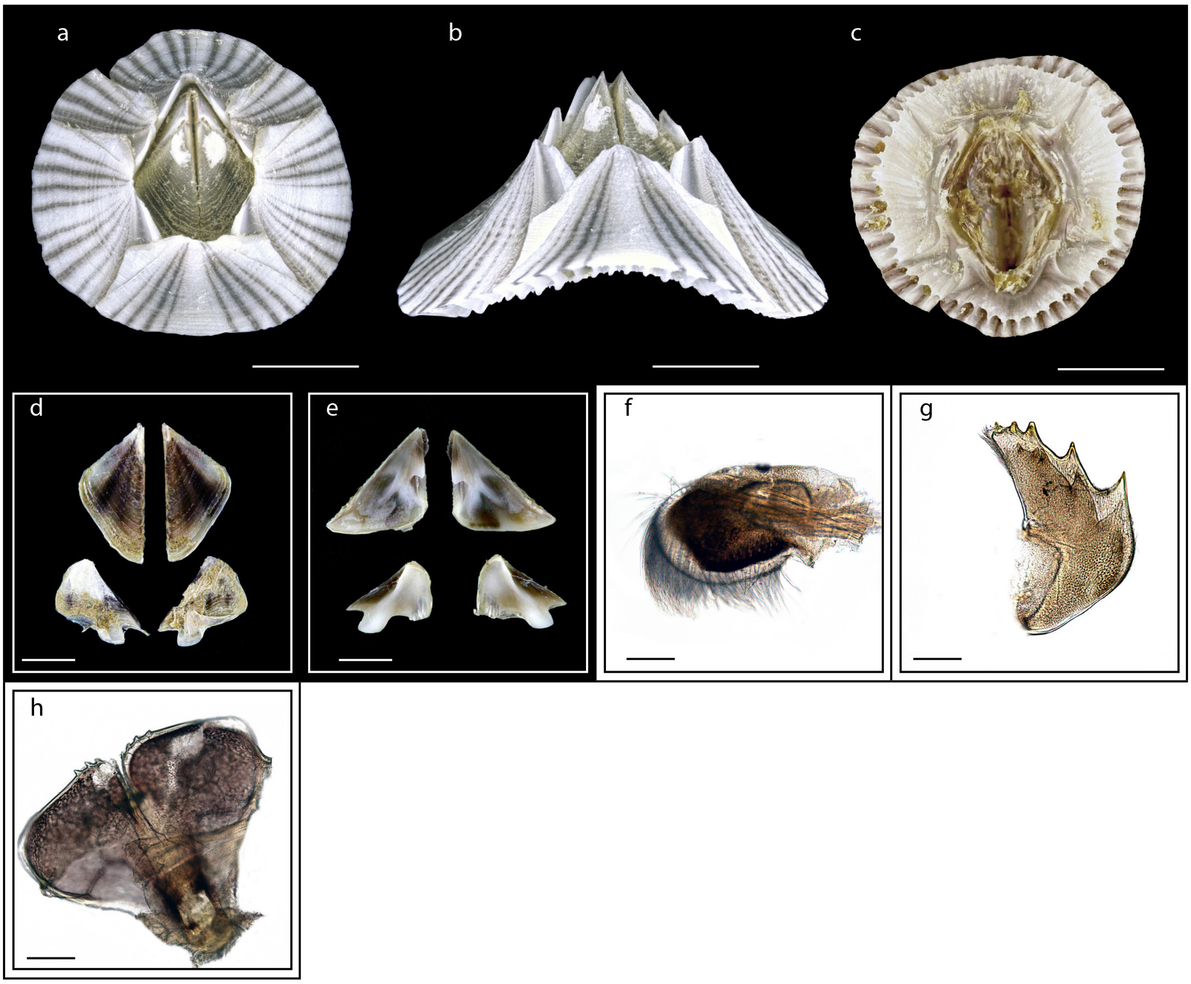

Figure 2.21. *Amphibalanus amphitrite* (Darwin, 1854) (MZB Cru Cir 005-4). (**a**) Upper view, (**b**) side view, (**c**) lower view, (**d**) external view of scutum and tergum, (**e**) internal view of scutum and tergum, (**f**) maxilla, (**g**) mandible, (**h**) labrum. Scale bars: a-c) 4 mm, d, e) 1 mm, f-h) 0.5 mm.

Distribution:

Amphibalanus amphitrite is commonly found on beaches and in estuaries, lives attached to harsh natural substrate, such as bedrock, rocks, shells of molluscs, as well as the roots and trunks of mangrove trees. Many specimens also stick to artificial substrates, such as ship hulls and the walls and pillars of docks. *Amphibalanus amphitrite* is spread globally tropical and subtropical waters (Zullo et al. 1972; Henry and McLaughlin 1975; Chen et al. 2014). In this study, *A. amphitrite* was found on the islands of Ambon (at Galala) and Saparua (at Desa Mahu, Negeri Mahu and Tuhaha) on stone, mollusc shells and the capitulum of *Lepas anserifera* (a map with the occurrence of *Amphibalanus amphitrite* in the Moluccas is shown in Supplementary Fig. 7.4).

Remarks:

Amphibalanus amphitrite is difficult to distinguish from two other members of the subgenus *Balanus*, i.e., *Balanus crenatus* Bruguière, 1789 and *Balanus trigonus* Darwin, 1854. However, *A. amphitrite* can usually be distinguished from the other species by the multi-denticulated labrum and also by the colour pattern of the parietes and sheath (Henry and McLaughlin 1975).

Amphibalanus reticulatus (Utinomi, 1967)

Figure 2.22a-o, Table 2.1: species no. 88

Balanus amphitrite var. (1) *communis* Darwin, 1854: 240, pl. 5 fig. 2e, h, l (part.).
Balanus amphitrite forma *communis*: Broch 1922: 314 (part.).
Balanus amphitrite forma *hawaiiensis* Broch, 1922: 314 (part.).
Balanus amphitrite communis: Hiro 1938a: 301, fig. 1a, b.
Balanus amphitrite cirratus: Zevina & Tarasov 1963: 89, fig. 10a-e.
Balanus amphitrite var. *variegatus*: Stubbings 1963a: 329, fig. 2a-e.
Balanus amphitrite variety: Southward & Crisp 1963: 43, fig. 23.
Balanus amphitrite tesselatus Utinomi, 1964: 52, pl. 26 fig. 11.
Balanus amphitrite var. *denticulata*: Karande & Palekar 1966: 145, fig. 7, pl.1 fig. 7, pl. 4 row 5 (part.).
Balanus variegatus tesselatus Utinomi & Kikuchi, 1966: 5.
Balanus amphitrite amphitrite: Stubbings 1967: 271, fig. 14d-f (part.).
Balanus reticulatus: Utinomi 1967: 216, figs 9a, b, 10a, b, 11a-e, pl. 6 figs 7, 8 (part.); Dong et al. 1982: 91, fig. A-C; Zevina et al. 1992: 92, fig. 63; Puspasari et al. 2001b.
Amphibalanus reticulatus: Pitombo 2004: 274; Chan, et al. 2009a: 234, fig. 200; Pochai et al. 2017: 26, fig. 10; Xu 2017: 43, figs 10, 39.

Material examined:

Ambon Island: 5 specimens, MZB Cru Cir 012, Yos Sudarso, 3°41’36.5”S 128°10’35.6”E, coll. P. Pitriana & D. Tala, 6 Sep 2016.

Diagnosis:

Primary parietal tubes with transverse septa; exterior of shell with longitudinal and horizontal striations; anterior margin of cirrus III with conical denticles, erect hooks below posterior angles of distal articles of rami present.

Description:

Shell conic or cylindric; six parietal plates, externally smooth, white with groups of well-spaced purple, or purple-pink vertical stripes intersecting with transverse striations (Fig. 2.22a, b); parietes with single row of internal tubes; alae with summits moderately oblique; radii narrow, summits oblique; orifice toothed; basis calcareous, porous; scutum triangular, externally flat, internally adductor ridge conspicuous, short, low, well separated from prominent articular ridge; tergum flat, spur narrow, short, basiscutal angle acute, scutal margin straight; scutum triangular, occluding margin toothed; tergum flat, basiscutal angle acute, scutal margin straight (Fig. 2.22c, d); cirrus II with simple spinules or conic teeth on outer face near anterior margin (Fig. 2.22f); maxilla bilobed, dense setae on margin (Fig. 2.22k); maxillule not notched, setae on upper and lower margins (Fig. 2.22l); mandible with four teeth (Fig. 2.22m); mandibular palp with setulae on lower margin, pinnate setae on upper margin; labrum simple with four teeth and setulae on crest on each side of deep notch (Fig. 2.22n). Basal length 7.7-16.3 mm; basal width 2.9-15.5 mm; height 3.2-10.5 mm. Orifice length 3.5-8.9 mm; orifice width 2.5-7.1 mm (measurements for five specimens are presented in Supplementary Table 7.21).

Distribution:

Amphibalanus reticulatus is native to the Indo-Pacific region and has been introduced by shipping to tropical-subtropical waters of the Eastern Pacific (Coles et al. 1999; Carlton et al. 2011). *A. reticulatus* can be found from Japan to the Malay Archipelago, east Asia from the Yellow Sea to Gulf of Siam, from Malaysia to southeast Africa, in the Mediterranean Sea, West Africa, the Southeast United States to the West Indies (Henry and McLaughlin 1975).

In this study, *A. reticulatus* was found on the islands of Ambon (at the port of Yos Sudarso) on stone and concrete wall of the port (a map with the occurrence of *Amphibalanus reticulatus* in the Moluccas is shown in Supplementary Fig. 7.2).

Remarks:

Amphibalanus reticulatus can be confused with *A. amphitrite.* However, the shell of *A. reticulatus* exhibits clear vertical and horizontal striations, whilst *A. amphitrite* shows only vertical purple striations on all shell plates (Henry and McLaughlin 1975).

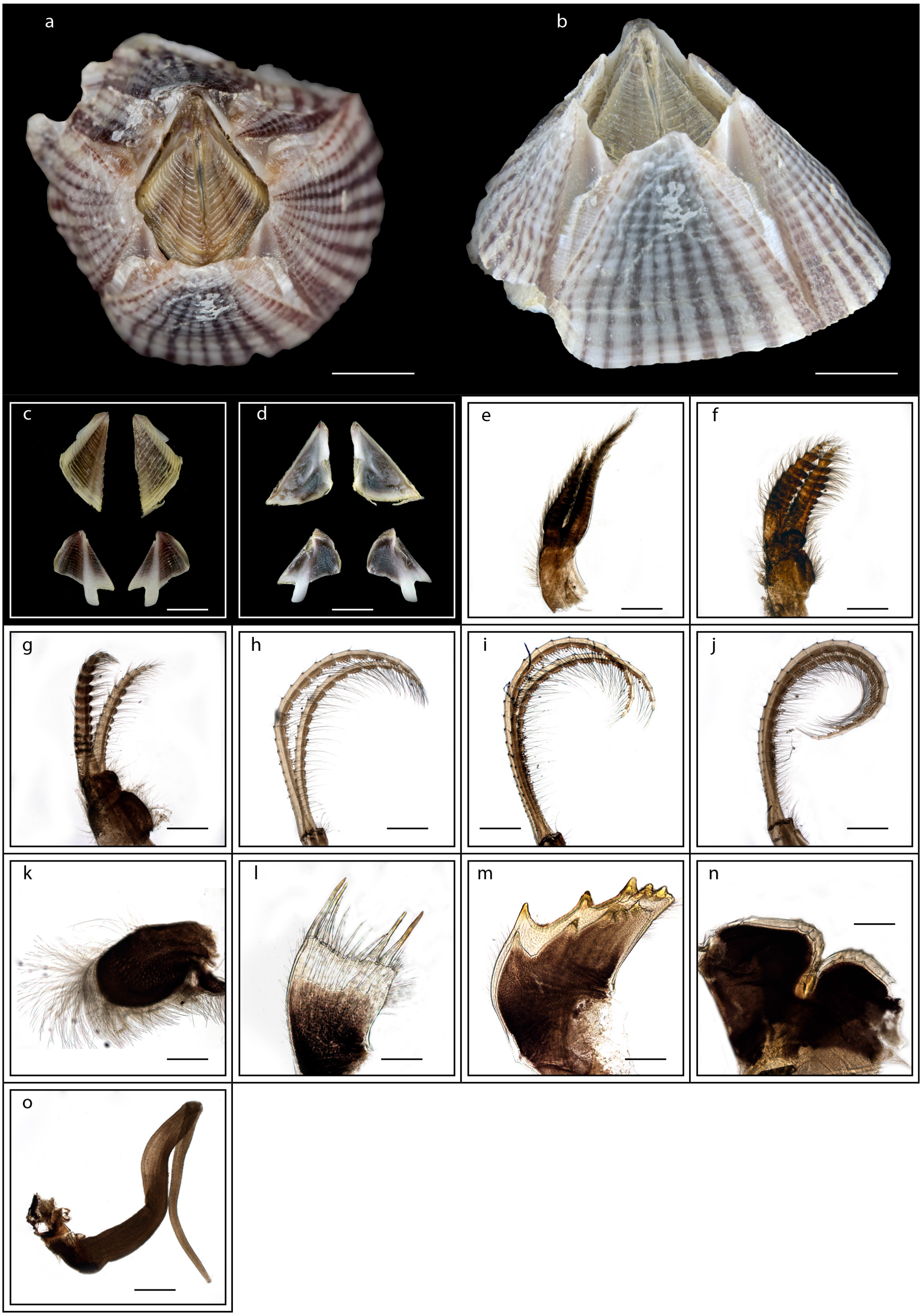

Figure 2.22. *Amphibalanus reticulatus* (Utinomi, 1967) (MZB Cru Cir 012-1). (**a**) Upper view, (**b**) side view, (**c**) external view of scutum and tergum, (**d**) internal view of scutum and tergum, (**e**) cirrus I, (**f**) cirrus II, (**g**) cirrus III, (**h**) cirrus IV, (**i**) cirrus V, (**j**) cirrus VI, (**k**) maxilla, (**l**) maxillule, (**m**) mandible, (**n**) labrum, (**o**) penis. Scale bars: a, b) 4 mm, c-g) 1 mm, h-j, o) 2 mm, k-n) 0.5 mm.

Amphibalanus variegatus (Darwin, 1854)

Figure 2.23a-p, Table 2.1: species no. 89

Balanus amphitrite var. (8) *variegatus* Darwin, 1854: 241.
Balanus amphitrite var. *stutsburi* Krüger, 1914: 437.
Balanus concavus sinensis Broch, 1931: 63, fig. 23.
Balanus amphitrite rafflesia Nilsson-Cantell, 1934a: 64.
Balanus amphitrite var. *cirratus*: Pope 1945: 362, pl. 28 fig. 6, pl. 29 fig. 6, pl. 30 figs 13, 14.
Balanus amphitrite cirratus: Skerman 1960: 610, figs 1, 3 (**non** *Balanus amphitrite cirratus* Darwin, 1854).
Balanus variegatus: Harding 1962: 291, pl. 10 figs a-k; Zevina et al. 1992: 92, fig. 64.
Balanus variegatus var. *cirratus*: Pope 1966: 179.
Balanus amphitrite: Foster 1967: 83 (part.).287
Balanus kondakovi: Henry & McLaughlin 1975: 78 (part., New Zealand specimens; non B. kondakovi Tarasov & Zevina, 1957).
Balanus variegatus variegatus: Foster 1979: 111, fig. 67, pl. 14b.
Balanus cirratus: Ren & Liu 1978: 145, figs 14, 15 (1-13), pl. 4 figs 15-20, pl. 5 figs 1-6.
non *Balanus amphitrite variegatus*: Nilsson-Cantell 1934a: 60.
non *Balanus variegatus*: Henry & McLaughlin 1975: 78, fig. 17, pls. 6, 7; Utinomi 1968b: 171 (= *B. cirratus*).
Amphibalanus variegatus: Pitombo 2004: 274; Horikoshi & Okamoto 2005: 49, fig.3.

Material examined:

- Ambon Island: 15 specimens, MZB Cru Cir 014, Waitatiri, 3°37’04.0”S 128°16’20.3”E, coll. P. Pitriana & D. Tala, 19 Sep 2017.
- Saparua Island: 10 specimens, MZB Cru Cir 015, Teluk Saparua, 3°34’25.7”S 128°39’25.8”E, coll. P. Pitriana & D. Tala, 22 Sep 2016.

  GenBank accession numbers: COI gene (MK995342 - MK995345), 18S (MK981355).

Diagnosis:

Primary parietal tubes with transverse septa; exterior of shell with longitudinal and horizontal striations; anterior margin of cirrus III without conical denticles, erect hooks below posterior angles of distal articles of rami absent.

Description:

Shell steeply conical, tubular in crowded populations; six parietal plates, smooth, thin, brownish purple externally with longitudinal stripes crosshatched by transverse bands, single row of internal tubes (Fig. 2.23b); carina forming a spout-like projection; radii wide, summits oblique, pink-purple; alae with summits oblique; orifice toothed (Fig. 2.23a-c); sheath purple with white bands, vesicular; basis calcareous, porous; scutum externally with growth lines prominent, internally with articular ridge high, adductor ridge moderately long; tergum with spur furrow, externally purple, margins white, spur pointed, basal margin deeply excavated on either side of spur, depressor muscle crests prominent(Fig. 2.23d, e); cirrus III without conical

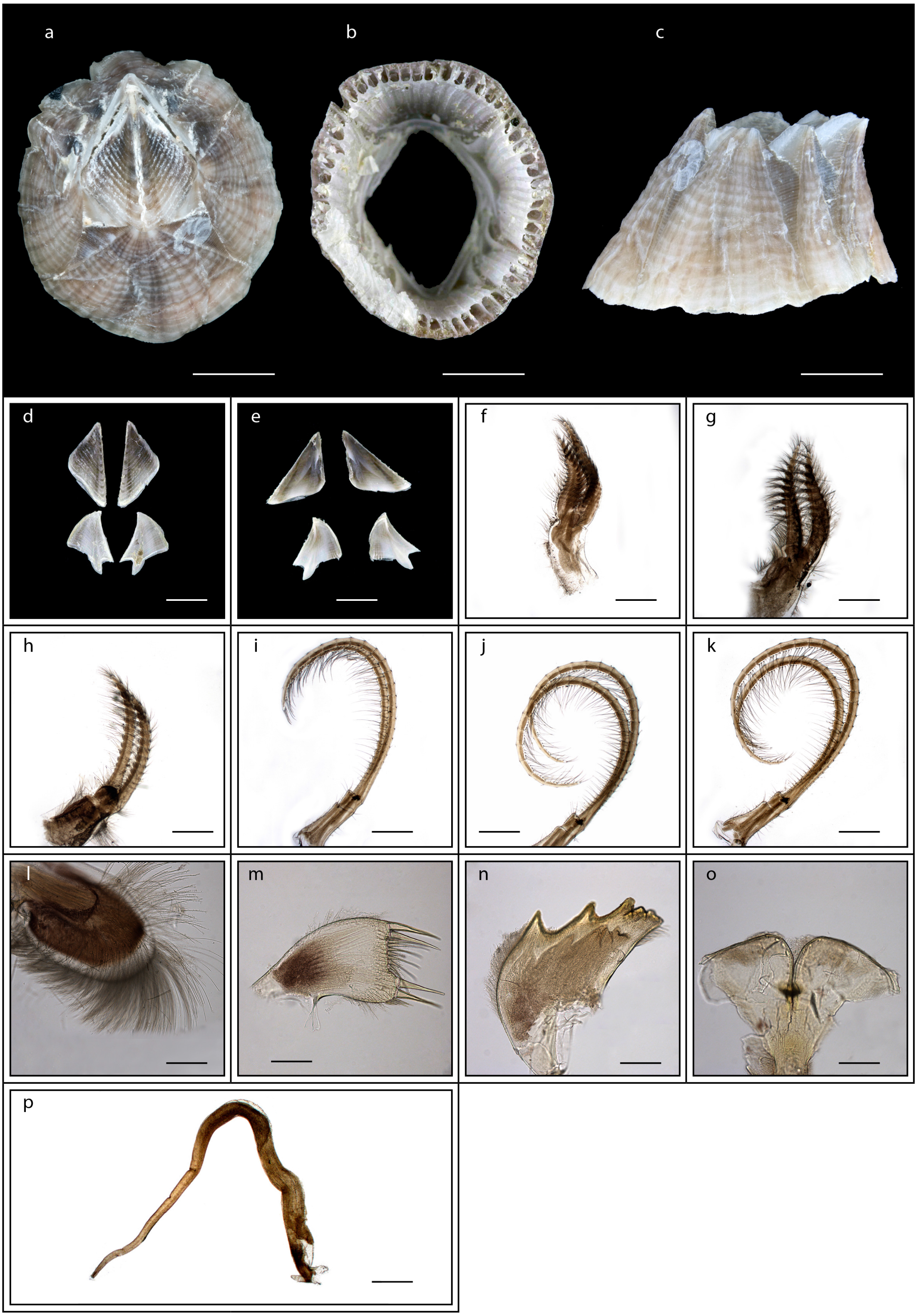

Figure 2.23. *Amphibalanus variegatus* (Darwin, 1854) (MZB Cru Cir 014-1). (**a**) Upper view, (**b**) lower view, (**c**) side view, (**d**) external view of scutum and tergum, (**e**) internal view of scutum and tergum, (**f**) cirrus I, (**g**) cirrus II, (**h**) cirrus III, (**i**) cirrus IV, (**j**) cirrus V, (**k**) cirrus VI, (**l**) maxilla, (**m**) maxillule, (**n**) mandible, (**o**) labrum, (**p**) penis. Scale bars: a-c) 3 mm, d-h) 1 mm, i-k, p) 2 mm, l-o) 0.5 mm.

denticles on anterior margin (Fig. 2.23h); maxilla without notch (Fig. 2.23l), mandible with four teeth (Fig. 2.23n), labrum notched, denticulate (Fig. 2.23o); penis with basidorsal point, with two apical setae (Fig. 2.23p). *Basal length (8.3-11.8 mm, basal width 6.9-10.4 mm, height 4.3-8.4 mm; orifice* length 4.8-11.8 mm; orifice width 3.4-5.3 mm (measurements for ten specimens are presented in Supplementary Table 7.22).

Distribution:

Amphibalanus variegatus has been reported from the Indo-west Pacific: Bay of Bengal; Sumatra; New Zealand, Australia; Indonesia; Singapore; Vietnam; Gulf of Siam; Hong Kong; W Kyushu; Vladivostok; and is a common fouling species (Henry and McLaughlin 1975; Jones and Hosie 2016). *In this study, A. variegatus was found on the islands of Ambon (at Waitatiri) and Saparua (at Teluk Saparua) on stones and a plastic bag (a* map with the occurrence of *Amphibalanus variegatus* in the Moluccas is shown in Supplementary Fig. 7.4).

Remarks:

Amphibalanus variegatus is a member of the *Balanus amphitrite* complex, whose members can be difficult to distinguish morphologically. *Amphibalanus variegatus* can be differentiated by its vesicular sheath, and from *A. reticulatus* by features of the tergum, armature of cirrus II and the lack of erect teeth below the posterior distal angles of cirri III-VI (Henry and McLaughlin 1975).

Amphibalanus zhujiangensis (Ren, 1989)

Figure 2.24a-j, Table 2.1: species no. 90

Balanus zhujiangensis Ren, 1989a: 467, fig. 2 (1-14).
Amphibalanus zhujiangensis: Pitombo 2004: 274; Puspasari et al. 2002: 235, figs 1A-G, 2A-H; Liu and Ren 2007: 501; Chan et al. 2009a: 238, fig. 204.

Material examined:

- Ambon Island: 10 specimens, MZB Cru Cir 016, Galala, 3°41’22.2”S 128°10’52.6”E, coll. P. Pitriana & D. Tala, 6 Sep 2016; 3 specimens, MZB Cru Cir 017, Laha, 3°43’22.5”S 128°05’02.5”E, coll. P. Pitriana & D. Tala, 5 Sep 2016; 6 specimens, MZB Cru Cir 018, Talake, 3°41’59.4”S 128°10’19.2”E, coll. P. Pitriana & D. Tala, 5 Sep 2016.
- Saparua Island: 10 specimens, MZB Cru Cir 019, Desa Pia, 3°30›20.4»S 128°36›55.0»E, coll. P. Pitriana & D. Tala, 21 Sep 2016; 7 specimens, MZB Cru Cir 020, Negeri Mahu, 3°31’52.9”S 128°41’12.4”E, coll. P. Pitriana & D. Tala, 11 Apr 2016; 1 specimen, MZB Cru Cir 021, Desa Mahu, 3°32’19.6”S 128°41’17.3”E, coll. P. Pitriana & D. Tala, 11 Apr 2016.
- Seram Island: 5 specimens, MZB Cru Cir 022, Desa Kasie, 2°51’05.5”S 128°32’54.1”E, coll. P. Pitriana & D. Tala, 20 Sep 2017; 3 specimens, MZB Cru Cir 010, Lepas Pantai Kawa, 2°57’32.5”S 128°05’33.4”E, coll. P. Pitriana & D. Tala, 19 Sep 2017.

  GenBank accession numbers: COI gene (MK995334, MK995336, MK995337, MK995339), 18S (MK981347, MK981349, MK981350, MK981352).

Diagnosis:

Primary parietal tubes without transverse septa; exterior of shell with longitudinal striations; scutum without adductor ridge, external surface scutum with row of pits; anterior margin of cirri III with conical denticles, erect hooks below posterior angles of distal articles of rami present; cirrus IV with erect hooks on posterodistal angles of articles.

Description:

Shell six-plated, conic, purplish-white with longitudinal stripes of purple, not cross-hatched by transverse striations; parietes externally smooth, parietal tubes lacking transverse septa and subsidiary tubes; radii wide with slightly oblique summits; orifice rhomboidal, toothed (Fig. 2.24a-c); scutum trigonal, exterior of scutum with single row of pits extending down centre of valve, occluding margin toothed, inner surface smooth, adductor ridge lacking; tergum with carinal margin convex, spur furrow open, basal margin straight on both sides of spur (Fig. 2.24d, e); cirrus III without complex setae; cirri III–VI with erect hooks around posterior angle; first maxilla without notch, mandible with five teeth (Fig. 2.24h). *Basal length* 5.8-21.6 *mm; basal width* 4.8-19.2 *mm; height* 2.1-16.5 *mm;* orifice length 3.0-10.0 mm; orifice width 2.6-7.6 mm (measurements for eleven specimens are presented in Supplementary Table 7.23).

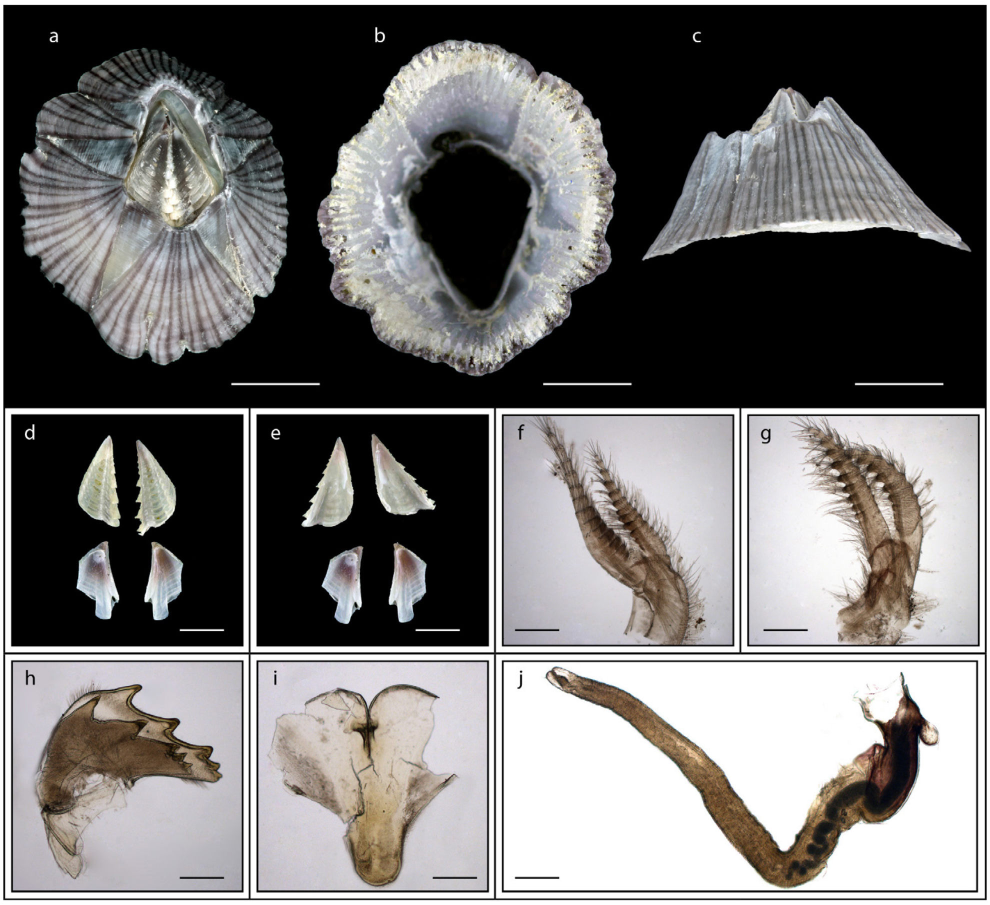

Figure 2.24. *Amphibalanus zhujiangensis* (Ren, 1989) (MZB Cru Cir 018-5). (**a**) Upper view, (**b**) lower view, (**c**) side view, (**d**) external view of scutum and tergum, (**e**) internal view of scutum and tergum, (**f**) cirrus I, (**g**) cirrus II, (**h**) mandible, (**i**) labrum, (**j**) penis. Scale bars: a-c) 6 mm, d-g) 1 mm, h, i) 0.5 mm, j) 2 mm.

Distribution:

Amphibalanus zhujiangensis was first recorded from the estuary of the Zhujiang River, South China Sea (Puspasari et al. 2002). Afterwards found on Okinawa Island, Japan and Taiwan (Chan et al. 2009a). In this study, *A. zhujiangensis* was found on the islands of Ambon Island (at Galala, Laha, and Talake), Saparua Island (at Dusun Pia, Negeri Mahu, Desa Mahu), and Seram Island (at Desa Kasie, Lepas Pantai Kawa) on stone and capitulum of *Lepas anserifera* (a map with the occurrence of *Amphibalanus zhujiangensis* in the Moluccas is shown in Supplementary Fig. 7.8).

Remarks:

The presence of a row of pits on the external surface of the scutum and the absence of an adductor ridge on the scutum are diagnostic for *A. zhujiangensis*. The species can be distinguished from *A. variegatus* by characters of the shell, cirri III and cirri IV; on *A.* reticulatus by characters of the shell and first maxilla. *Amphibalanus zhujiangensis* is distinct from *A. thailandicus* in lacking transverse septa in the longitudinal tubes and a notch on the first maxilla (Puspasari et al. 2002).

Amphibalanus sp.

Figure 2.25a-o, Table 2.1: species no. 91

Material examined:

- Ambon Island: 1 specimen, MZB Cru Cir 135, Talake, 3°41’59.4”S 128°10’19.2”E, coll. P. Pitriana & D. Tala, 5 Sep 2016; 1 specimen, MZB Cru Cir 136, Waitatiri, 3°37’04.0”S 128°16’20.3”E, coll. Adin, 19 Sep 2017.
- Seram Island: 2 specimens, MZB Cru Cir 137, Dermaga Pelita Jaya, 3°00’13.5”S 128°07’09.2”E, coll. P. Pitriana & D. Tala, 21 Sep 2017.
  GenBank accession numbers: COI gene (MK995349 - MK995351, MK995353), 18S (MK981356 - MK981358, MK981360).

Diagnosis:

Primary parietal tubes with transverse septa, exterior of shell with longitudinal striations; orifice toothed; scutum without adductor ridge; anterior margin of cirri III with conical denticles, erect hooks below posterior angles of distal articles of rami present; cirrus IV with erect hooks on posterodistal angles of articles; basidorsal of penis absent.

Description:

Shell six-plated, conical, whitish with dark purple transverse stripes (Fig. 2.25a, b); orifice slightly toothed; scutum trigonal, occluding margin toothed; tergum with closed spur furrow (Fig. 2.25c, d); mandible with five teeth (Fig. 2.25n); maxilla bilobed with dense setae only on lower margin (Fig. 2.25l). Basal length 7.4-12.2 mm, basal width 6.3-11.8 mm, height 5.5-9.4 mm; orifice length 3.6-8.3 mm; orifice width 2.6-5.9 mm (measurements for four specimens are presented in Supplementary Table 7.24).

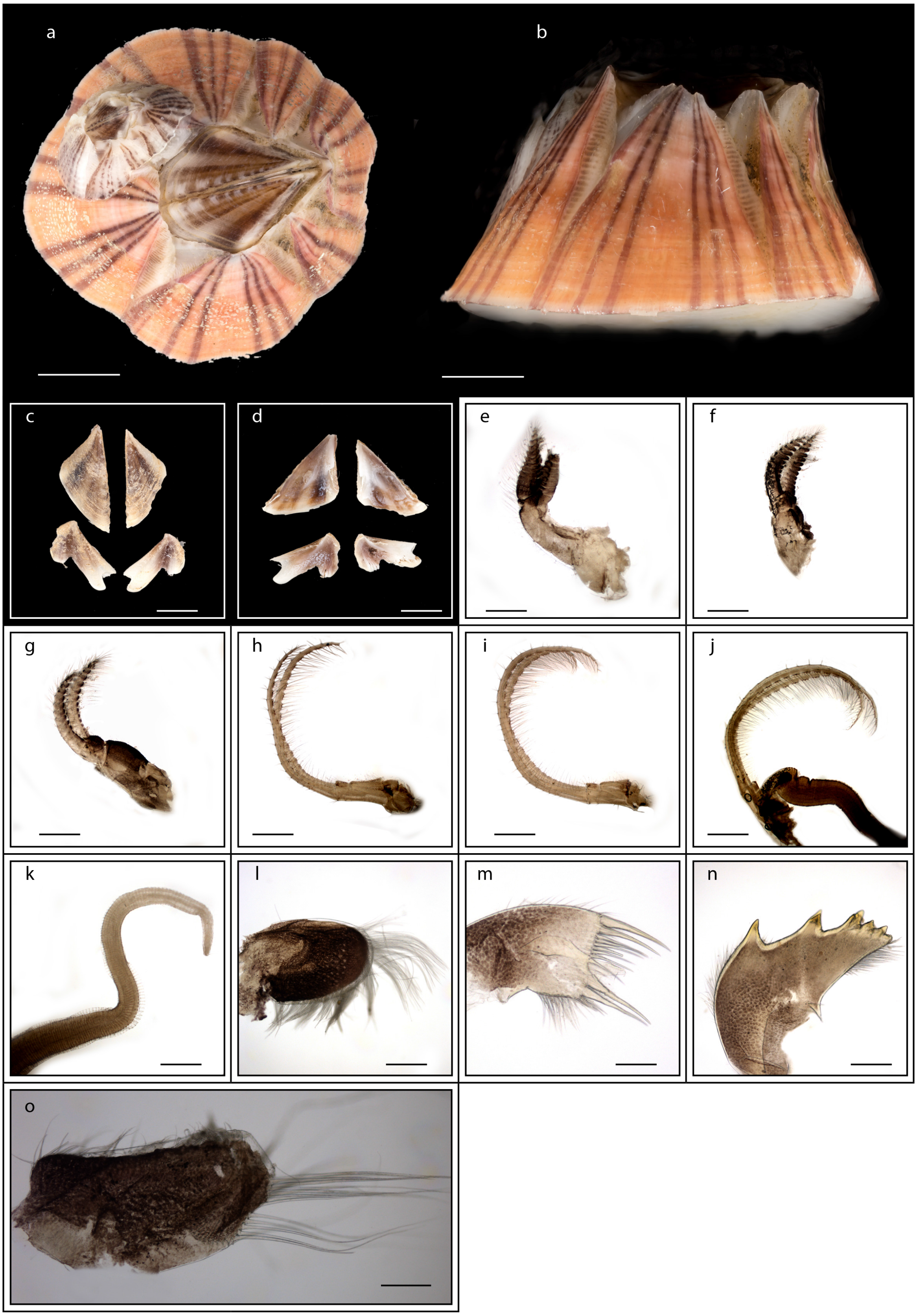

Figure 2.25. *Amphibalanus* sp. (MZB Cru Cir 135). (**a**) Upper view, (**b**) side view, (**c**) external view of scutum and tergum, (**d**) internal view of scutum and tergum, (**e**) cirrus I, (**f**) cirrus II, (**g**) cirrus III, (**h**) cirrus IV, (**i**) cirrus V, (**j**) cirrus VI, (**k**) penis, (**l**) maxilla, (**m**) maxillule, (**n**) mandible, (**l**) mandibular palp. Scale bars: a, b) 3 mm, c-g) 1 mm, h-k) 2 mm, l-o) 0.5 mm.

Distribution:

In this study, *Amphibalanus* sp. was found on Ambon (at Talake and Waitatiri) and Seram islands (at Dermaga Pelita Jaya) (a map with the occurrence of *Amphibalanus* sp. in the Moluccas is shown in Supplementary Fig. 7.9).

Remarks:

In the molecular phylogeny, *Amphibalanus* sp. forms a well-supported clade in both, the COI and the 18S tree (Figs 2.28-29). This species also has different maxilla than those of *A. amphitrite*, *A. reticulatus* and *A. variegatus*, which have setae on its upper and lower margins.

Subfamily Megabalaninae Newman, 1979

Genus *Megabalanus* Hoek, 1913

Megabalanus tintinnabulum (Linnaeus, 1758)

Figure 2.26a-e, Table 2.1: species no. 96

Balani Rhumphius, 1705: 121, pl. 41 figs A, C, D.
Balanus tintinnabuliformis laevis Lang, 1772: 4.
Balanus cylindraceus unicum thalamum efformans, magnis ventricosus Gaultierus, 1742: un-numbered page, pl. 106, fig. H.
Glands de mer de la grande espèce Dezallier d'Argenville, 1742: 364, pl. 30 fig. A; 1757: 364, pl. 26 fig. A.
Lepas Tintinnabulum Linnaeus, 1758: 668; Chemnitz 1785 (part.): pl. 97 figs 830, 831 (non figs 828, 829).
Lepas calyciformis orientalis Ellis, 1758: 845, pl. 34 figs 8, 9.
Balanus tintinnabulum: Bruguière 1789 (part.): 165; Holthuis & Heerebout 1972: 24, pl. 1.
Lepas tintinnabulum: Wood 1815: 38, pl. 6 figs 1, 2.
Lepas spinosa Wood, 1815 (part.): pl. 7 fig. 4 (large shell only; small shells = M. spinosus).
Balanus tintinnabulum var. (1) *communis* Darwin, 1854: 195, pl. 1 figs a, b, f supra, pl. 2 figs 1 a, 1 c–e, 1 i, 1 k.
Balanus tintinnabulum var. *communis*: Gruvel 1905a: 211
Balanus tintinnabulum tintinnabulum: Pilsbry 1916: 55, fig. 9, pl. 10 figs 1a-e; Dong et al. 1982: 86.
Balanus tintinnabulum antillensis Pilsbry, 1916: 63, pl. 13 figs 1-2 e.
Balanus (*Megabalanus*) *tintinnabulum* forma *communis* Broch, 1931: 56.
Balanus tintinnabulum var. *tintinnabulum*; Oliveira 1941: 11, fig. 1, pl. 2 figs 1, 2, pl. 4 fig. 1, pl. 5 fig. 3, pl. 8 fig. 6.
Megabalanus antillensis Newman & Ross, 1976: 67.
Balanus (*Megabalanus*) *tintinnabulum tintinnabulum*: Ren & Liu 1978: 121, fig. 1, pl. 1 figs 1-5.
non *Lepas tintinnabulum*: Spengler 1790: 180 [= *Megabalanus occator* (Darwin, 1854)]
non *Lepas tintinnabulum* var. a: Spengler 1790: 181 (*incertae sedis*).
non *Lepas tintinnabulum* var. b: Spengler 1790: 182 [= *Striatobalanus amaryllis* (Darwin, 1854)]
non *Lepas tintinnabulum*: Chemnitz 1785: pl. 97, figs 828, 829 [= *Austromegabalanus nigrescens* (Lamarck, 1818)].
non *Balanus tintinnabulum*: Chenu 1843: pl. 2 fig. 8, pl. 3 fig. 5, pl. 2 fig. 8 [= *Megabalanus ajax* (Darwin, 1854)]; pl. 3 fig. 5 [= *Megabalanus tulipiformis* (Darwin, 1854)].

non *Balanus tintinnabulum* var. *communis*: Krüger 1911a: 46, pl. 3 figs 31 a1-31 b2 [= *Megabalanus volcano* Pilsbry, 1916)].
non *Balanus* (*Megabalanus*) *tintinnabulum*: Withers 1924: pl.6 figs 4-7 [= *Megabalanus linzei* (Foster, 1979)].
non *Balanus tintinnabulum antillensis* Pilsbry, 1927: 38, fig. 3 a-c [= *Megabalanus stultus* (Darwin, 1854)]
non *Balanus tintinnabulum tintinnabulum*: Linzey 1942: 279 [= *Megabalanus linzei* (Foster, 1979)].
non *Balanus tintinnabulum*: Foster 1967: 81, fig. 2a, b [= *Megabalanus linzei* (Foster, 1979)].
Megabalanus tintinnabulum: Newman & Ross 1976: 68; Henry & McLaughlin 1986: 17, figs 1e, 2a, g, h, 3a-c, 5 a-l; Zevina et al. 1992: 99, fig. 67; Pitombo 2004: 175; Chan et.al 2009a: 259, fig. 224; Pochai et.al 2017: 28, fig.11.

Material examined:

- Ambon Island: 3 specimens, MZB Cru Cir 066, Laha, 3°43’22.5”S 128°05’02.5”E, coll. P. Pitriana & D. Tala, 5 Sep 2016.
- Saparua Island: 1 specimen, MZB Cru Cir 067, Desa Pia, 3°30’20.4”S 128°36’55.0”E, coll. P. Pitriana & D. Tala, 21 Sep 2016.

Diagnosis:

Shell relatively large, lightly ribbed; radii wide; surface smooth without spines; tergum wider than scutum with spur narrow and long, crests for depressor muscle weakly to moderately well developed.

Description:

Shell cylindrical to conical, parietes purplish, smooth, with longitudinal purple striations, tubiferous (Fig. 2.26a); radii wide, usually horizontally striated, summits horizontal, sutural edges with regular denticles; summits of alae oblique; orifice rhomboidal, moderately small to large, one-third to two-thirds basal diameter, subcircular to subtriangular; scutum triangular, external surface with horizontal striations, inner surface with conspicuous articular ridge; tergum triangular, frequently wider than scutum, external surface with horizontal striations, spur long, narrow, external surface with median furrow, scutal margin denticulate (Fig. 2.26b-e); mandible with five teeth, labrum with deep cleft, three teeth on each side. Basal length 26.0-49.2 mm, basal width 29.0-43.1 mm, height 20.1-49.4 mm. Orifice length 13.7-16.3 mm, orifice width 10.4-15.9 mm (measurements for four specimens are presented in Supplementary Table 7.25).

Distribution:

Megabalanus tintinnabulum is a cosmopolitan species and widely distributed worldwide (Pochai et al. 2017). In this study, *M. tintinnabulum* was found on Ambon Island (at Laha) and in Saparua Island (at Desa Pia) on concrete bridge at the port, stones and reef surface (a map with the occurrence of *Megabalanus tintinnabulum* in the Moluccas is shown in Supplementary Fig. 7.4).

Remarks:

The name *Megabalanus* was given by Hoek (1913), referring to the largest form of existing Balani. With the exception of *Balanus amphitrite*, Darwin (1854) considered *Balanus tintinnabulum* as the most difficult and variable species in the genus *Balanus* (Henry and McLaughlin 1986). *Megabalanus tintinnabulum* can be distinguished by its large shell plates and purple surface with irregular, unclear longitudinal stripes (Pochai et al. 2017).

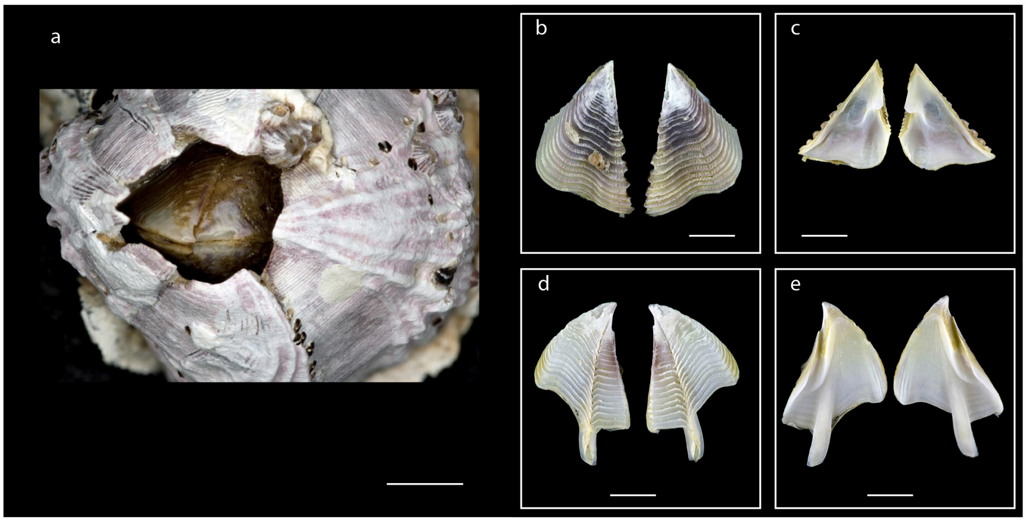

Figure 2.26. *Megabalanus tintinnabulum* (Linnaeus, 1758) (MZB Cru Cir 066-3). (**a**) Upper view, (**b**) external view of scutum, (**c**) internal view of scutum, (**d**) external view of tergum, (**e**) internal view of tergum. Scale bars: a) 8 mm, b-e) 5 mm.

Megabalanus zebra (Darwin, 1854)

Figure 2.27a-c, Table 2.1: species no. 97

Balanus tintinnabulum var. (4) *zebra* Darwin, 1854: 195. pl. 1 fig. g.

Balanus tintinnabulum zebra: Pilsbry 1916: 57, pl. 10 figs 2, 3; Stubbings 1967: 264; Dong et al. 1982: 86, fig. A-C.

Balanus tintinnabulum var. *zebra* Karande & Palekar, 1966: 143, pl.I, fig. 2.

Megabalanus zebra: Newman & Ross 1976: 69; Henry & McLaughlin 1986: 47, figs 2f, 4j-k, 12e-l; Pitombo 2004: 275; Chan et al. 2009a: 265, fig. 232; Pitombo et al. 2017: 135, figs 2, 4, 5, 6, 7, 8.

Material examined:

Ambon Island: 4 specimens, MZB Cru Cir 068, Galala, 3°41’22.2”S 128°10’52.6”E, coll. P. Pitriana & D. Tala, 6 Sep 2016; 4 specimens, MZB Cru Cir 069, Laha, 3°43’22.5”S 128°05’02.5”E, coll. P. Pitriana & D. Tala, 5 Sep 2016.

Diagnosis:

Parietes reddish purple with strong longitudinal white ribs; radii and sheath dark purple to reddish brown; scutum with narrow tergal segment slightly inflected; tergum approximately as wide as scutum, crest for depressor muscle prominent.

Description:

Shell conic, six-plated; parietes smooth, purple with well-developed white ribs and dark purple interspaces; radii wide, summits horizontal, white with dark purple spots on proximal side (Fig. 2.27a); orifice rhomboidal; scutum triangular, external surface withe intersecting horizontal and longitudinal striations; tergum triangular, white with purple spots in some areas, scutal margin slightly curved, basal margin inclined, spur short (Fig. 2.27b, c); mandible with five teeth, labrum with deep cleft, three teeth on each side. Basal length 5.4-19.0 mm, basal width 5.0-20.0 mm, height 4.4-13.1 mm. Orifice length 3.1-7.6 mm, orifice width 1.7-6.2 mm (measurements for eight specimens are presented in Supplementary Table 7.26).

Distribution:

Megabalanus zebra is a well-known fouling species of ship hulls, floating structures, moveable oil platforms, etc., and has been widely recorded from the Atlantic Ocean; W Africa; Indo-west Pacific: Indian Ocean; Australia; Thailand; China; Philippines; Taiwan (Pilsbry 1896, 1916; Stubbings 1961; Karande and Pakelar 1966; Foster and Willan 1979; Chan et al. 2009a; Jones and Hosie 2016; Pitombo et al. 2017). In this study, *Megabalanus zebra* was found on Ambon Island (at Galala and Laha) on stones and the capitulum of *Lepas anserifera* (a map with the occurrence of *Megabalanus zebra* in the Moluccas is shown in Supplementary Fig. 7.1).

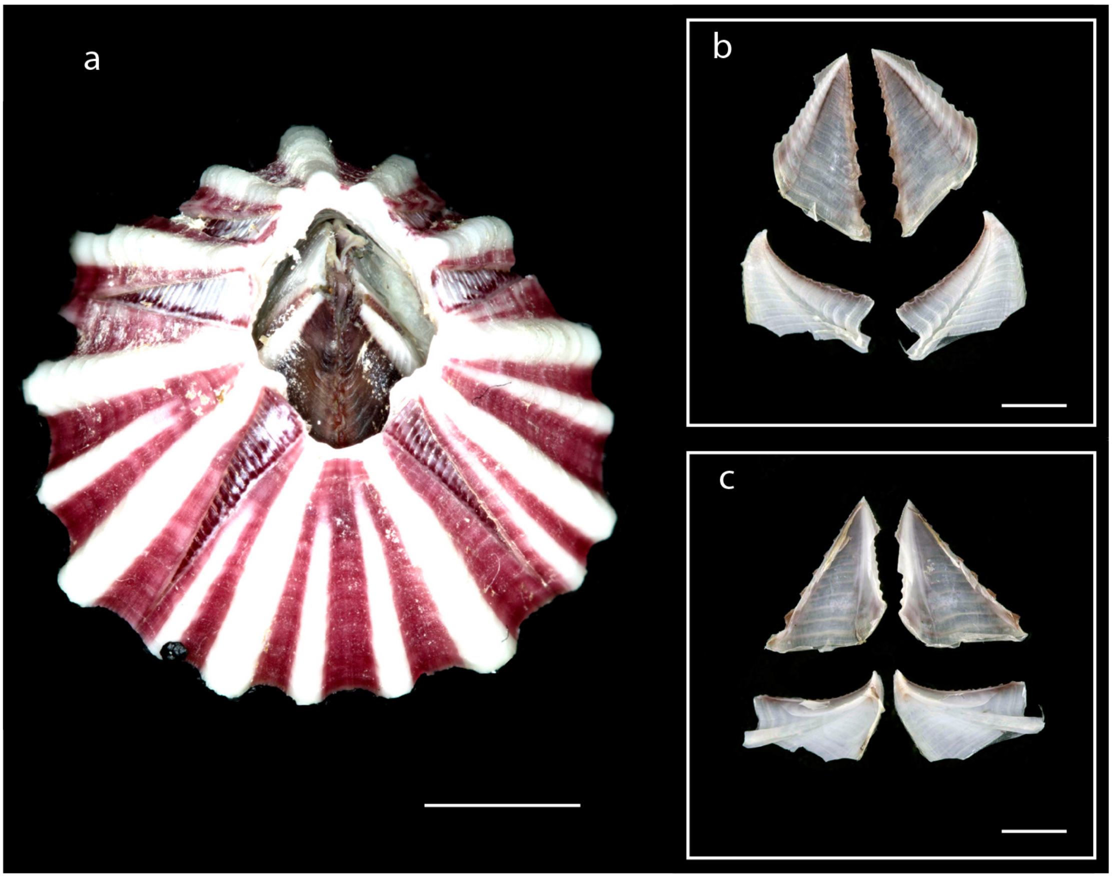

Figure 2.27. *Megabalanus zebra* (Darwin, 1854) (MZB Cru Cir 068-3). (**a**) Upper view, (**b**) external view of scutum and tergum, (**c**) internal view of scutum and tergum. Scale bars: a, b) 4 mm, c, -d) 2 mm.

Remarks:

Megabalanus zebra can be distinguished from other species in the *Megabalanus* group by, for example, the inflection of the tergal segment of the scutum and the position of the spur (Henry and McLaughlin 1986). *M. zebra* can also be differentiated by an intermediate shape of the tergum and scutum compared to *M. tintinnabulum* and *M. coccopoma* (Pitombo et al. 2017).

2.4.2 Molecular results

In total, we produced 120 new sequences for this study (COI = 62 sequences, 18S = 58 sequences; Supplementary Table 7.1; Figs 2.28, 2.29). We downloaded a total of 172 sequences from GenBank (COI = 84 sequences, 18S = 88 sequences). The final COI alignment used for phylogenetic analyses was 641 bp long, and included 156 sequences from 50 species (Fig. 2.29). The 18S alignment was 1918 bp long and included 154 sequences from 83 species (Fig. 2.28).

In general, support values (bootstrap and posterior probability) were low for both markers, with the majority of internal nodes receiving support values below 50% bootstrap or 0.5 posterior probability. However, there are several highly supported nodes throughout (> 70% bootstrap; > 0.85 posterior probability), which allow us to gain insights into the evolutionary history of the group. In general, and as expected, COI (Fig. 2.29) provided higher resolution at terminal nodes but low resolution at deeper nodes (rapidly evolving marker), whereas 18S (Fig. 2.28) provided higher resolution than COI at basal nodes (slowly evolving marker). The trees resulting from the BEAST and RaxML analyses were fully congruent, with no highly supported relationships being favoured in one analysis but not the other. The main purpose of our phylogenetic analyses was to find out where the new accessions from the Moluccas sequenced for this study are retrieved on the barnacle tree, and to see whether putative species are retrieved as monophyletic. We therefore show multiple accessions per species on the trees. The trees resulting from RaxML analyses and the concatenated analyses are given in the Supplementary material (Supplementary Figs 7.10-13).

2. 5 Molecular study of Moluccan barnacles

The vast majority of new samples from the Moluccas produced in this study matched sequences from the same species that are available on GenBank. For example, DNA sequence of our *Heteralepas japonica* matched the sequence of *H. japonica* EU884146.1 and EU884169.1 from Chan, et al. (2009c); and our *Nesochathamalus intertextus* matched the sequence of *N. intertexus* JX083869.1 from Perez-Losada, et al. (2012). This applies to all species for which we have new sequences. The only exception is *Chthamalus moro*, for which one of our samples in the 18S tree does not match the GenBank samples of that species. However, for this particular case, the support values of that clade in the tree are very low, therefore the odd positioning is not strongly supported (that clade is essentially a polytomy).

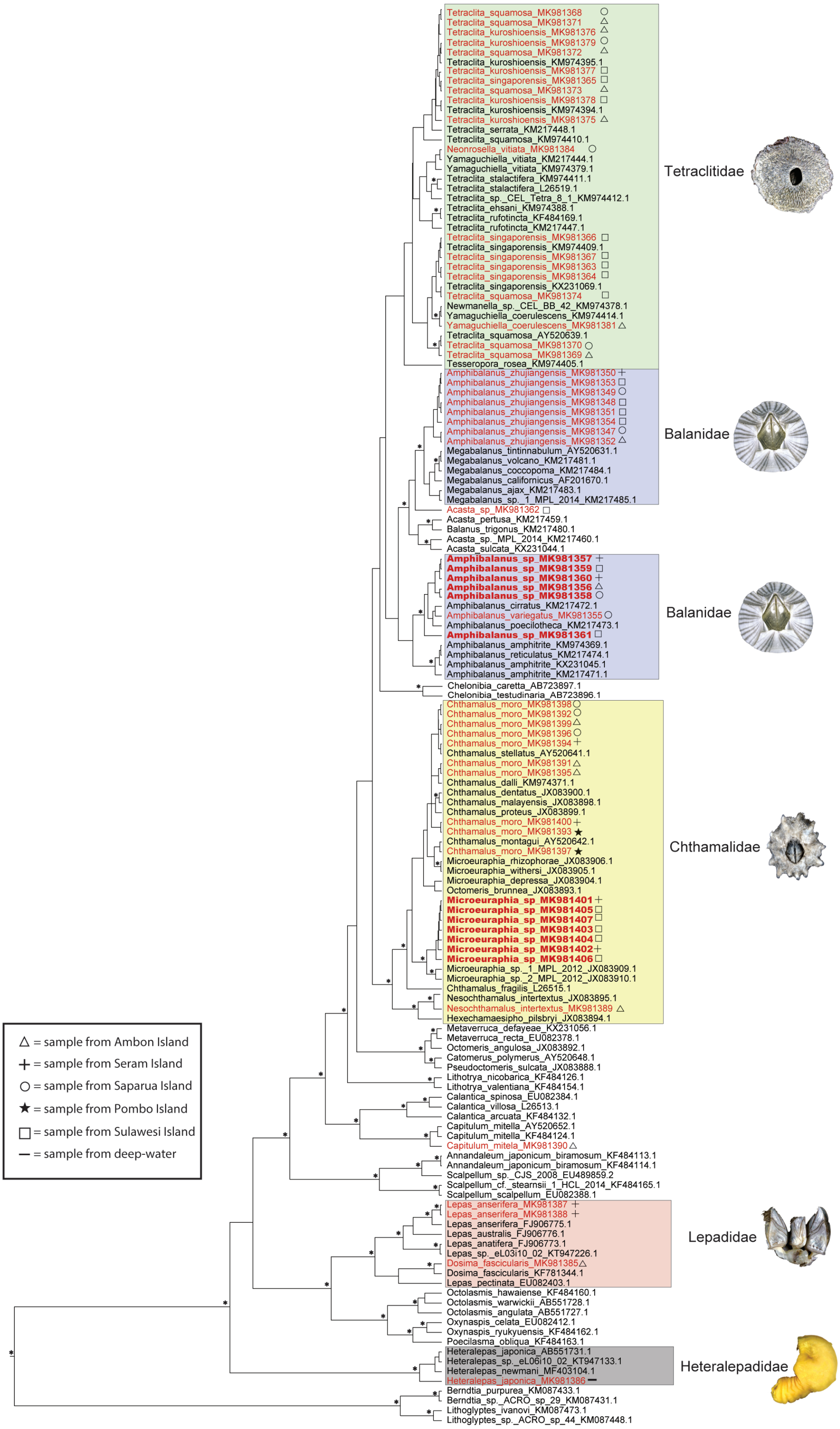

Figure 2.28. Bayesian phylogeny of 18S gene sequences. High Bayesian posterior probabilities (≥ 0.85) are indicated by an asterisk at the respective node. Families with relevance for this study are highlighted by coloured rectangles. Sample labels in red indicate sequences newly generated for this study. Species names in bold indicate potential new species.

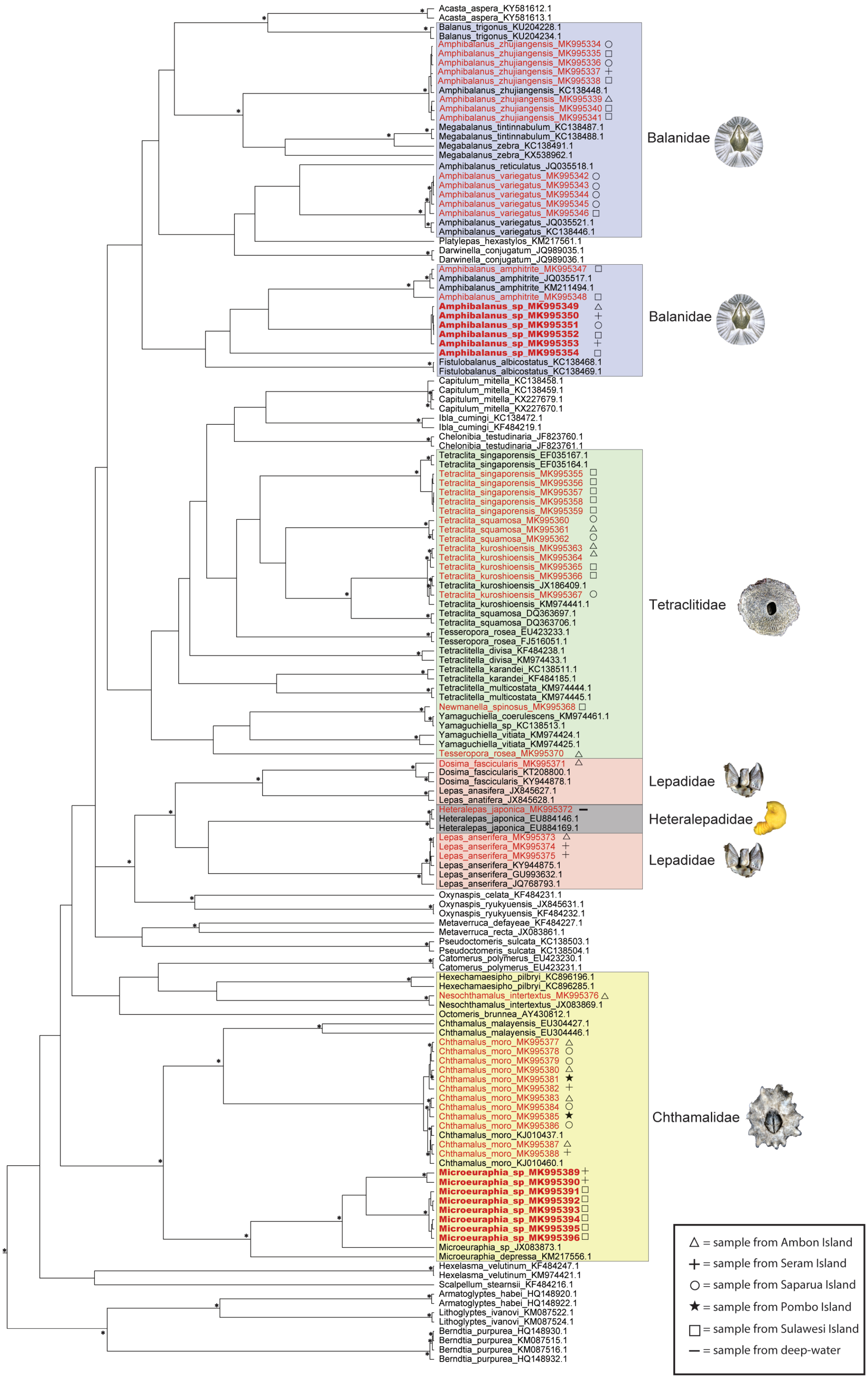

Figure 2.29. Bayesian phylogeny of COI gene sequences. High Bayesian posterior probabilities (≥ 0.85) are indicated by an asterisk at the respective node. Families with relevance for this study are highlighted by coloured rectangles. Sample labels in red indicate sequences newly generated for this study. Species names in bold indicate potential new species.

Two taxa for which we sequenced multiple accessions, but for which we could not assign a species name, were retrieved in positions on the tree that lead us to propose these may constitute new unidentified species. The first one is *Amphibalanus* sp., clustering as a unit in both COI and 18S trees (Figs 2.28, 2.29; Supplementary Figs 7.10-13). The other was *Microeuraphia* sp., which formed well supported and separated clades in the COI tree, and was clustered in the same unresolved clade in 18S (Figs 2.28, 2.29; Supplementary Figs 7.10-13).

The K2P distances within *Microeuraphia* sp. were 1.74%±0.51% for the COI sequences. The K2P distances between *Microeuraphia* sp. and other species ranged from 10.90% to 22.70%; and overall averaged distances between the species and other species were 13.82% (Supplementary Table 7.27). Whilst for *Amphibalanus* sp. the K2P distances within the species were 0.22%±0.13% for the COI sequences. The K2P distances between *Amphibalanus* sp. and other species ranged from 13.34% to 18.33%; and overall averaged distances between the species and other species were 14.37% (Supplementary Table 7.28).

2.6 Discussion

This checklist lists 97 species, including 23 new records the Moluccas and two of which still await their species descriptions. The past record on barnacles from these islands dates back to the *Challenger* (1872-1876) and *Siboga* (1899-1900) expeditions (Hoek 1913). Later, Kolosváry (1950) only mentioned some balanids living in corals collected during *Snellius* Expedition (1929-1930), which contrasts reports from other groups numerously collected during the same expedition, such as in decapod crustaceans and Foraminifera.

Hoek (1913) listed a total of 210 species from the Malay Archipelago that were collected during the *Challenger* and *Siboga* expeditions. Among these, 45 species were found in the Moluccas. However, the majority of the Moluccan species listed by Hoek (32 species) were deep-water barnacles found at depths of 204-2,798 m, while 10 species barnacles were found at depths of 9-90 m, and only three inshore species were recorded: *Temnaspis fissum* (Darwin, 1851) from Ternate; *Yamaguchiella coerulescent* (Spengler, 1790) and *Tetraclitella costata* (Darwin, 1854) from Banda Island. In contrast, sampling for this study focused on inshore habitats with only two deep-sea locations. In consequence to the different sampling approaches, we found 24 inshore species and only one deep-sea species among the new samples.

A comparison of the number of species previously recorded from Ambon, Seram, and Banda by Hoek (1913) and Jones (2001, 2016) with those recorded in this study indicates that species diversity for each island has been heavily underestimated. On Ambon, for example, seven species were previously known compared to the 24 species listed here. For other smaller islands such as Saparua and Pombo, no barnacle species was previously recorded. Given the size of the Moluccan Archipelago, with ca. 1,000 islands, many of which have never been sampled despite including relatively large islands such as Haruku, Buru, Yamdena or Wetar, a much higher number of species can be expected in the Moluccas.

The molecular results also indicate that the barnacle fauna of the region is understudied. In addition to evidence for two potentially new species (see above), the generic assignment of some described species is also challenged. For example, *Amphibalanus zhujiangensis* was found to be more closely related to *Megabalanus* than to other *Amphibalanus* species, suggesting the need to conduct in-depth research on this species to clarify its taxonomy. However, we must caution against over interpretation of our phylogenetic trees, because the markers we used revealed low node support overall.

The molecular phylogeny failed to reveal any biogeographic pattern of barnacles from the Moluccas, which is not surprising given the limited scope of sampling. These points all underline again the necessity of a more comprehensive approach to sampling in the region as well as the need to explore more molecular markers for a truly integrative taxonomy of barnacles, not just in the Moluccas.

2.7 Acknowledgements

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Barnacle samples were collected by the first author with permit numbers as follows: 488/IPK.3/KP/V 2016 for Banda Island; 694/IPK.3/AP/IX/2016 for the islands of Ambon and Pombo; 737/IPK.3/AP/IX/2016 for Saparua Island; B-671/IPK.3/KP.01.06/IX72017 for South Sulawesi; B-684/IPK.5/KP.01.06/IX/2017 for Seram Island.

CHAPTER 3

New insights gained from museum collections: Deep-sea barnacles (Crustacea, Cirripedia, Thoracica) in the Muséum National d'Histoire Naturelle, Paris, collected during the *Karubar* expedition in 1991

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3.1 Abstract

An examination of the deep-sea barnacles (Cirripedia, Thoracica) collected by the *Karubar* expedition to Indonesia (1991) and deposited in the Muséum National d'Histoire Naturelle, Paris, identified 40 species contained in three families of stalked and five families of acorn barnacles. Information on these species is presented, including descriptions, updated distributions and images to aid species identification. Thirty of the species, treated herein, are new records for the Indonesian Kei Islands and Tanimbar Island, which increases the total number of species recorded from Kei Islands, Aru Island and Tanimbar Island to 40. This study demonstrates the value of museum collections as a resource in biodiversity science.

3.2 Introduction

In 1991, scientists from France and Indonesia conducted collaborative research through the *Karubar* expedition in Indonesia. The acronym for this expedition, which collected the material reported on herein, is a contraction of the names of the Kei, Aru and Tanimbar Islands. These Islands attracted attention after Professor Th. Mortensen's Danish expedition to the Kei Islands (1914–16). Mortensen suggested that the Islands were an ideal place for a marine laboratory to study deep-sea fauna, as he had found stalked crinoids, elasipods and other abyssal creatures at depths of 200–400 m around the Kei Islands (Crosnier et al. 1997).

The *Karubar* expedition was part of the MUSORSTOM-Tropical Deep-Sea Benthos programme (1976–present). This programme was a collaboration between the Muséum National d'Histoire Naturelle (MNHN), Paris and the Institut de Recherche pour le Développement (IRD) (formerly ORSTOM), to explore the deep-sea fauna of the tropical Indo-Pacific. As the programme was inspired and guided by carcinologists, it is not surprising that ~ 33% of the papers resulting from these cruises concern crustaceans, especially crabs, lobsters and shrimps (Richer de Forges et al. 2013).

Publications on the thoracic barnacles collected by the *Karubar* expedition are those of Buckeridge (1994, 1997) who focused on barnacles from the suborder Verrucomorpha. He reported six species of verrucomorph barnacles: *Newmaniverruca albatrossiana* (Pilsbry, 1912), *Altiverruca navicula* (Hoek, 1913), *Brochiverruca dens* (Broch, 1932), *Metaverruca recta* (Aurivillius, 1898), *Rostratoverruca intexta* (Pilsbry, 1912) and *R. kruegeri* (Broch, 1922). Here, we present a study of the remaining barnacle material collected by the *Karubar* expedition, to cover the entire taxonomic range of deep-sea barnacles collected by this expedition.

3.3 Material and Methods

In total, 459 specimens were studied at the Muséum National d'Histoire Naturelle (MNHN), of which 89 specimens were studied in detail at the Museum für Naturkunde (MfN), Berlin, Germany. Species were determined on external shell morphology and mouthpart and arthropodal characters, as described in Darwin (1852, 1854), Hoek (1883, 1907, 1913), Pilsbry (1890, 1907, 1916), Annandale (1905, 1906, 1908, 1909, 1910, 1913, 1916), Broch (1916, 1922, 1931), Foster (1974, 1978, 1980, 1981), Newman and Ross (1971, 1976), Rosell (1981, 1989, 1991), Calman (1918, 1919), Ren (1989), Chan et al. (2009, 2010) and Shalaeva and Boxshall (2014).

Hard body parts, such as the shell (parietes) and the opercular plates, were studied using a Leica M125 stereomicroscope. Soft body parts, such as mouthparts and cirri, were studied using an Axioskop 20 light microscope. Mouthparts and cirri were mounted on glass slides and examined under a light microscope. Images were taken using a stereomicroscope with a digital camera (Leica Microsystems M205C and Leica Z16 APo-A).

In the "Taxonomic account" section, the diagnosis is followed by description, type species and localities and known distributions for each species are given. Each species is listed under its current valid binomen and all known synonyms are also provided. Photographs of each species are provided to facilitate their recognition.

In the "Material examined" section, there are four station codes dependent on the type of dredge used and are listed as follows: DW for dredge Warén, ED (drague épibenthique) for epibenthic dredge, CP (chalut à perche) for beam trawl and CC (chalut à crevettes) for otter trawl (shrimp).

Measurements were made using digital callipers (accurate to 0.1 mm) as follows: for acorn barnacles, basal length of shell (LB), basal width (WB), orifice length (LO), orifice width (WO) and carinal height (H); for stalked barnacles, total height (TH), capitular height (CH), diameter of base of capitulum (DBC), distance between carina and scutum (CS), scutal length (LS), scutal width (WS), tergal length (LT) and tergal width (WT).

3.4 Results

Morphological analyses of all the samples revealed 40 species from three families of stalked barnacles (Heteralepadidae: two genera, three species; Poecilasmatidae: four genera, five species; Scalpellidae: twelve genera, 21 species) and five families of acorn barnacles (Verrucidae: two genera and species; Pachylasmatidae: one genus and species; Archaeobalanidae: three genera, six species; Pyrgomatidae: one genus and species; Balanidae: one genus and species).

A list of the species of Cirripedia collected during the *Karubar* expedition and deposited in the Muséum National d'Histoire Naturelle (MNHN) Paris is presented, including additional information on substrate, as well as the depth where the sample was found (Supplementary Table 7.29).

Taxonomic account

Class Hexanauplia Oakley, Wolfe, Lindgren & Zaharoff, 2013
Subclass Thecostraca Gruvel, 1905
Infraclass Cirripedia Burmeister, 1834 (= Cirrhipèdes Lamarck, 1806)
Superorder Thoracica Darwin, 1854

Order Lepadiformes Buckeridge & Newman, 2006
Suborder Heteralepadomorpha Newman, 1987

Diagnosis:

Capitulum and peduncle without calcareous armament. According to Buhl-Mortensen and Mifsud (2017), Heteralepadomorpha consists of seven families of poorlyknown Pedunculata.

Family Heteralepadidae Nilsson-Cantell, 1921

Heteralepadidae Nilsson-Cantell, 1921: 245
Lepadidae Darwin, 1852: 8 (part.)

Diagnosis:

Capitulum naked, thick-walled, globular, supported by stout peduncle; filamentary appendage at base of cirrus I; caudal appendage multi-segmented; cirri ctenopod or acanthopod, rarely lasiopod.

Type genus:

Heteralepas Pilsbry, 1907a.

Remarks:

The family consists of two genera: *Heteralepas* Pilsbry, 1907a and *Paralepas* Pilsbry, 1907a.

Genus *Heteralepas* Pilsbry, 1907

Alepas Darwin, 1852: 156, pl. III, figs 5, 6.
Heteralepas (Heteralepas) Pilsbry, 1907a: 100.
Heteralepas s. str. — Newman 1960: 109.

Diagnosis:

Filamentary appendage present at base of cirrus I, short; posterior rami of cirri V and VI shorter and more slender than anterior rami.

Type species:

Alepas rex Pilsbry, 1907c: 186, fig. 3, pl. IV fig. 7; type locality: Kauai Island, Hawaiian waters.

Heteralepas japonica (Aurivillius, 1892)

Figure 3.1

Alepas japonica Aurivillius, 1892: 125. — 1894: 28, pl. II figs 14, 15, pl. VIII, figs 3, 7, pl. IX, fig. 3.
Alepas indica Gruvel, 1901: 259. — 1905a: 162, fig. 179.
Heteralepas (*Heteralepas*) *japonica*. — Pilsbry 1907a: 101.
Heteralepas (*Heteralepas*) *japonica* var. *alba* Krüger, 1911: 34, pl. 1, fig. 2b.
Heteralepas (*Heteralepas*) *dubia* Broch, 1922: 288, fig. 38.
Heteralepas japonica. — Pilsbry 1911: 71, fig. 4. — Zevina et al. 1992: 31, fig. 19. — Chan et al. 2009a: 61. — Chan et al. 2009b: 88–91, figs 2A–D, 3A–D, 4, 5. — Pitriana et al. 2020a: 12, fig. 3.

Material examined:

Tanimbar Island: 1 specimen, MNHN-IU-2019-4877, stn. CP 46, 08°01'S, 132°51'E, 271–273 m depth, 29 October 1991.

Diagnosis:

Capitulum rounded, plates absent; wall of capitulum thick; orifice crenulated with no more than two crests on carinal region; cirrus VI with caudal appendage; maxillule strongly notched.

Description:

Capitulum and peduncle yellowish. Orifice slightly protuberant, crenulated, occupying one half to one third capitular length, parallel to or at oblique angle to capitulum; integument thick, chitinous. Cirrus I with anterior rami (20-segmented) shorter than posterior rami (25-segmented); cirrus VI with long caudal appendage, 24-segmented, 2/3 length of anterior ramus. Mandibles with four large teeth excluding inferior angle; maxillule strongly notched, two large setae at upper angle, blade-shaped setae on cutting margin; labrum concave with numerous teeth. Measurements of specimen: height of capitulum 18.50 mm, width 12.82 mm, thickness 5.97 mm; length of peduncle 15.26 mm, width 5.55 mm.

Distribution:

Singapore; Indo-west Pacific: Indian Ocean; Australia; Malay Archipelago; Vietnam; Condor Island; South China Sea; East China Sea; Taiwan, Philippines; South Japan; NE New Zealand; fouling hard rock substrata, crabs, gorgonians, antipatharians, deep-sea cables; 48–500 m depth (Jones and Hosie 2016). Recently, the species has also been recorded from the Lifamatola Sea and the Halmahera Sea, Indonesia (Pitriana et al. 2020a). In this study, *Heteralepas japonica* was found at Tanimbar Island, Indonesia.

Type locality:

Hirado Strait, Japan, 146 m depth (Aurivillius 1892).

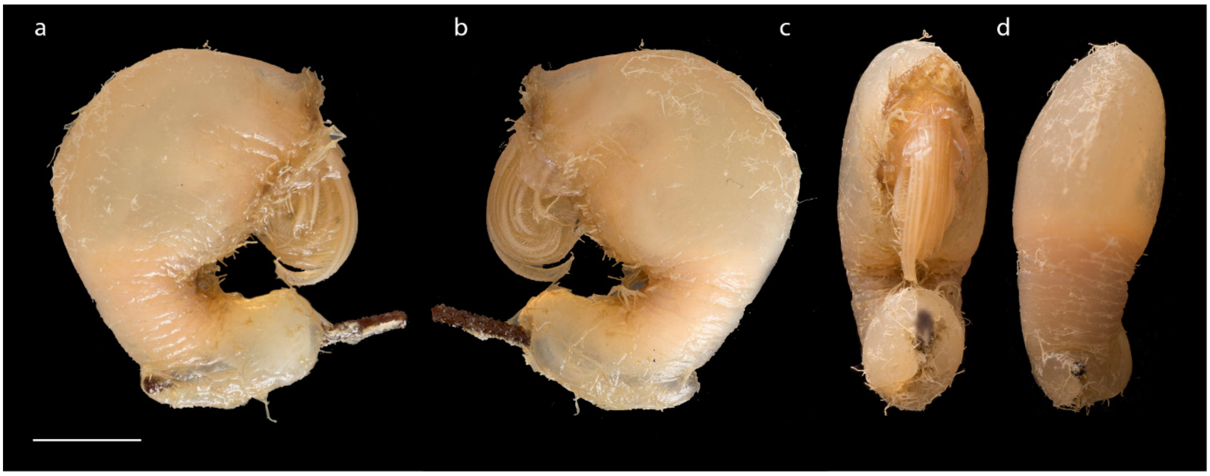

Figure 3.1. *Heteralepas japonica* (Aurivillius, 1892) (MNHN-IU-2019-4877). (**a**) left lateral view showing the capitulum and peduncle, (**b**) right lateral view showing the capitulum and peduncle, (**c**) anterior view, orifice, (**d**) posterior view, capitulum and peduncle. Scale bars: a–d) 6 mm.

Genus *Paralepas* Pilsbry, 1907

Alepas Darwin, 1852: 156 (part.).

Heteralepas (*Paralepas*) Pilsbry, 1907a: 100, fig. 34A.

Paralepas s. str. — Newman 1960: 108.

Diagnosis:

Maxillule slightly notched; filamentary appendages well-developed; posterior and anterior rami of cirri V and VI similar in length; segments of cirri V and VI square-shaped, each armed with semi-circular brush of many setae on anterior face.

Type species:

Alepas percarinata Pilsbry, 1907c: 185, fig. 2, pl. IV, fig. 8; type locality: Molokai, Hawaiian waters.

Paralepas minuta (Philippi, 1836)

Figure 3.2

Alepas minuta Philippi, 1836: 254, pl. 12, fig. 23.
Alepas (*Paralepas*) *minuta*. — Weltner 1897: 239.
Heteralepas (*Paralepas*) *minuta*. — Broch 1927b: 18, fig. 4, pl. 1, figs 1, 2.
Paralepas minuta nipponica Utinomi, 1970: 342.
Paralepas minuta. — Stubbings 1967: 240. — Newman 1960: 109. — Chan et al. 2009b: 66, figs 55–57.

Material examined:

- Kei Islands: 6 specimens, MNHN-IU-2019-4882, Stn. CP 25, 05°30’S, 132°52’E, 336–346 m depth, 26 October 1991, attached to dead stem of gorgonian.
- Tanimbar Island: 4 specimens, MNHN-IU-2019-4883, Stn. CP 85, 09°22’S, 131°14’E, 240–245 m depth, 4 November 1991, attached to spine of sea urchin.

Diagnosis:

Capitulum yellowish with globular shape; anterior and posterior rami of cirrus V and VI similar in length.

Description:

Capitulum yellowish, globose, small-sized, externally smooth; orifice crenulated; peduncle rather short. Segments of rami of cirrus I wide, anterior ramus (9-segmented) shorter than posterior ramus (13-segmented); cirrus VI with short caudal appendage, 8-segmented. Penis annulated, setae sparsely distributed over most of surface, a few longer setae towards tip. Maxillule notched, two large and one small setae at upper angle; mandible with four major teeth; labrum concave, with numerous teeth. Measurements of specimen: height of capitulum 8.34 mm, width 6.67 mm, thickness 4.53 mm; length of peduncle 3.84 mm, width 2.60 mm.

Distribution:

Java Sea (Indonesia); Mediterranean Sea; West Africa; Indo-west Pacific: Indian Ocean; Australia; Malay Archipelago; Taiwan; Japan; Philippines; Northern New Zealand; 485–736 m depth; attached to spines of cidarids (Jones and Hosie 2016). In this study, *Paralepas minuta* was found at Kei Islands and Tanimbar Island, Indonesia.

Type locality:
Mediterranean Sea (Chan et al. 2009b).

Remarks:
Paralepas minuta (Philippi, 1836) can be distinguished from *Paralepas ovalis* (Hoek, 1907) by the presence of triangular scutal areas and from *Paralepas nodulosa* Broch, 1922 by the absence of "well defined, scanty, almost thorn-like warts" (Broch 1922).

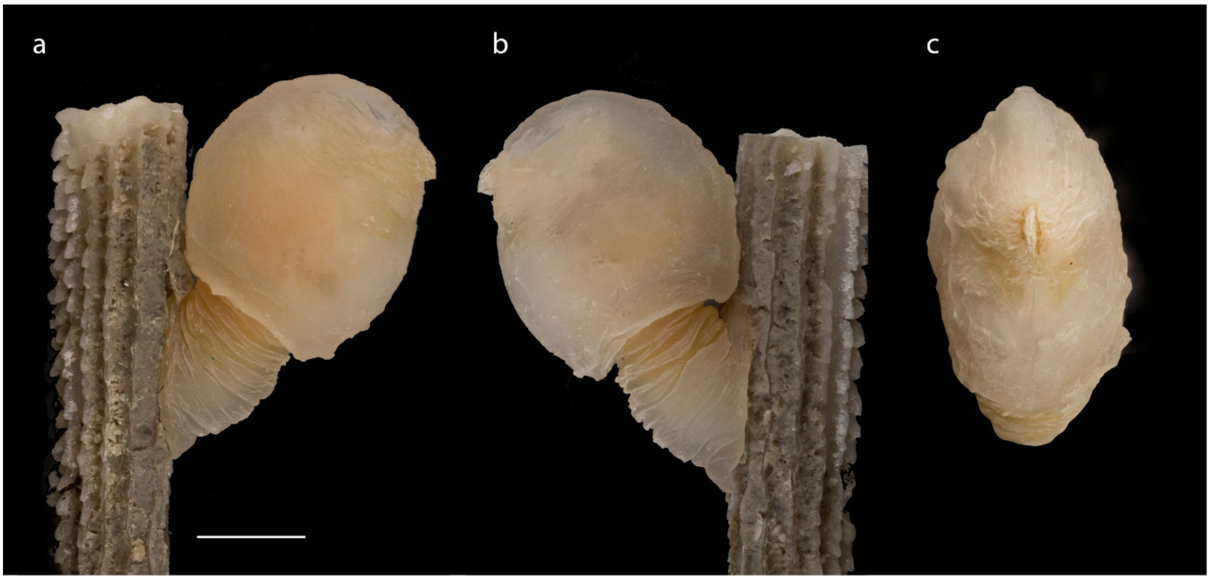

Figure 3.2. *Paralepas minuta* (Philippi, 1836) (MNHN-IU-2019-4882). (**a**) left lateral view, capitulum and peduncle, (**b**) right lateral view, capitulum and peduncle, (**c**) anterior view, orifice. Scale bars: a–c) 5 mm.

Paralepas morula (Hoek, 1907)
Figure 3.3

Alepas morula Hoek, 1907: 35, pl. IV, figs 9–12.
Heteralepas (*Paralepas*) *morula*. — Broch 1922: 28, fig. 34.
Paralepas morula. — Newman 1960: 109.

Material examined:
- Tanimbar Island: 45 specimens, MNHN-IU-2019-4878, Stn. CP 54, 08°21'S, 131°43'E, 836–869 m depth, 30 October 1991, attached to spine of sea urchin.

Diagnosis:
Capitulum globular with numerous tubercles on surface, scuta absent, orifice small, not protuberant, peduncular length more than half capitular length.

Description:
Capitulum and peduncle yellowish. Capitulum globular with thick, chitinous, large warts all over surface. Peduncle rather long, narrower than capitulum; surface bearing tubercles,

smaller than those of capitulum. Cirrus I placed rather far from cirrus II; cirri II–VI similar, length and number of segments slightly increasing from second to sixth; cirrus VI with 7-segmented caudal appendage. Penis indistinctly segmented, few long hairs towards tip. Maxillule notched, two large setae on upper notch; mandibles with three major teeth, inferior angle considered as fourth tooth; labrum with continuous row of numerous short, strong, blunt teeth. Measurements of specimen: height of capitulum 5.14 mm, width 3.69 mm, thickness 1.81 mm; length of peduncle 5.08 mm, width 1.31 mm.

Distribution:

Flores Sea (Indonesia); Philippines; Bass Strait, N of Tasmania; attached to spines of echinoids, for example, *Histocidaris elegans* (Agassiz, 1879); 182–538 m depth (Jones and Hosie 2016). In this study, *Paralepas morula* was found at Tanimbar Island, Indonesia.

Type locality:

Bali Sea, North of Lombok; 538 m depth (Hoek 1907).

Remarks:

Most of the smaller specimens do not show the warts that are characteristic of this species.

Figure 3.3. *Paralepas morula* (Hoek, 1907) (MNHN-IU-2019-4878). (**a**) left lateral view, capitulum and peduncle, (**b**) right lateral view, capitulum and peduncle. Scale bars: a, b) 3 mm.

Suborder Lepadomorpha Pilsbry, 1916

Lepadomorpha Pilsbry, 1916: 14 (Lepadidae *sensu* Darwin, 1852).
Lepadoidea Darwin, 1852: 8 (*nom. trans.* Zevina 1978a, b).

Family Poecilasmatidae Annandale, 1910

Lepadidae Darwin, 1852: 8 (part.). — Pilsbry 1907a: 72 (part.).
Lepadinae. — Gruvel 1905: 104 (part.).
Poecilasmatinae Annandale, 1910a: 84.

Poecilasmatidae. — Nilsson-Cantell 1921: 253.
Trilasmatidae Nilsson-Cantell, 1934: 40. — Hiro 1937a: 79. — Krüger 1940: 29.

Diagnosis:

Capitulum with up to five plates, including tergum and scutum; scutum in some species split into two (resulting in seven plates); some or all plates may be degenerate or absent; umbos of terga apical, those of carina and scuta fundamentally basal; peduncle without calcareous scales; maxillule not stepped; cirrus I widely separated and much shorter than posterior cirri; caudal appendages uniarticulate, spinose.

Type genus:

Poecilasma Darwin, 1852: 99.

Genus *Dianajonesia* Koçak & Kemal, 2008

Temnaspis Fischer, 1884: 357. — Broch 1931: 30.
Poecilasma (part). — Darwin 1852: 99. — Pilsbry 1907a: 82. — Nilsson-Cantell 1921: 253.
Dianajonesia Koçak & Kemal, 2008: 2.

Diagnosis:

Capitulum with five plates, approximate or variously reduced; scutum divided into two parts; apex of carina extending to, or slightly overlapping basal end of terga, basally terminating in disc.

Type species:

Poecilasma fissa Darwin, 1852: 109, pl. II, fig. 4, pl. X, fig. 29.

Dianajonesia amygdalum (Aurivillius, 1894)

Figure 3.4

Poecilasma amygdalum Aurivillius, 1894: 10, pl. 1, figs 4–6, pl. 8, fig. 4. — Nilsson-Cantell 1921: 262, fig. 46 d–g, pl. 3, fig. 6.
Poecilasma fissum (non Darwin). — Hoek 1907: 8 (part.).
Trilasmis fissum hawaiense. — Pilsbry 1928: 306, pl. 24, figs 1–8.
Trilasmis (Temnaspis) amygdalum. — Hiro 1937a: 85, fig. 69.
Temnaspis amygdalum amygdalum. — Zevina: 1982: 70, fig. 62.
Temnaspis amygdalum. — Utinomi 1966: 5. — Dong et al. 1982: 77.
Dianajonesia amygdalum. — Koçak & Kemal, 2008: 2.

Material examined:

- Tanimbar Island: 2 specimens, MNHN-IU-2019-4861, Stn. CP 79, 09°16’S, 131°22’E, 239–250 m depth, 3 November 1991, attached to crab leg.

Diagnosis:

Capitulum broadly oval, with five smooth plates; carina not extending to area between terga; peduncle with circles of small protuberances; cirri short.

Description:

Capitulum yellowish, with five tranparent, smooth plates. Scutum bilobed, occludent segment narrow, bow-shaped; tergum sub-triangular, nearly half as broad as long. Carina very narrow, slightly curved downwards, end blunt. Peduncle yellow, plainly ringed, spines absent. Cirrus I with anterior ramus wider than posterior ramus. Maxillule notched, with two strong teeth in upper part; mandible with four teeth, fourth pectinated, placed very close to inferior angle; labrum with row of minute teeth. Measurements of specimen: basal diameter of capitulum 0.94 mm; capitular height 7.03 mm; total height 10.40 mm; scutal width 4.11 mm; scutal length 5.85 mm; tergal width 1.00 mm; tergal length 3.13 mm.

Distribution:

Indo-west Pacific: Indian Ocean; Madagascar through Malaysia, Hong Kong, South China Sea; Taiwan; Philippines; South Japan; tropical West and central Pacific Ocean to Fiji and Hawaii; attached to decapod crustaceans; shallow water (Jones and Hosie 2016). In this study, *Dianajonesia amygdalum* was found at Tanimbar Island, Indonesia.

Type locality:

Nordwachter Island, Thousand Islands, Java Sea (Aurivillius 1894).

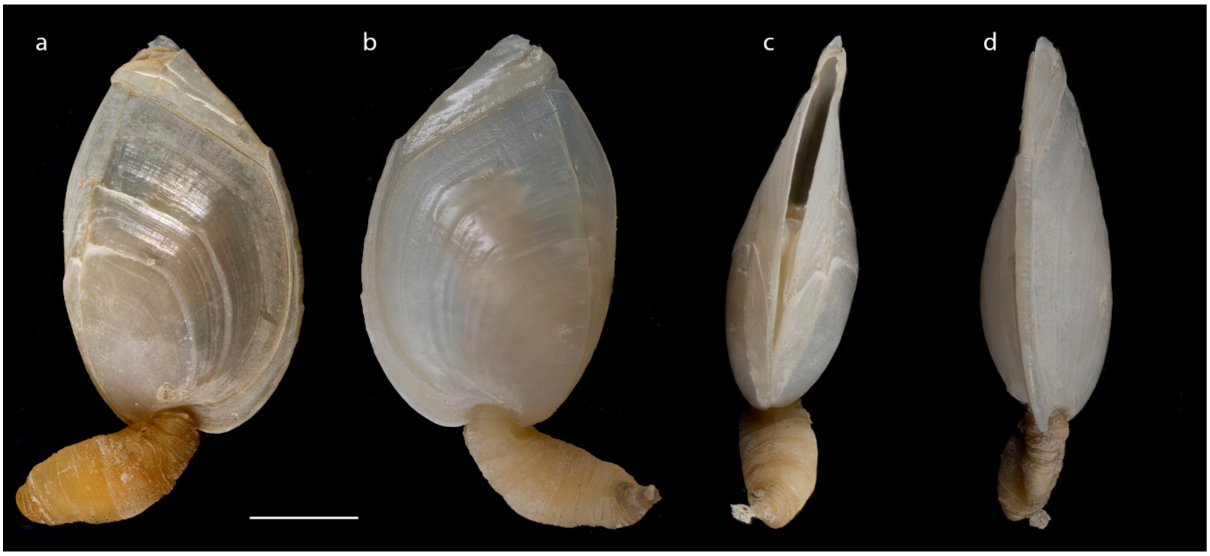

Figure 3.4. *Dianajonesia amygdalum* (Aurivillius, 1894) (MNHN-IU-2019-4861). (**a**) left lateral view, capitulum and peduncle, (**b**) right lateral view, capitulum and peduncle, (**c**) anterior view, orifice (**d**) posterior view, carina. Scale bars: a–d) 2 mm.

Dianajonesia excavatum (Hoek, 1907)

Figure 3.5

Poecilasma excavatum Hoek, 1907: 10, pl. I, figs 5–10.
Poecilasma tridens. — Weltner 1922: 80, pl. 4, fig. 19 (*non* Aurivillius).
Poecilasma (Temnaspis) excavatum. — Nilsson-Cantell 1925: 16, fig. 5, pl. 1, fig. 1.

Trilasmis (Temnaspis) excavatum. — Hiro 1937b: 412.
Dichelaspis (Dichelaspis) tridens. — Stubbings 1936: 7, fig. 2. (*non* Aurivillius).
Trilasmis excavatum. — Nilsson-Cantell 1938: 9.
Temnaspis excavatum. — Broch 1931: 31, fig. 10. — Dong et al. 1982: 77.
Dianajonesia excavatum. — Koçak & Kemal, 2008: 2.

Material examined:

- Tanimbar Island: 3 specimens, MNHN-IU-2019-4859, Stn. CP 78, 09°06'S, 131°24'E, 284-295 m depth, 3 November 1991.

Diagnosis:

Capitulum with scutum divided into two segments parallel to occludent margin; tergum with excavation in scutal margin near occludent margin, receiving tip of occludent segment of scutum.

Description:

Capitulum oval, apex pointed, slightly thick, swollen. Scutum with larger segment strongly bowed, basal margin short, apex pointed; smaller segment bowed, terminating in point at base, tergal margin rounded, fitting exactly into excavation of tergum. Tergum triangular, characteristic excavation at scutal margin near occludent margin. Carina narrow, terminating in spatula-shaped disc. Cirrus I with anterior and posterior rami subequal (each five-segmented); cirri II–VI longer, more slender; cirrus VI with caudal appendages. Penis thick, ringed, especially mid-length, terminating in narrower, curved part. Maxillule notched, two large teeth on upper side; mandible with four teeth, largedistance between first and second teeth. Labrum convex, with numerous blunt teeth. Measurements of specimen: basal diameter of capitulum 1.06 mm; capitular height 7.12 mm; total height 12.69 mm; scutal width 3.08 mm; scutal length 6.09 mm; tergal width 1.30 mm; tergal length 3.47 mm.

Distribution:

Indo-west Pacific: East coast of Africa (Zanzibar); Gulf of Aden; Indonesia; Malay Archipelago; South China Sea; East China Sea; Philippines; South Japan (Goto Island); attached to echinoid spines, crustaceans; palinurids and cirripedes; 189–600 m depth (Jones and Hosie 2016). In this study, *Dianajonesia excavatum* was found at Tanimbar Island, Indonesia.

Type locality:

Siboga station 253; 5°48.2' S, 132°15' E; depth: 304 m; bottom: grey clay, hard and crumbly (Hoek 1907).

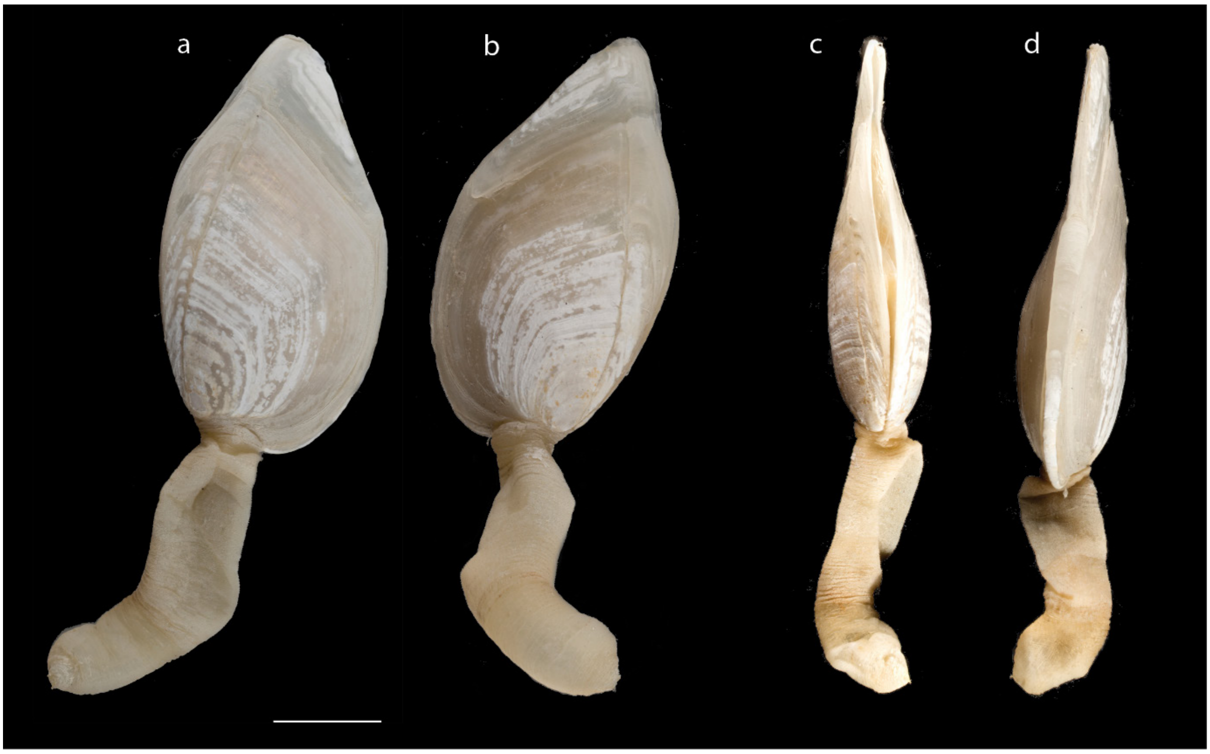

Figure 3.5. *Dianajonesia excavatum* (Hoek, 1907) (MNHN-IU-2019-4859). (**a**) left lateral view showing the capitulum and peduncle, (**b**) right lateral view showing the capitulum and peduncle, (**c**) anterior view, orifice, (**d**) posterior view, carina. Scale bars: a–d) 2 mm.

Genus *Dichelaspis* Darwin, 1852

Dichelasmis Darwin, 1852: 115.
Heptalasmis. Agassiz, 1842: 178.
Octolasmis Gray, 1825: 100. — Pilsbry 1907a: 93.

Diagnosis:

Capitulum with five plates; scutum with two distinct segments, united at rostral angle; carina generally extending up between terga, terminating downwards as imbedded disc (fork- or cup-shaped).

Type species:

Octolasmis warwicki Gray, 1825: 100. — 1830: pl. VI, fig. 16.

Dichelaspis orthogonia Darwin, 1852

Figure 3.6

Dichelaspis orthogonia Darwin, 1852: 130, pl. II, fig. 10a, b.
Dichelaspis versluysi Hoek, 1907: 28, pl. III, figs 8–13.
Octolasmis (Dichelaspis) orthogonia. — Pilsbry 1907a: 94.
Octolasmis orthogonia. — Krüger 1911: 462. — Pilsbry 1911: 70, pl. 11, figs 6–7. — Broch 1922: 279. — 1931: 38, fig. 14. — Nilsson-Cantell 1925: 21, fig. 8. — 1928: 18, fig. 8. — Hiro 1933: 55, fig. 16, pl. 2, fig. 5a, 5. — 1937a: 91, fig.71. — 1937b: 415, fig. 12. — Stubbings 1963: 327, fig. 1. — Dong et al. 1982: 79. — Zevina et al. 1992: 26, fig. 15. — Chan 2009: 68, fig. 2 B and fig. 17 A–F.

Material examined:

- Kei Islands: 4 specimens, MNHN-IU-2019-4864, Stn. CP 27, 05°33'S, 132°51'E, 314–304 m depth, 27 October 1991.
- Tanimbar Island: 6 specimens, MNHN-IU-2019-4862, Stn. DW 24, 05°32'S, 132°51'E, 230-243 m depth, 26 October 1991.

Diagnosis:

Capitulum flattened; five plates, separated by thin membrane; scutum consisting of two distinct segments, with point of junction perfectly calcified; base of carina oval.

Description:

Capitulum and peduncle yellowish. Scutum with basal segment narrow, L-shaped; tergum triangular, three prominent ridges at scutal margin; base of carina crescent-formed cup. Cirrus I with anterior ramus (6-segmented) shorter than posterior ramus (8-segmented); cirrus VI with small caudal appendage. Maxillule notched, three large setae on upper notch; mandible with four teeth, inferior angle produced into single strong spine; labrum concave, with numerous teeth. Measurements of specimen: basal diameter of capitulum 1.89 mm; capitular height 8.69 mm; total height 10.47 mm; scutal width 3.5 mm; scutal length 7.16 mm; tergal width 0.80 mm; tergal length 6.53 mm.

Distribution:

Indo-west Pacific: East and South African Coast, Indian Ocean, Australia, Indonesia, Malay Archipelago, Vietnam, South China Sea, East China Sea, Philippines, Taiwan, South Japan; attached to hydroid, gorgonians, antipatharians, sea urchin spines, nylon cord, sometimes fouling; 14–818 m depth (Jones and Hosie 2016). In this study, *Dichelaspis orthogonia* was found at Kei Islands and Tanimbar Island, Indonesia.

Type locality:

Unknown.

Remarks

The type locality of this species is unknown. The species was re-discovered in the Malay Archipelago by the *Siboga* Expedition in 40–112 m depth (Hoek 1907) and the *Albatross* Expedition, off Kagoshima Gulf, Japan, in 87 m depth (Pilsbry 1907d).

Figure 3.6. *Dichelaspis orthogonia* Darwin, 1852 (MNHN-IU-2019-4864). (**a**) left lateral view capitulum and peduncle, (**b**) right lateral view, capitulum and peduncle. Scale bars: a–b) 2 mm.

Genus *Glyptelasma* Pilsbry, 1907

Glyptelasma Pilsbry, 1907a: 87.

Diagnosis

Capitulum with five approximate, fully calcified plates; scutum quadrangular, umbone subcentral; carina becoming larger towards base; peduncle short.

Type species:

Megalasma (*Glyptelasma*) *subcarinatum* Pilsbry, 1907a: 91, pl. VII, figs 1–5; type locality: Atlantic Ocean, East of New Jersey, USA.

Glyptelasma gracile (Hoek, 1883)

Figure 3.7

Poecilasma gracile Hoek, 1883: 46, pl. II, figs 2–4.
Megalasma gracile gracilius. — Pilsbry 1907a: 88, pl. V, fig.16, pl. VII, figs 6–9.
Megalasma gracile. — Nilsson-Cantell 1938: 10.
Megalasma (*Glyptelasma*) *gracile*. — Zevina 1982: 84, fig. 74.
Glyptelasma gracile. — Jones et al. 2001: 239.

Material examined:

- Tanimbar Island: 14 specimens, MNHN-IU-2019-4873, Stn. CP 54, 08°21’S, 131°43’E, 836–869 m depth, 30 October 1991, attached to spine of sea urchin; 1 specimen, MNHN-IU-2019-4875, Stn. CC 57, 08°19’S, 31°53’E, 603–620 m depth, 31 October 1991; 3 specimens (1 adult, 2 juveniles), MNHN-IU-2019-4876, Stn. CP 73, 08°29’S, 131°33’E, 840-855 m depth, 2 November 1991, attached to spines of sea urchins.

Diagnosis:

Capitulum with five plates; carina enlarged, keel-shaped; tergum with basal point truncated; maxillule notched; caudal appendages with relatively-long spines at tip.

Description:

Capitulum whitish, peduncle brownish. Capitulum compressed, striated, about twice as long as broad. Scutum with apex pointed; tergum basally truncated, flat, oblong. Carina flat, very narrow, enlarged, keel-shaped in basal region. Cirrus I with anterior and posterior rami equal length; cirrus II–VI long, slender; cirrus VI with small caudal appendages. Penis with few long hairs towards tip. Maxillule notched, with strong teeth on upper side; mandible with four teeth; labrum with row of small teeth on crest. Measurements of specimen: basal diameter of capitulum 1.45 mm; capitular height 10.44 mm; total height 13.99 mm; scutal width 4.79 mm; scutal length 9.01 mm; tergal width 1.87 mm; tergal length 5.07 mm.

Distribution:

West-southwest Pacific: from Australia (Sydney) to Indonesia (Sumbawa) and the Philippines (northwest Panay Island); East Indian Ocean; attached to glassy spicule of hexactinellid sponge, fragments of sea urchin tests, spines of cidarids; 395–935 m depth (Jones and Hosie 2016). In this study, *Glyptelasma gracile* was found at Tanimbar Island, Indonesia.

Type locality:

Challenger expedition Station 164a (off Sydney, Australia); 34°13’S, 151°38’E; depth 125 m; bottom: grey ooze (Hoek 1883).

Figure 3.7. *Glyptelasma gracile* (Hoek, 1883) (MNHN-IU-2019-4875). (**a**) left lateral view, capitulum and peduncle, (**b**) right lateral view, capitulum and peduncle, (**c**) anterior view, orifice, (**d**) posterior view, carina. Scale bars: a–d) 2 mm.

Genus *Megalasma* Hoek, 1883

Megalasma Hoek, 1883: 50. — Pilsbry 1907a: 87.

Diagnosis:

Capitulum with five strong, calcified plates; scutal umbones subcentral; apex of carina sometimes slightly overlapping basal end of terga, progressively becoming broader towards base; peduncle very short.

Type species:

Megalasma striatum Hoek, 1883: 51, pl. II, figs 5–9, pl. VII, figs 8–9.

Megalasma striatum Hoek, 1883

Figure 3.8

Megalasma striatum Hoek, 1883: 51, pl. II, figs 5–9, pl. VII, figs 8, 9. — Broch 1931: 270, figs 29–30.
Megalasma (*Megalasma*) *elegans*. — Zullo & Newman 1964: 355, fig. 2 a–i.
Megalasma (*Megalasma*) *striatum*. — Zevina 1982: 80, fig. 71. — Chan 2009: 66, figs 2A, 16 A–H.

Material examined:

- Kei Islands: 1 specimen, MNHN-IU-2019-4868, Stn. CP 09, 05°23'S, 132°29'E, 368–389 m depth, 23 October 1991; 1 specimen, MNHN-IU-2019-4869, Stn. CP 16, 05°17'S, 132°50'E, 315–349 m depth, 24 October 1991, attached to sea urchin spine; 2 specimens, MNHN-IU-2019-4866, Stn. CP 17, 05°15'S, 133°01'E, 439–459 m depth, 24 October 1991.
- Tanimbar Island: 1 specimen, MNHN-IU-2019-4867, Stn. CP 46, 08°01'S, 132°51'E, 271–273 m depth, 29 October 1991; 4 specimens (3 attached to sea urchin spine), MNHN-IU-209-4870, Stn. DW 49, 08°00'S, 132°59'E, 206-210 m depth, 29 October 1991; 6 specimens, MNHN-IU-2019-4871, Stn. CP 85, 09°22'S, 131°14'E, 240–245 m depth, 4 November 1991, attached to spines of sea urchin.

Diagnosis:

Capitulum ovate, occludent margin almost same length as carinal margin; capitular plates heavily calcified, markedly sculptured with radial striations between grooves of growth lines; peduncle short, covered by capitulum.

Description:

Capitulum white, with five calcified plates, surfaces strongly striated. Scutum with basal margin rotated; tergum triangular in lateral view; carina with dorsal roof widening apically on either side of midline groove. Cirrus I with anterior ramus wider than posterior ramus. Maxillule with three strong setae at upper angle separated by wide notch; mandible with four teeth, lower angle sharp. Measurements of specimen: basal diameter of capitulum 2.14 mm; capitular height 9.36 mm; total height 9.36 mm; scutal width 3.81 mm; scutal length 7.28 mm; tergal width 1.58 mm; tergal length 4.29 mm.

Distribution:

West-southwest Pacific, Indo-west Pacific, East coast of Africa, Indian Ocean, north Australia, Indonesia, Malay Archipelago, East China Sea, South China Sea, Taiwan, Philippines, south Japan to New Zealand; attached to echinoid spines, antipatharians, gorgonians, glassy spicule of hexactinellid sponges, corallines; 125–984 m depth (Jones and Hosie 2016). In this study, *Megalasma striatum* was found at Kei Islands and Tanimbar Island, Indonesia.

Type Locality:

Philippine Archipelago (Hoek 1883).

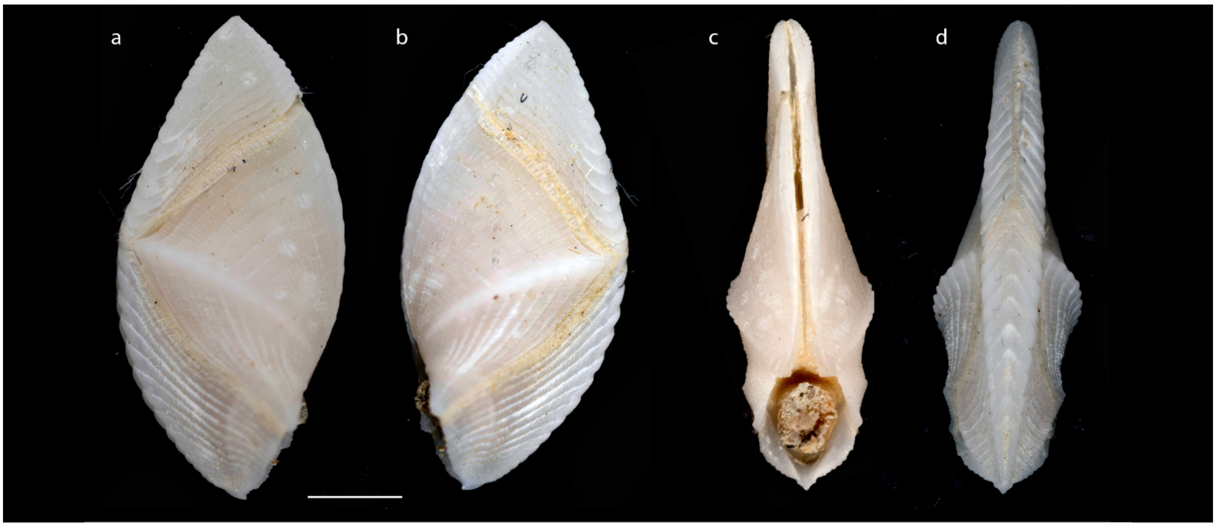

Figure 3.8. *Megalasma striatum* Hoek, 1883 (MNHN-IU-2019-4868). (a) left lateral view, capitulum, (b) right lateral, capitulum, (c) anterior view, capitulum and peduncle, (d) posterior view, carina. Scale bars: a–d) 2 mm.

Order Scalpelliformes Buckeridge & Newman, 2006

Scalpelloidea Pilsbry, 1916: 14 (*nom. trans.* Zevina, 1978).

Scalpelliformes Buckeridge & Newman, 2006: 22.

Family Scalpellidae Pilsbry, 1907

Pollicipedidae Gray, 1825: 100 (part.). — Annandale 1909: 63 (part.).

Lepadidae Darwin, 1852: 8 (part.).

Polyaspidae Gruvel, 1905: 8, 16 (part.; rejected by Pilsbry, 1907a, because family group name not derived from generic name).

Scalpellinae Pilsbry, 1907a: 3 (part.).

Scalpellidae. — Krüger 1911: 7. — Pilsbry 1916: 4. — Nilsson-Cantell 1921: 162. — Foster 1978: 38. — Zevina 1978a: 999. — Buckeridge 1983: 27. — Gale 2016: 296.

Diagnosis:

Capitulum with fully or partially calcified plates; peducle with calcareous or phosphorus scales. According to Gale (2016), the Scalpellidae have a maximum of 14 plates i.e. carina, rostrum, paired scuta, terga, upper latera, carinolatera, rostrolatera and inferior median latera; and rarely 13 plates, due to secondary loss of the rostrum.

Subfamily Scalpellinae Pilsbry, 1907

Scalpellinae Pilsbry, 1907a: 4. — Zevina 1978a: 1002. — Zevina 1981: 93. — Gale 2016: 296.
Pollicipedidae. — Annandale 1909: 63 (part.).

Diagnosis:

Formerly, the subfamily was characterised by a subapical carinal umbo, inflexed carina and subapical umbones of the upper and inframedian latus (Zevina 1978a). Gale (2016) characterised the subfamily by the broad, low, straplike and gently incurved rostrolatus. The rostrum is broader than high, rectangular, trapezoidal or triangular and its large, triangular, lateral surfaces contact the interior of the rostrolatus. The articulation surface between the rostrum and rostrolatus extends over the entire height of both plates.

Type genus:

Scalpellum Leach, 1817: 68.

Genus *Diotascalpellum* Gale, 2016

Diotascalpellum Gale, 2016: 297.

Diagnosis:

Scalpellines without specialised contact between carina and carinolatus, merely a cresentic concavity on interior of plate that forms a rim slightly overlapping the upper latus; umbo of carinolatus upright, only slightly incurved, dorsal margin gently convex; inframedian surface of carinolatus well demarcated, slightly inset.

Diotascalpellum rubrum (Hoek, 1883)

Figure 3.9

Scalpellum rubrum Hoek, 1883: 91, pl. IV fig. 18. — Pilsbry 1911: 62, text-fig. 1, pl. VIII, figs 1–4. — Calman 1918b: 122–123. — Broch 1922: 237. — Nilsson-Cantell 1927: 745–747, text-fig. 2. — 1931: 2.

Trianguloscalpellum rubrum. — Zevina 1981: 316–317, fig. 240. — Rosell 1986: 89, text-fig. 1a. — 1991: 22, fig. 1f–g. — Huang 1994: 517. — 2001: 318. — Jones et al. 2001: 254. — Young 2001: 464, fig. 7. — Jones 2007: 292. — Shalaeva & Boxshall 2014: 49, fig. 34.

Diotascalpellum rubrum. — Gale 2016: 297, figs 2A, 6U–Y, 11Q–T, 13K–M, 18A–G.

Material examined:

- Kei Islands: 2 specimens, MNHN-IU-2019-4925, Stn. CP 09, 05°23’S, 132°29’E, 368–389 m depth, 23 October 1991; 1 specimen, MNHN-IU-2019-4926, Stn. CP 16, 05°17’S, 132°50’E, 330–350 m depth, 24 October 1991, attached to gorgonian.

Diagnosis:

Capitulum with 14 plates, smooth, white and reddish coloured; carina simply, strongly bowed, roof slightly convex with umbo at apex; rostrum triangular, distinct; upper latus quadrangular, large; infra-median latus triangular.

Description:

Capitulum flat, rather broad, not covered by distinct membrane. Scutum with occludent margin arched, forming with tergal margin a triangular portion projecting over tergum. Tergum surpassing scutal area with occludent margin almost straight. Upper latus quadrangular, angle at apex between scutal and tergal margins distinctly projecting over scutum. Rostrum small, triangular; rostrolatus very low, quadrangular; infra-median latus small, triangular, umbo at apex; carinal latus larger than other latera with carinal margin arched. Cirrus I with anterior and posterior rami almost same length; cirrus VI with long caudal appendages. Maxillule not notched, with large spine on upper side, cutting edge almost straight; mandible with three large teeth excluding inferior angle. Measurements of two specimens: height of capitulum 12.51–20.57 mm, width 7.39–10.55 mm, thickness 4.09–6.51 mm; length of peduncle 5.10–7.76 mm, width 4.36–6.62 mm.

Distribution:

Java Sea, Indonesia. Pacific: western central and northwest; Philippines; Kagoshima Sea and Sagami Bay, Japan; 133–551 m depth (Shalaeva and Boxshall 2014). In this study, *Diotascalpellum rubrum* was found at Kei Islands, Indonesia.

Type locality:

Philippines, 12°43'N, 122°10'E.; depth, 180 m and 207 m; bottom, mud (near Luzon) (Hoek 1883).

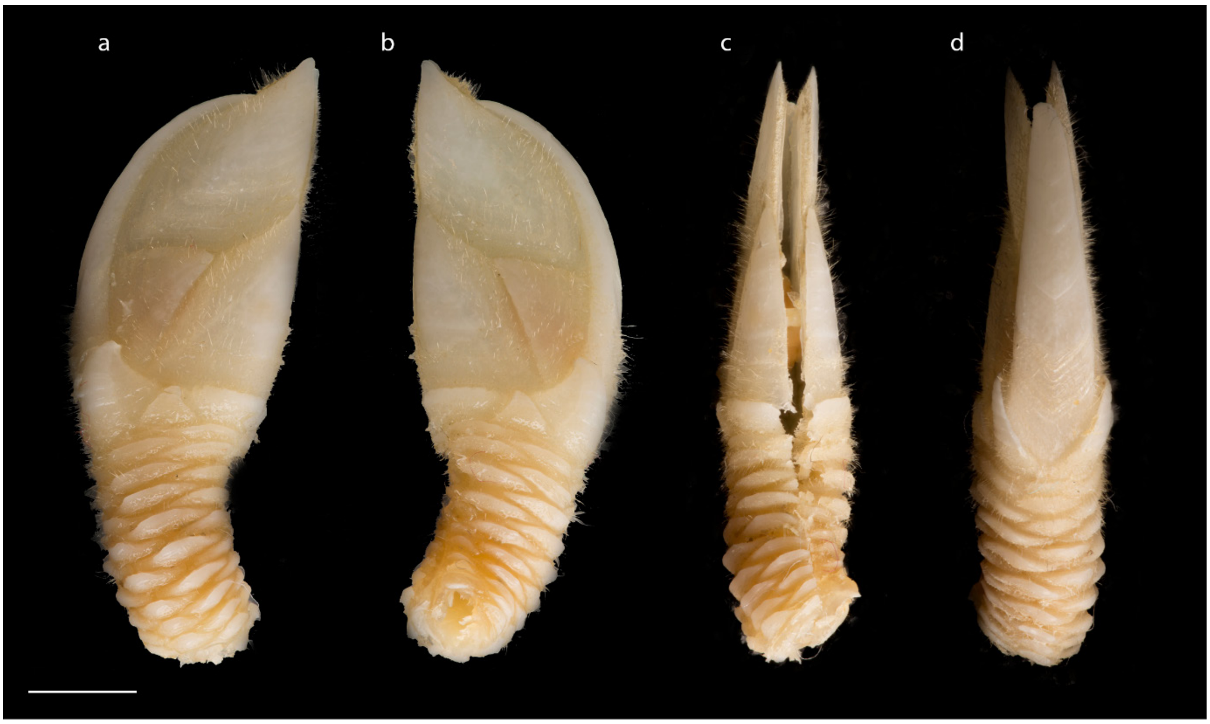

Figure 3.9. *Diotascalpellum rubrum* (Hoek, 1883) (MNHN-IU-2019-4925). (**a**) left lateral view showing the capitulum and peduncle, (**b**) right lateral view showing the capitulum and peduncle, (**c**) rostral view showing the capitulum and peduncle, (**d**) carinal view. Scale bars: a–d) 5 mm.

Genus *Regioscalpellum* Gale, 2016

Regioscalpellum Gale, 2016: 298.

Diagnosis:

Concave scalpellines; internal surface upper latus covered by epidermis, short carinal margin present on carinolatus; carinolatus with incurved umbones, lateral margin strongly convex.

Type species:

Scalpellum regium Thomson, 1873; type locality: Stn 61: Atlantic, Western Central (North Western Atlantic Basin); 5,210 m depth.

Regioscalpellum moluccanum (Hoek, 1883)

Figure 3.10

Scalpellum moluccanum Hoek, 1883: 104, pl. V figs 3–4; 1907: 56, 85, pl. VII, fig. 13. — Gruvel 1905: 76, fig. 85. — Nilsson-Cantell 1927: 747, fig. 3.

Arcoscalpellum moluccanum. — Newman & Ross 1971: 60. — Jones et al. 1990: 6, 27. — Jones 1992: 172–175, figs 18–19.

Trianguloscalpellum moluccanum. — Jones 2012: 371, table 2. — Shalaeva & Boxshall 2014: 45, fig. 31.

Regioscalpellum moluccanum. — Gale 2016: 298.

Material examined:

- Tanimbar Island: 3 specimens, MNHN-IU-2019-4909, Stn. CP 38, 07°40'S, 132°27'E, 620–666 m depth, 28 October 1991; 1 specimen, MNHN-IU-2019-4910, Stn. DW 49, 08°00'S, 132°59'E, 206-210 m depth, 29 October 1991; 1 specimen, MNHN-IU-2019–4911, Stn. CC 57, 08°19'S, 131°53'E, 603–620 m depth, 31 October 1991; 1 specimen, MNHN-IU-2019-4912, Stn. CP 52, 08°03'S, 131°48'E, 1244–1266 m depth, 30 October 1991.

Diagnosis:

Capitulum with 14 plates, surface covered by chitinous, almost smooth membrane; carina simply, not strongly bowed, apex projecting freely, roof not flat; umbo of the carina apical; upper latus almost triangular.

Description:

Capitulum inflated, subtriangular, apices of plates projecting freely through membrane, growth lines fairly distinct. Scutum trapezioid, umbo apical. Tergum large, oval, truncated, very pointed, extending between upper latus and carina. Carina simply, slightly bowed, roof slightly convex, apex projecting freely. Upper latus quadrangular; rostrum very small, carinate; rostral latus trapeziform; infra-median latus triangular, moderately small; carinal margins of carinal latera convex, touching each other at base and below middle of carina. Peduncle stout, slightly thinner below apex. Cirrus I unequal, anterior ramus oval, posterior ramus more slender; cirrus VI with long caudal appendages. Maxillule not notched, large spine on upper side, cutting edge almost straight; mandible with three large teeth excluding inferior angle. Measurements of five specimens: height of capitulum 7.88–14.89 mm, width 4.81–10.65 mm, thickness 2.15–5.24 mm; length of peduncle 3.38–9.13 mm, width 2.09–6.04 mm.

Distribution:

Pacific, Central and Southwest; Tasman Sea, north-eastern Australia; 788–2,745 m depth (Jones 2012; Shalaeva and Boxshall 2014). In this study, *Regioscalpellum moluccanum* was found at Tanimbar Island, Indonesia.

Type locality:

Banda Sea (4°21’S, 129°7’E); Challenger stn 195; 2,606 m depth: bottom temp. 3°C; substrate grey ooze (Hoek 1883).

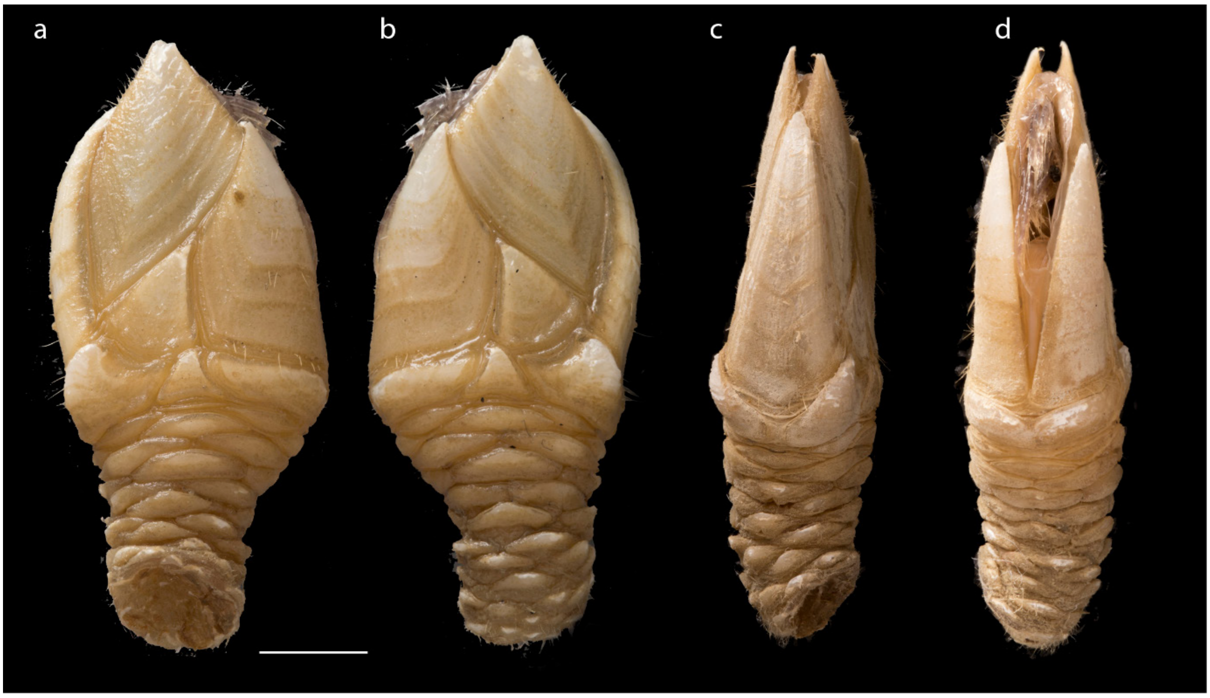

Figure 3.10. *Regioscalpellum moluccanum* (Hoek, 1883) (MNHN-IU-2019-4909). (**a**) left lateral view showing the capitulum and peduncle, (**b**) right lateral view showing the capitulum and peduncle, (**c**) carinal view showing the capitulum and peduncle, (**d**) rostral view showing the capitulum and peduncle. Scale bars: a–d) 4 mm.

Genus *Scalpellum* Leach, 1817

Scalpellum Leach, 1817: 68. — Darwin 1852: 21. — Hoek 1883: 59. — Gruvel 1905: 23. — Pilsbry 1907d: 181. — Tarasov & Zevina 1957: 126. — Zevina 1978a: 1002. — 1981: 94. — Gale 2016: 297.
Strictoscalpellum Broch, 1924: 14.

Diagnosis:

Scalpellines with carinal and scutal umbones subapical; carinolatus with horn-like projection, often recurved, extending beyond carinal margin; inframedian latus rectangular to slightly trapezoidal, with low umbo; upper latus rhomboidal with subapical umbo; rostrum rectangular, pyramidal, with large sub-umbonal surface.

Type species:

Lepas scalpellum Linnaeus, 1767: 1109.

Type locality:

Unknown.

Scalpellum sp.

Figure 3.11

Material examined:

- Tanimbar Island: 1 specimen, MNHN-UI-2019-4929, Stn. DW 49, 08°00’S, 132°59’E, 206-210 m depth, 29 October 1991.

Diagnosis:

Capitulum with 14 fully calcified plates; tergum triangular; inframedian latus broad, quadrilateral with umbo near to basal; upper latus rhomboidal, umbo sub-apical; carinal lateral horn-shaped, with angle extending beyond carina.

Description:

Capitulum subtriangular, covered by membrane. Tergum triangular, occludent and basal margins slightly convex; scutum quadrangular, basal and upper latus margins concave; upper latus pentagonal; rostrolatus quadrangular; inframedian latus broad, rectangular, umbo close to basal margin; carinolatus horn-shaped with slightly deep transverse furrows, umbo at basi-carinal angle; carina convex, umbo apical. Cirrus I with rami unequal, anterior ramus broader than posterior ramus; both rami densely covered with long setae. Maxilla subtriangular, with dense long setae; maxillule notched, with numerous setae; mandible with three teeth, inferior angle with large cuspidate setae. Measurements of specimen: height of capitulum 15.90 mm, width 10.29 mm, thickness 4.58 mm; length of peduncle 6.97 mm, width 5.67 mm.

Distribution:

In this study, *Scalpellum* sp. was found in Tanimbar Island, Indonesia.

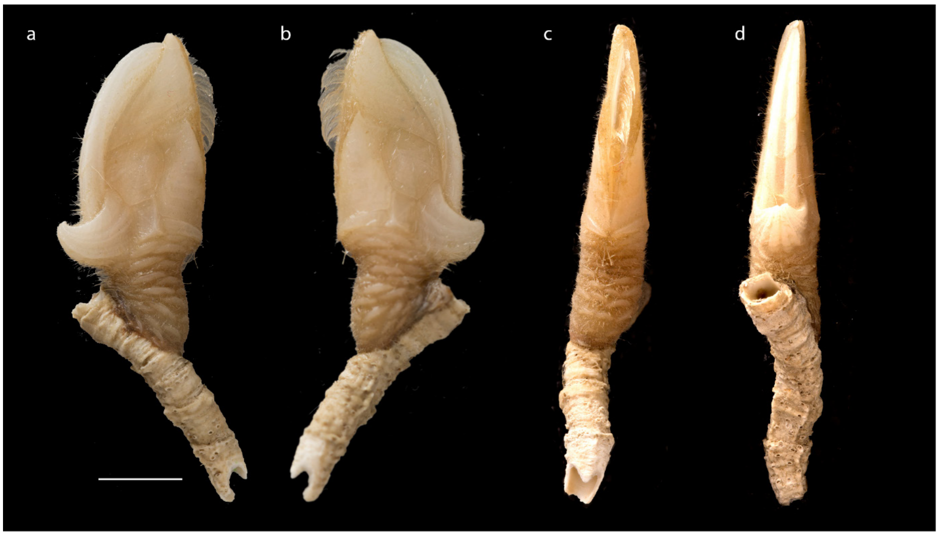

Figure 3.11. *Scalpellum* sp. (MNHN-UI-2019-4929). (**a**) left lateral view, capitulum and peduncle, (**b**) right lateral view, capitulum and peduncle, (**c**) rostral view, capitulum and peduncle, (**d**) carinal view. Scale bars: a–d) 7 mm.

Scalpellum stearnsi Pilsbry, 1890

Figure 3.12

Scalpellum magnum Darwin, 1852: 18, pl. I, fig. 1.
Scalpellum calcariferum Fischer, 1891: 116.
Scalpellum stearnsii var. *gemina* and var. *robusta* Hoek, 1907: 69, pl. VI, figs 2–3, 8–12.
Scalpellum stearnsii var. *inerme* Annandale, 1916a: 293.
Scalpellum stearnsii forma *typica* Broch, 1931: 16.
Scalpellum stearnsii Pilsbry, 1890a: 96. — 1890b: 441, pl. IV, figs 1–5. — 1907a: 14, pl. 4, figs 1-5. — Nilsson-Cantell, 1921: 175. — 1934: 33. — Broch, 1922: 235, fig. 6. — Hiro, 1933: 22, fig. 4, pl. 1, figs 5, 5a. — 1939a: 237. — Zevina 1981: 98, fig. 68. — Rosell 1991: 15. — Jones 1992: 146, figs 1, 2. — Liu & Ren 2007: 226, fig. 95. — Chan et al. 2009b: 89, figs 73–76. — Chan et al. 2010: 24, figs 2C, 18A–G.
Scalpellum stearnsi: Gruvel, 1905: 44, fig. 46. — Gale 2016: fig. 5, table 1.

Material examined:

- Tanimbar Island: 1 specimen, MNHN-IU-2019-4888, Stn. CP 71, 08°38’S, 131°44’E, 477–480 m depth, 2 November 1991; 1 specimen, MNHN-IU-2019-4889, Stn. CC 58, 08°19’S, 132°02’E, 457–461 m depth, 31 October 1991; 6 specimens, MNHN-IU-2019–4890, Stn. CC 42, 07°53’S, 132°42’E, 350–354 m depth, 28 October 1991; 3 specimens, MNHN-IU-2019-4891, Stn. CP 69, 08°42’S, 131°53’E, 356–368 m depth, 2 November 1991; 5 specimens, MNHN-IU-2019-4892, Stn. CC 41, 07°45’S, 132°42’E, 393-401 m depth, 28 October 1991; 5 specimens, MNHN-IU-2019-4893, Stn. CP 59, 08°20’S, 132°11’E, 399-405 m depth, 31 October 1991, 2 specimens attached to glass rope sponge.
- Kei Islands: 8 specimens, MNHN-IU-2019-4894, Stn. CP 06, 05°49’S, 132°21’E, 287-298 m depth, 22 October 1991.

Diagnosis:

Capitulum rhomboidal, compressed; carina strongly angled at umbo; scutum large, umbo at tergo-occludent angle; tergum triangular; inframedian latus pentagonal; carinolateral horn-shaped.

Description:

Capitulum with 14 fully calcified plates. Scutum large, longer than broad, apex slightly projecting over tergum; tergum large, triangular, apex erect, slightly recurved. Carina distinctly bent near middle, umbo distant from apex. Cirrus I with anterior ramus oval (12-segments), posterior ramus slender, long (15-segments); cirri II–VI slender, long, rami almost equal length; cirrus VI with short caudal appendages (six segments). Maxillule not notched, with numerous setae; mandible with six teeth excluding inferior angle. Measurements of five specimens: height of capitulum 31.69–52.00 mm, width 28.20–40.11 mm, thickness 11.19–18.56 mm; peduncle length 28.29–86.59 mm, width 11.39–17.94 mm.

Distribution:

Indo-west Pacific: Indian Ocean, off Nicobar Island; Indonesia: Java Sea, Bali Straits; north west & north east Australia; Malay Archipelago; Celebes; Sulu Arch.; Sulu Sea; South China Sea; East China Sea; Philippines; Taiwan; east coast of south Japan, Sagami Bay, off Hondo; attached to mollusc shells, anchor filaments of hexactinellid sponges, telegraph cables, carapaces of crabs, stones; 146–2117 m depth (Jones and Hosie 2016). In this study, *Scalpellum stearnsi* was found at Tanimbar Island and Kei Islands, Indonesia.

Type locality:

East coast of Japan, between the Bay of Tokyo and the Inland Sea (Jones 1992).

Remarks:

For the first time, *Scalpellum stearnsi* was found in Japan and described by Pilsbry (1890). During the *Siboga* expedition (1899), *S. stearnsi* was collected from different locations in the Malay Archipelago with the depths varying from 204 m to 450 m. Hoek (1907) found intraspecific variations of the shell plate morphology. He then divided *S. stearnsi* into two groups, i.e. variety *robusta* and var. *gemina*, which differed in the shape of the tergum. The species *S. stearnsi* in this study belongs to the group of var. *gemina* because of the V-shaped tergum.

Scalpellum stearnsi has a low period of larval development (Ozaki et al. 2008) and a slow growth rate (Yusa et al. 2018). This can result in the broad geographical distribution of this species. Recently, Lin et al. (2020) examined the diversity and genetic differentiation of populations of *S. stearnsi* from the East China Sea, West Philippine Basin, Sulu Sea and Caroline Trenches, which resulted in four distinct clades of *S. stearnsi*.

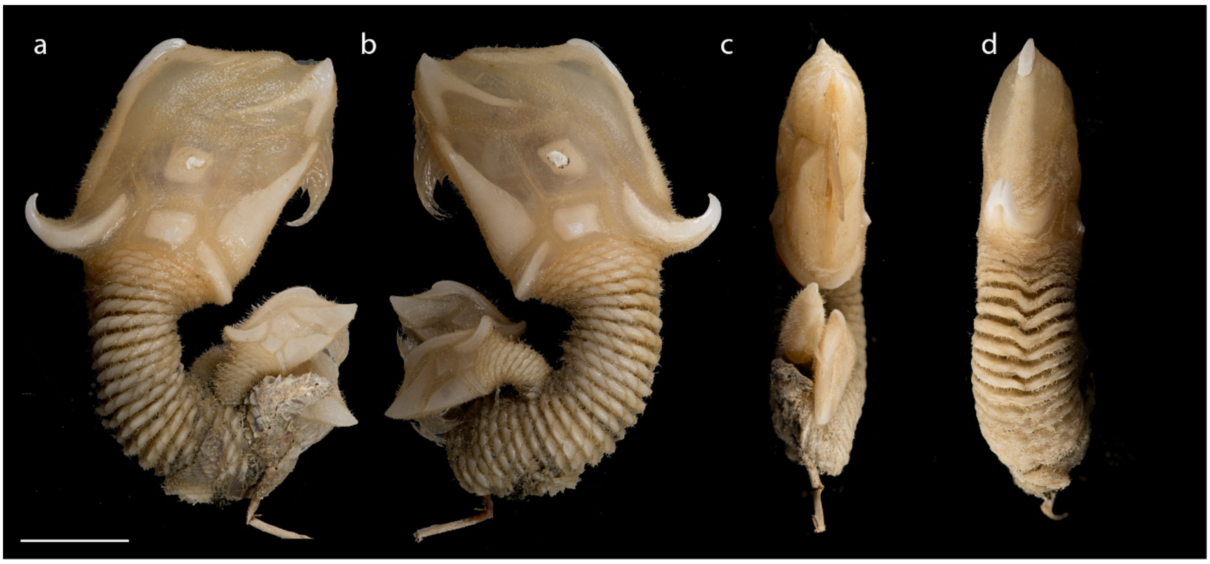

Figure 3.12. *Scalpellum stearnsi* Pilsbry, 1890 (MNHN-IU-2019-4888). (**a**) left lateral view, capitulum and peduncle, (**b**) right lateral view, capitulum and peduncle, (**c**) rostral view, capitulum and peduncle, (**d**) carinal view. Scale bars: a–d) 14 mm.

Subfamily Meroscalpellinae Zevina, 1978

Meroscalpellinae Zevina, 1978b: 1343.

Diagnosis:

Capitulum with 14 or 13 plates, reduced in differing stages or proportions; carina with two umbo positions; females considered rarer than hermaphrodites; males saclike, usually without plates, rarely with two or four reduced plates.

Type genus:

Meroscalpellum Zevina 1978b: 1346.

Genus *Alcockianum* Zevina, 1978

Alcockianum Zevina, 1978b: 1345.

Diagnosis:

Plates strongly reduced; partly obscured under heavy cuticle; tergum double branched, depressed at base; scutum triangular; upper lateral triangular; midlateral very small, umbo apical; caudal appendages very long; hermaphrodites.

Type species:

Scalpellum alcockianum Annandale, 1905: 82; type locality: Gulf of Manaar and Andaman Sea.

Alcockianum persona (Annandale, 1916)

Figure 3.13

Scalpellum persona Annandale, 1916a: 295, pl. IV, fig. 3; pl. V, figs 7, 8; pl. VI, figs 3–5. — Calman 1918b: 120. — Nilsson-Cantell 1934: 44, pl. 5, fig. 2.

Graviscalpellum persona Foster, 1980: 527, figs 1e, 2.

Alcockianum persona Zevina, 1978b: 1345. — 1981: 150–151, fig. 107. — Jones 1992: 151–154, figs 4, 5.

Material examined:

- Tanimbar Island: 2 specimens, MNHN-IU-2019-4903, Stn. CP 71, 08°38’S, 131°44’E, 477–480 m depth, 2 November 1991; 5 specimens, MNHN-IU-2019-4904, Stn. CC 21, 05°14’S, 133°00’E, 688–694 m depth, 25 October 1991 attached to glass rope sponge; 1 specimen, MNHN-IU-2019-4905, Stn. CC 40, 07°46’S, 132°31’E, 443–468 m depth, 28 October 1991; 5 specimens, MNHN-IU-2019-4906, Stn. CC 57, 08°19’S, 131°53’E, 603–620 m depth, 31 October 1991.

Diagnosis:

Capitulum with plates buried or obscure; plates reduced in size; tegum reduced, forming four-pointed star; scutum small; peduncle armed with distinct circles of large, calcareous scales.

Description:

Capitulum brownish, large, ovoid, inflated, with 13 capitular plates, including a vestigial rostrum, plates embedded and mostly concealed by thick, opaque membrane. Scutum small, widely separated from all remaining plates except tergum, margins not excavated or deeply concave; tergum reduced in form as four-pointed star, with two rays greatly and two rays slightly produced. Carina reduced in size, apex approaching terga, widely separated from remaining plates. Peduncle cylindrical, similar length to capitulum, with large calcareous scales arranged in alternating rows. Cirrus I with anterior ramus oval (8-segments), posterior ramus slender, long (12-segments); cirri II–VI slender, long, rami almost equal length; cirrus VI with caudal appendages; caudal appendages 1/3 length of cirrus VI, 15-segmented, tapering distally. Penis rather short, smooth, pointed. Maxilla bilobed, dense setae on margin. Maxillule relatively large, with broad, shallow excavation on lower margin occupying more than half margin, remainder of margin obliquely subtruncate; mandible with three main teeth in addition to inner angle, which is variously divided, broad as a whole. Measurements of five specimens: height of capitulum 17.71–35.06 mm, width 12.91–28.06 mm, thickness 4.96–18.20 mm; length of peduncle 13.42–28.67 mm, width 6.66–10.79 mm.

Distribution:

Indonesian Seas, eastern Australia, New Zealand; 109–915 m depth (Jones 1992). In this study, *Alcockianum persona* was found at Tanimbar Island, Indonesia.

Type Locality:

Timor Sea (10°22’30”S, 120°7’30”E); 109–366 m depth: bottom temp. 13.1°C (Jones 1992).

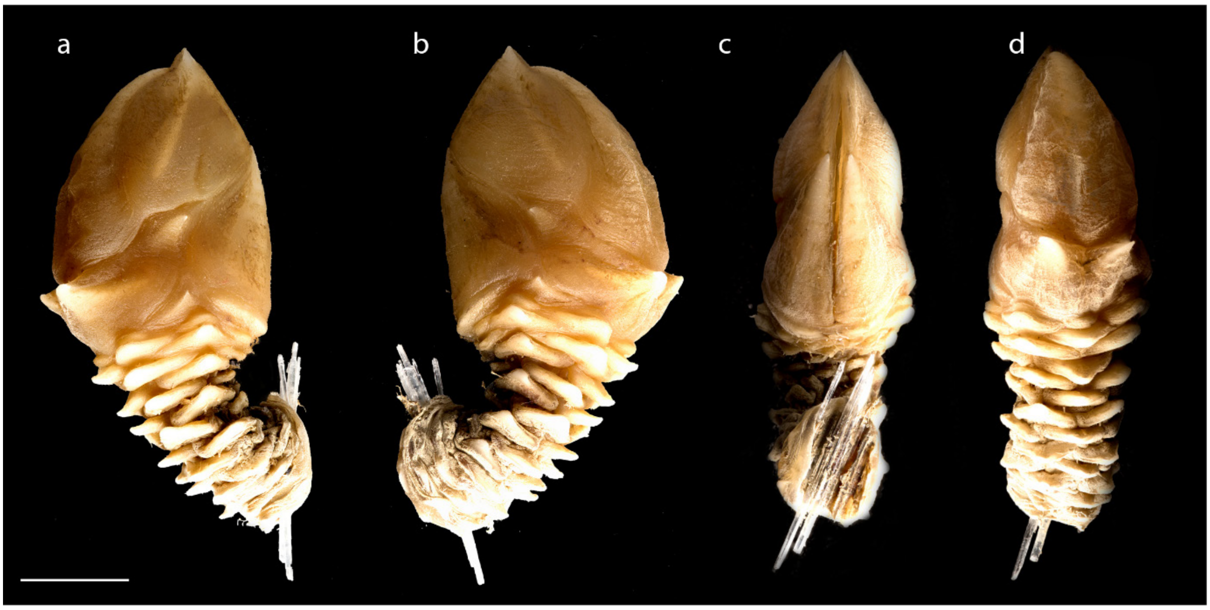

Figure 3.13. *Alcockianum persona* (Annandale, 1916) (MNHN-IU-2019-4903). (a) left lateral view, capitulum and peduncle, (b) right lateral view, capitulum and peduncle, (c) rostral view, capitulum and peduncle, (d) carinal view. Scale bars: a–d) 9 mm.

Genus *Annandaleum* Newman & Ross, 1971

Annandaleum Newman & Ross, 1971: 122. — Zevina, 1978b: 1346.

Diagnosis:

Capitulum of female with 14 partially calcified plates; tergum in shape of inverted V; scutum with moderately long apicolateral arm, 1/4 to 1/2 length of tergal margin; basal margin of scutum entire; upper latus pentagonal to triangular or subrectangular, with or without short depending arm; carinolatus as high as or slightly higher than wide, umbo at basicarinal angle; inframedian latus higher than wide, vase-shaped, umbo submedial to basal; rostrolatus wider than high, commonly less than twice height of inframedian latus; caudal appendage relatively long.

Type species:

Scalpellum subflavum Annandale, 1906.

Annandaleum japonicum (Hoek, 1883)

Figure 3.14

Scalpellum japonicum Hoek, 1883: 67, pl. III, figs 9–10. — Annandale 1906: 131, fig. 3. — Pilsbry 1911: 66, pl. II, figs 1–3. — Weltner 1922: 69, taf. II, fig. 4. — Hiro 1937 b: 392. — Tarasov & Zevina, 1957: 144, figs 46–47. — Zevina 1969: 68. — 1970: 257–259, figs 5–6.

Scalpellum chitinosum Hoek, 1907: 73.

Scalpellum curiosum Hoek, 1907: 49.

Scalpellum japonicum biramosum Pilsbry, 1911: 68, fig. 4. — Weltner 1922: 69, taf. II, fig. 5. — Nilsson-Cantell 1938: 7.

Scalpellum japonicum metapleurum Pilsbry, 1907b: 360.

Annandaleum japonicum biramosum Chan et al., 2009b: 98–99, fig. 80. — Chan et al. 2010: 17–18, figs 2A, 14, 15.

Annandaleum japonicum. — Newman & Ross 1971: 122. — Zevina 1981: 166–167. — Jones et al. 2001: 251. — Young 2001: 465, fig. 8. — 2007: 23, fig. 22.

Material examined:

- Tanimbar Island: 4 specimens, MNHN-IU-2019-4932, Stn. CP 53, 08°18’S, 131°41’E, 1026–1053 m depth, 30 October 1991.

Diagnosis:

Capitulum with 14 partly calcified plates; carina with flat roof; apex of tergum curved towards carina; rostral latus trapezoidal in shape; peduncle short.

Description:

Capitulum yellowish, with 14 plates separated by broad, chitinous spaces. Peduncle short, curved, scales large, not numerous. Scutum long, narrow; umbo apical, divided into two segments, occludent segment large, increasing in width from upper to lower part, other segment very narrow. Tergum divided into occludent and carinal segments, with triangular, chitinous portion between, umbo apical, distinctly recurved. Cirrus I unequal, anterior ramus oval, posterior ramus slender long; cirrus VI with caudal appendages. Maxillule slightly notched, two long and one short setae on upper side; mandible with three teeth excluding inferior angle; labrum cutting edge straight, very fine teeth on cutting edge. Measurements of the four specimens: height of capitulum 9.56–12.73 mm, width 4.67–7.13 mm, thickness 1.85–3.21 mm; length of peduncle 3.37–4.77 mm, width 1.83–3.27 mm.

Distribution:

Eastern Indian Ocean; Northwest and Western Central Pacific; Malay Archipelago; Japan; Taiwan; Indonesia; attached to shell of gastropod, gorgonians, rocks; 805–6,810 m depth (Jones and Hosie 2016). In this study, *Annandaleum japonicum* was found at Tanimbar Island, Indonesia.

Type locality:

Pacific, Northwest (off Nagoya, south of Japan); 1,017 m depth (Shalaeva and Boxshall 2014).

Figure 3.14. *Annandaleum japonicum* (Hoek, 1883) (MNHN-UI-2019-4932). (**a**) left lateral view showing the capitulum and peduncle, (**b**) right lateral view showing the capitulum and peduncle, (**c**) rostral view showing the capitulum and peduncle, (**d**) carinal view. Scale bars: a–d) 2 mm.

Annandaleum laccadivicum (Annandale, 1906)

Figure 3.15

Scalpellum laccadivicum Annandale, 1906b: 393. — 1908: pl. I, figs 3, 4. — 1913: 235; 1916b: 129, pl. vii, fig. 6. — Calman, 1918b: 124. — Hiro, 1933: 31, text figs 7, 8, pl. I, figs 11–11b. — 1937b: 392. — Stubbings 1936: 26. — Nilsson-Cantell 1938: 25.

Scalpellum subflavum Annandale, 1906b: 397. — Newman & Ross 1971: 122.

Scalpellum polymorphum Hoek, 1907: 80, pl. 7, figs 9–11. — Weltner 1922: 72.
Scalpellum molliculum Pilsbry, 1911: 68, pl. 10, figs 4, 5.
Annandaleum laccadivicum Rosell, 1991: 16, fig 1a. — Zevina 1981: 170, fig. 121. — Jones et al. 2001: 251. — Chan et al. 2009b: 102–103.

Material examined:

- Tanimbar Island: 1 specimen, MNHN-IU-2019-4931, Stn. CP 54, 08°21'S, 131°43'E, 836–869 m depth, 30 October 1991, attached to gastropod shell.

Diagnosis:

Capitulum regularly oval; carina simply bowed; tergum almost triangular; scutum subtriangular; upper latus large, perfectly calcified part irregularly triangular, constricted above; rostral latus quadrangular; peduncle at least half as long as capitulum.

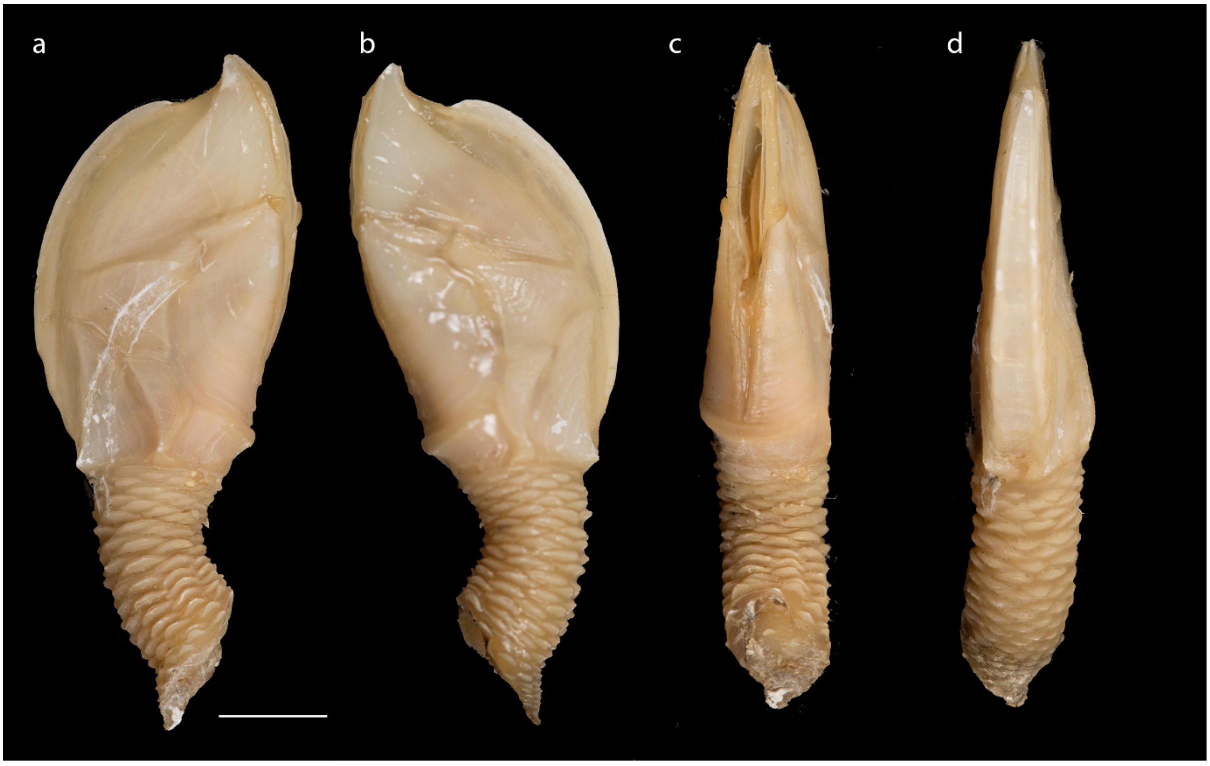

Figure 3.15. *Annandaleum laccadivicum* (Annandale, 1906) (MNHN-IU-2019-4931). (**a**) left lateral view showing the capitulum and peduncle, (**b**) right lateral view showing the capitulum and peduncle, (**c**) rostral view showing the capitulum and peduncle, (**d**) carinal view. Scale bars: a–d) 5 mm.

Description:

Capitulum compressed; 13 plates completely covered by fine, hairless membrane. Peduncle half length of capitulum, stout, cylindrical, armed with small, transversely elongated plates. Scutum subtriangular, lateral margin excavated with tooth above excavation blunt, short, simple; tergum almost triangular, scutal margin excavated, but not very boldly, occludent margin slightly, regularly convex outwards. Carina simply bowed, umbo subterminal, in contact with terga above or just entering between them. Cirrus I unequal, anterior ramus oval, posterior ramus slender, long; cirri II–VI slender, long, rami almost equal lengths; cirrus VI with long, slender caudal appendages. Maxillule slightly notched, two major setae on upper side; mandible with four teeth. Measurements of specimen: height of capitulum 18.88 mm, width 11.41 mm, thickness 6.30 mm; length of peduncle 11.45 mm, width 4.89 mm.

Distribution:

Gulf of Oman, Arabian Sea, Sri Lanka, Japan (Chan et al. 2009b). In this study, *Annandaleum laccadivicum* was found at Tanimbar Island, Indonesia.

Type locality:

Laccadive Sea, 2,077 m depth; on living shells of Dentalium (Annandale 1906).

Annandaleum lambda (Annandale, 1910)

Figure 3.16

Scalpellum lambda Annandale, 1910b: 115. — 1916a: pl. VII, figs 6, 6a, pl. VIII, figs 12–15.
Scalpellum longius Annandale, 1913: 234.
Annandaleum lambda. — Newman & Ross, 1971: 122. — Jones, 1992: 154, fig. 6.

Material examined:

- Tanimbar Island: 10 specimens, MNHN-IU-2019-4915, Stn. CP 52, 08°03’S, 131°48’E, 1244–1266 m depth, 30 October 1991; 1 specimen, MNHN-IU-2019-4913, Stn. CP 53, 08°18’S, 131°41’E, 1026–1053 m depth, 30 October 1991; 1 specimen, MNHN-IU-2019-14, Stn. CP 89, 08°39’S, 131°08’E, 1058-1084 m depth, 5 November 1991, attached to pumice.

Diagnosis:

Capitulum narrow; carinal margin strongly curved; laterally compressed; bearing fourteen imperfectly formed, thin, smooth, translucent plates, eight formed like a Greek lambda.

Description:

Capitulum with 14 plates. Peduncle shorter than capitulum, cylindrical, rather slender, expanded at base. Tergum lambda-shaped, with prominent tooth on carinal margin just above point where apex of carina approaches it. Scutum shaped similarly, but occludent branch much stouter, with vertical ridge running nearer to lateral than occludent margin. Cirrus I unequal, anterior ramus oval, posterior ramus slender, long; cirri II–VI slender, long, with rami almost equal length; cirrus VI with long, slender caudal appendages. Maxillule not notched, two major setae on upper side; mandible with four teeth including inner angle. Measurements of five specimens: height of capitulum 16.61–24.27 mm, width 8.73–14.49 mm, thickness 3.17–6.31 mm; length of peduncle 5.54–15.27 mm, width 3.73–6.26 mm.

Distribution:

Indo-Pacific from off Zanzibar, Indian Ocean, eastern Australia; Sumbawa, Indonesia; Malay Arch.; SW of Calatagan Pt, Philippines; S Japan (S of Honda I.), SW Pacific; attached to shells of bivalves; 234–2077 m depth (Jones and Hosie 2016). In this study, *Annandaleum lambda* was found at Tanimbar Island, Indonesia.

Type locality:

Eastern Indian Ocean (13°54’15”N, 94°02’15”E), Investigator Stn. 372; 1,176 m depth (Jones 1992).

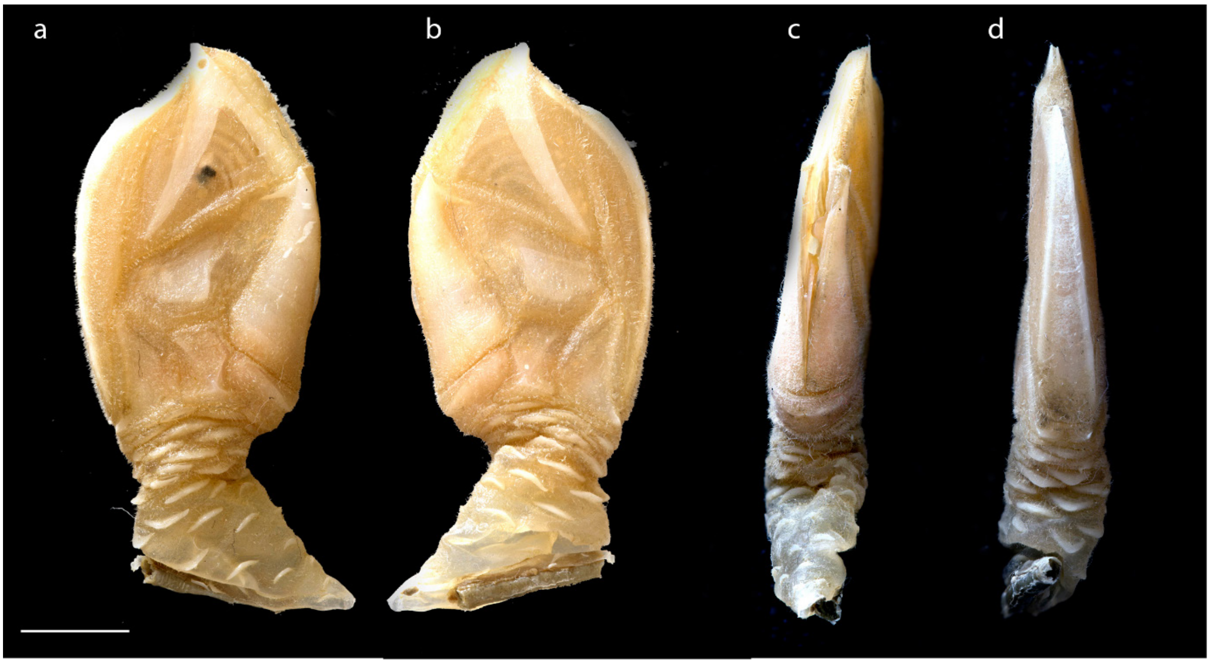

Figure 3.16. *Annandaleum lambda* (Annandale, 1910) (MNHN-IU-2019-4915). (**a**) left lateral view showing the capitulum and peduncle, (**b**) right lateral view showing the capitulum and peduncle, (**c**) rostral view showing the capitulum and peduncle, (**d**) carinal view. Scale bars: a–d) 6 mm.

Genus *Litoscalpellum* Newman & Ross, 1971

Litoscalpellum Newman & Ross, 1971: 108. — Zevina 1978b: 1344. — Liu & Ren 1985: 196. — 2007: 228.

Diagnosis:

Capitulum with 14 plates, mostly not reduced; tergum with straight basal margin or shallow notch; scutum with straight, smooth basal margin; upper latus triangular or elongate, commonly with slightly hollowed-out basal margin, rarely with deep notch; inframedian latus narrow, triangular or quadrilateral, umbo apical; caudal appendages present.

Type species:

Litoscalpellum fissicarinatum Newman & Ross, 1971: 108, pl. XC, text-fig. 55.

Litoscalpellum juddi (Calman, 1918)

Figure 3.17

Scalpellum juddi Calman, 1918b: 116, text-figs 5–7.
Scalpellum regulus Calman, 1918b: 113, text-fig. 4.
Litoscalpellum juddi Zevina, 1981:135–136, fig. 94.

Material examined:

- Tanimbar Island: 5 specimens, MNHN-IU-2019-4896, stn. CC 56, 08°16’S, 131°59’E, 549-552 m depth, 31 October 1991; 1 specimen, MNHN-IU-2019-4898, stn. CP 71, 08°38’S, 131°44’E, 477–480 m depth, 2 November 1991; 6 specimens, MNHN-IU-2019-4901, stn. CP 72, 08°36’S, 131°33’E, 676-699 m depth, 2 November 1991.

Diagnosis:

Capitulum compressed, oval, notched above; surface covered with very short velvety pubescence, areas of valves defined by grooves, lines of growth strongly marked; carina flattened.

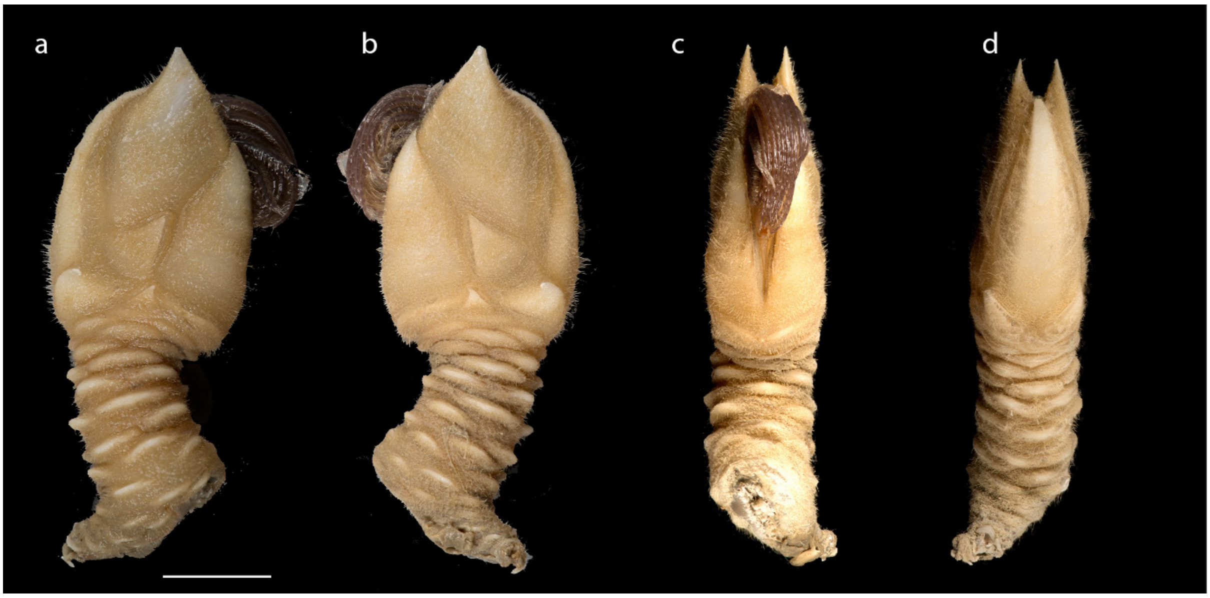

Figure 3.17. *Litoscalpellum juddi* (Calman, 1918) (MNHN-UI-2019-4898). (**a**) left lateral view showing the capitulum and peduncle, (**b**) right lateral view showing the capitulum and peduncle, (**c**) rostral view showing the capitulum and peduncle, (**d**) carinal view. Scale bars: a–d) 11 mm.

Description:

Capitulum with 14 plates, cartilaginous thick. Terqum irregularly triangular, apex projecting above carina, recurved. Scutum triangular, basal width more than half height, apex overlapping tergum. Carina evenly curved, apex projecting freely for short distance, touching or entering between terga, its base rounded, widely separated from carinal latera; roof strongly convex. Upper latus triangular with base convex. Rostrum triangular; inframedian latus small, triangular, base deeply embedded. Peduncle with large transverse plates, not overlapping (widely spaced). Cirrus I unequal, anterior ramus oval, posterior ramus slender, long; cirrus VI with caudal appendages. Maxillule with oral edge sinuous, a large seta at its proximal third, another at its distal end; mandible with four teeth. Measurements of five specimens: height of capitulum 16.94–39.25 mm, width 11.39–28.28 mm, thickness 5.20–19.89 mm; length of peduncle 15.02–52.02 mm, width 5.63–16.87 mm.

Distribution:

In this study, *Litoscalpellum juddi* was found at Tanimbar Island, Indonesia.

Type locality:

11°0’S, 121°30’E (Java-Australia), 720 m depth (Calman 1918b).

Litoscalpellum recurvirostrum (Hoek, 1883)

Figure 3.18

Scalpellum recurvirostrum Hoek, 1883: 77–79, pl. III, figs 11–12, pl. VIII, figs 9–10.
Arcoscalpellum recurvirostrum. — Newman & Ross 1971: 79–80, fig. 39.
Litoscalpellum recurvirostrum. — Zevina 1974: 214. — 1981: 127–128, fig. 88. — Shalaeva & Boxshall 2014: 13, fig. 6.

Material examined:

- Kei Islands: 1 specimen, MNHN-IU-2019-4934, Stn. CP 05, 05°49’S, 132°18’E, 296–299 m depth, 22 October 1991; 1 specimen, MNHN-IU-2019-4936, Stn. CP 09, 05°23’S, 132°29’E, 368–389 m depth, 23 October 1991.
- Tanimbar Island: 4 specimens, MNHN-IU-2019-4935, Stn. CP 83, 09°23’S, 131°00’E, 285–297 m depth, 4 November 1991; 16 specimens, MNHN-IU-2019-4937, Stn. CP 69, 08°42’S, 131°53’E, 356–368 m depth, 2 November 1991.

Diagnosis:

Capitulum plates separated, covered by fine membrane; carina slightly angularly bent; upper latus trapeziform; inframedian latus triangular; peduncle with scattered, calcareous scales.

Description:

Capitulum with 14 plates, lines of growth not distinct, plates separated by broad, membranous interspaces. Scutum elongate quadrangular, broader at base than in upper half; umbo apical, slightly projecting outwards. Tergum triangular; carina bowed; upper latus trapeziform; inframedian latus very small, triangular. Peduncle cylindrical with numerous calcareous scales scattered over surface. Cirrus I with rami unequal, anterior ramus oval, posterior ramus slender, long, segments very hairy. Maxilla bilobed; maxillule notched, two large setae above notch; mandible with three teeth, inferior angle pectinated. Measurements of five specimens: height of capitulum 16.15–26.05 mm, width 9.24–16.59 mm, thickness 4.45–8.18 mm; length of peduncle 7.25–20.90 mm, width 4.13–8.95 mm.

Distribution:

Indian Ocean, Antarctic and Southern (South of the Kerguelen Islands); known depth range 195 to 274 m (Shalaeva and Boxshall 2014). In this study, *Litoscalpellum recurvirostrum* was found at Kei Islands and Tanimbar Island, Indonesia.

Type locality:

Between Kerguelen and Heard Islands; 52°4’S, 71°22’E; depth: 270 m; bottom temperature: 1.8°C; bottom: rocks (Hoek 1883).

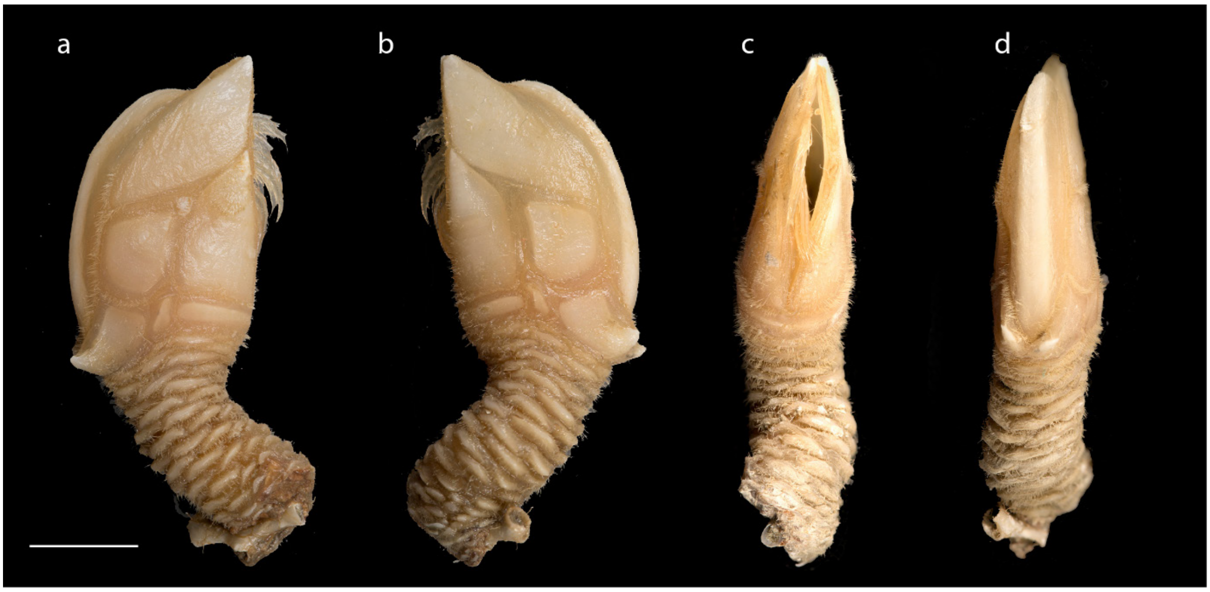

Figure 3.18. *Litoscalpellum recurvirostrum* (Hoek, 1883) (MNHN-UI-2019-4934). (**a**) left lateral view showing the capitulum and peduncle, (**b**) right lateral view showing the capitulum and peduncle, (**c**) rostral view showing the capitulum and peduncle, (**d**) carinal view. Scale bars: a–d) 6 mm.

Litoscalpellum walleni Newman & Ross, 1971

Figure 3.19

Litoscalpellum walleni Newman & Ross, 1971: 116, pl. X E text-fig. 60.

Material examined:

- Tanimbar Island: 1 specimen, MNHN-IU-2019-4927, Stn. CP 91, 08°44’S, 131°05’E, 884–891 m depth, 5 November 1991.

Diagnosis:

Capitulum with 14 plates; inframedian latus triangular, very small, narrow; carina with flat roof; rostrum minute; scutum lacking prominent apicolateral arm; maxilla subtriangular, slightly trilobate; maxilulle slightly notched with teeth diverging laterally from cutting edge; caudal appendage multi-articulate, slightly shorter than first segment of cirrus VI.

Description:

Capitulum elongate, higher than broad; plates ornamented with growth lines. Carina bowed, roof slightly convex, bounded by angles. Tergum triangular; scutum with lateral margin concave; upper latus roughly quadrangular; carinal latus higher than wide; rostral latus quadrangular, slightly broader than high; rostrum minute, narrow, essentially rectangular. Cirrus I unequal, anterior ramus shorter, broader than posterior ramus; both rami densely covered with long setae. Mandible with four teeth including inferior angle, inferior angle serrate along basal margin with four spines. Measurements of specimen: height of capitulum 14.56 mm, width 8.09 mm, thickness 2.50 mm; length of peduncle 7.52 mm, width 3.89 mm.

Distribution:

Southeast Pacific Ocean (Newman and Ross 1971). In this study, *Litoscalpellum walenni* was found at Tanimbar Island, Indonesia.

Type locality:

Northeast of Peter I Island, southeast Pacific Ocean; 65° 50› S, 88° 56› W; depth: 4,502 m (Newman and Ross 1971).

Figure 3.19. *Litoscalpellum walleni* Newman & Ross, 1971 (MNHN-UI-2019-4927). (**a**) left lateral view showing the capitulum and peduncle, (**b**) right lateral view showing the capitulum and peduncle, (**c**) rostral view showing the capitulum and peduncle, (**d**) carinal view. Scale bars: a–d) 4 mm.

Subfamily Arcoscalpellinae Zevina, 1978

Arcoscalpellinae Zevina, 1978b: 1346. —1981: 184. — Liu & Ren 2007: 238.

Diagnosis:

Capitulum with plates packed very closely; carina slightly convex; umbo of scutum and tergum apical.

Type genus:

Arcoscalpellum Hoek, 1907: 57.

Genus *Amigdoscalpellum* Zevina, 1978

Arcoscalpellum Hoek, 1907: 85 (in part). — Newman & Ross 1971: 42 (part).
Amigdoscalpellum Zevina, 1978b: 1349. — Foster 1980: 527. — Liu & Ren 1985: 206. — 2007: 251.

Diagnosis:

Capitulum of female or hermaphrodite with 13 or 14 completely calcified plates; scutum and tergum with umbones apical; carina evenly bent, umbo apical or subapical; middle latera narrowly triangular, baton-like, small, umbo apical, not reaching upper latera; carinolatera typically with umbo orientated in middle part of carinal area, not extending beyond rim of capitulum; caudal appendages usually uni-articulate, but possibly absent or extended to seven segments; basically females with dwarf males.

Type species:

Scalpellum manum Zevina, 1973: 843, figs 1–7; type locality: Indian Ocean, 12°18’S, 112°43’E.

Amigdoscalpellum costellatum (Withers, 1935)

Figure 3.20

Scalpellum elongatum Hoek 1883: 93, pl. IV, figs 8–9. — Nilsson-Cantell 1928: 8, fig. 4. — 1931: 3, text-fig.1. — 1938: 7.
non *Scalpellum (Arcoscalpellum) elongatum*. — Steenstrup, 1837: 409.
Scalpellum (Scalpellum) elongatum. — Stubbings 1936: 25, text-fig. 10.
Scalpellum (Arcoscalpellum) costellatum Withers, 1935: 279.
Arcoscalpellum buccinum Newman & Ross, 1971: 55, pl. VIII, figs 22–23.
Arcoscalpellum costellatum. — Foster 1978: 56, pl. 7B–C, fig. 33.
Amigdoscalpellum costellatum. — Foster 1980: 527–529, fig. 3J. — Zevina 1981: 270–271, fig. 204. — Jones et al. 1990: 5 — Jones 2012: 371, 376 — Poltarukha 2013: 52–53, fig. 1. —Shalaeva & Boxshall 2014: 16, fig. 9.

Material examined:

- Tanimbar Island: 2 specimens, MNHN-IU-2019-4922, Stn. CC 21, 05°14’S, 133°00’E, 688–694 m depth, 25 October 1991, attached to glass rope sponge.

Diagnosis:

Capitulum triangular; plates ornamented with radial ridges, covered by sparsely hirsute integument; carina with roof deeply grooved; scutum with apex overlapping tergum; inframedian latus triangular, very small.

Desciption:

Capitulum yellowish, with 13 fully calcified plates. Peduncles short with scales slightly overlapping in the middle part. Scutum with pit for complemental males, above shallow pit for adductor muscle. Carina wide in lower part, ribbed in upper part. Upper latus with straight sides; rostrum appearing externally as inverted triangle. Cirrus I unequal, anterior ramus oval, posterior ramus slender, long; cirrus VI with very short caudal appendages. Maxillule with notch between two or three stout setae at upper angle, group of more slender setae on cutting edge; mandible with three teeth excluding inferior angle; labrum cutting edge slightly concave, numerous pointed teeth on cutting edge. Measurements of two specimens: height of capitulum 12.44–13.88 mm, width 6.97–7.52 mm, thickness 2.77–3.47 mm; length of peduncle 2.99–3.15 mm, width 2.94–3.24 mm.

Distribution:

Indian Ocean, Eastern and Western; Pacific, Southwest and Western Central; Atlantic, Southeast and Eastern central; 110–2,397 m depth (Shalaeva and Boxshall 2014). In this study, *Amigdoscalpellum costellatum* was found at Tanimbar Island, Indonesia.

Type locality:

1. Station 135: Island of Tristan da Cunha; depth: 110 m, 137 m, 183 m, 274 m, 1,006 m, 1,829 m, 2,012 m; bottom: rocky, shells. 2. Station 164a: off Sydney, 34º13'S, 151°38'E; depth: 750 m; bottom: grey ooze. 3. Station 169: off East Cape, Auckland, 37°34'S, 179°22'E; depth: 1,280 m; bottom temperature: 4.2°C; bottom: grey ooze (Hoek 1883).

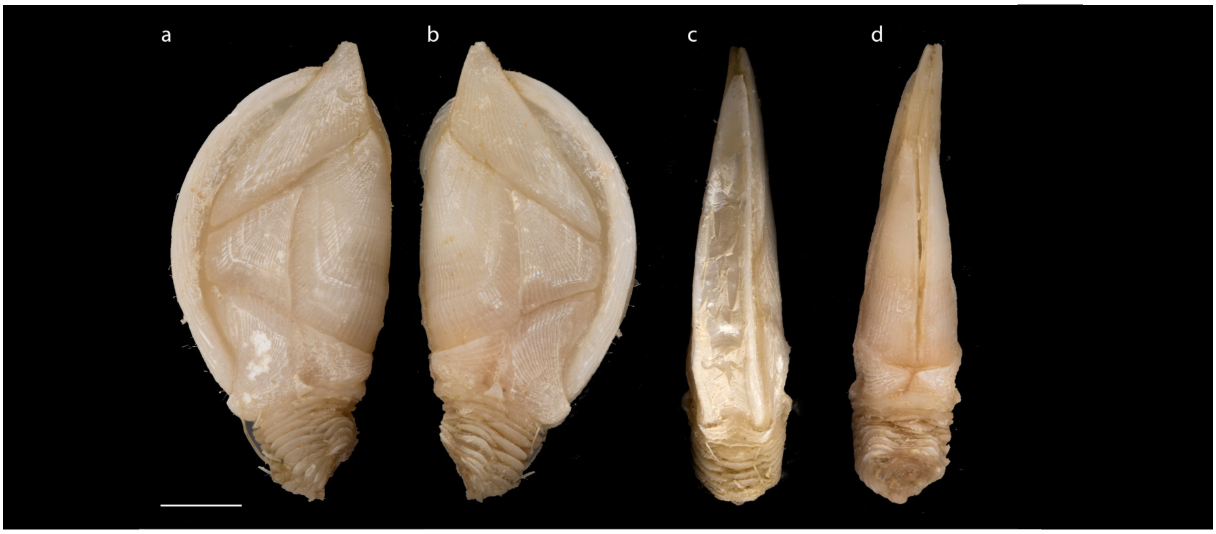

Figure 3.20. *Amigdoscalpellum costellatum* (Withers, 1935) (MNHN-IU-2019-4922). (**a**) left lateral view showing the capitulum and peduncle, (**b**) right lateral view showing the capitulum and peduncle, (**c**) carinal view, (**d**) rostral view showing the capitulum and peduncle. Scale bars: a–d) 3 mm.

Amigdoscalpellum tenue (Hoek, 1883)

Figure 3.21

Scalpellum tenue Hoek, 1883: 119, pl. IV, figs 20–21, pl. X, fig. 6. — Gruvel 1912: 345. — Nilsson-Cantell 1938: 8.

non *Scalpellum tenue* Annandale, 1906a: 142.

Amigdoscalpellum tenue. — Zevina 1981: 292–293, fig. 220 (2). — Shalaeva & Boxshall 2014: 17, fig. 10.

Material examined:

- Kei Islands: 1 specimen, MNHN-IU-2019-4921, Stn. CP 20, 05°15'S, 132°59'E, 769–809 m depth, 25 October 1991.

Diagnosis:

Capitulum with 13 fully calcified plates; carina slightly bowed, umbo at apex; upper latus trapeziform; inframedian latus small, narrow; carinal latus not projecting beyond carina; peduncle short, cylindrical.

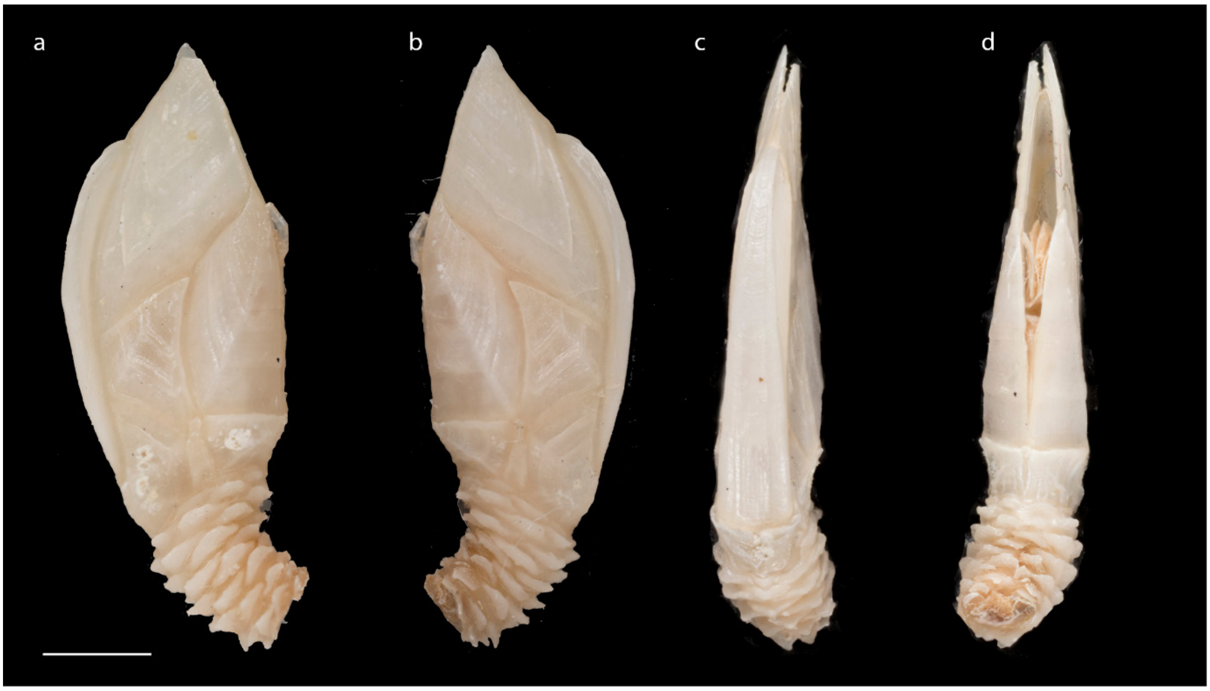

Figure 3.21. *Amigdoscalpellum tenue* (Hoek, 1883) (MNHN-IU-2019-4921). (**a**) left lateral view showing the capitulum and peduncle, (**b**) right lateral view showing the capitulum and peduncle, (**c**) carinal view showing the capitulum and peduncle, (**d**) rostral view showing the capitulum and peduncle. Scale bars: a–d) 2 mm.

Description:

Capitulum yellowish, elongate-oval shape; surface with distinct lines of growth. Carina large, simply bowed. Scutum with umbo at apex, slightly recurved, projecting slightly over tergum; tergum triangular, stout, broad, apex recurved, scutal margin almost straight. Upper latus quadrangular, apex slightly projecting over scutum. Rostral latus quadrangular, scutal and basal margins parallel. Carinal latus quadrangular, carinal margin almost straight. Cirrus I unequal, anterior ramus oval, posterior ramus more slender. Maxillule with notch between two or three stout setae at upper angle, a group of more slender setae on cutting edge; mandible with three teeth excluding inferior angle; labrum with numerous blunt teeth on straight, cutting edge. Measurements of specimen: height of capitulum 7.26 mm, width 3.74 mm, thickness 1.40 mm; length of peduncle 3.00 mm, width 1.99 mm.

Distribution:

Indian Ocean, Antarctic and Southern (North East of Prince Edward Island); known depth 2,516 m (Shalaeva and Boxshall 2014). In this study, *Amigdoscalpellum tenue* was found at Kei Islands, Indonesia.

Type locality:

46°46'S, 45°31'E; depth: 2,475 m; bottom temperature: 1.5°C; bottom: globigerina ooze (Hoek 1883).

Genus *Catherinum* Zevina, 1978

Acroscalpellum Hoek, 1907: 85. — Newman & Ross 1971: 42 (part). — Liu & Ren 1985: 202.
Catherinum Zevina, 1978b: 1348.

Diagnosis:

Capitulum with 13 or 14 plates; inframedian latus very narrow, bacilliform, umbo sub-medial; umbo of upper latus apical or sub-apical; carinal latus broad, umbo sub-basicarinal, not extending beyond carinal margin; caudal appendages long.

Type species:

Scalpellum recurvitergum Gruvel, 1902; type locality: Atlantic Ocean, SW of Azores.

Catherinum rossi (Rao & Newman, 1972)

Figure 3.22

Arcoscalpellum rossi Lakshmana Rao & Newman, 1972: 82, fig. 7.
Catherinum rossi. — Zevina 1978b: 1348. — Liu & Ren 1985: 203, fig. 12, pl. 2, figs 11–14. — 2007: 250, fig. 108. — Chan et al. 2009b: 113, figs 92–94.

Material examined:

- Tanimbar Island: 1 specimen, MNHN-IU-2019-4933, Stn. DW 02, 05°47'S, 132°13'E, 209–240 m depth, 22 October 1991.

Diagnosis:

Capitulum smooth, elongate, 14 fully calcified plates; inframedia latus rectangular, not constricted; rostrum large, ovo-triangular; caudal appendages short.

Description:

Capitulum long, narrow, sparsely covered with hairs, plates separated by narrow, chitinous interspaces, marked with growth lines. Occludent margin strongly convex; carinal margin irregularly straight; apex slightly retroverted towards carinal side. Carina long, simply bowed; roof flat; parietes well developed towards distal half of plate. Tergum triangular, occludent margin short, convex, scutal and basal margins almost straight, carinal margin concave. Scutum with umbo apical, overlapping occludent margin of tergum. Upper latus triangular; carinal latus twice as long as broad; inframedian latus rectangular; rostral latus nearly rectangular in outline; rostrum large, elongate triangular, broad above, pointed below. Cirrus I unequal, anterior ramus oval, posterior ramus more slender; cirrus VI with caudal appendages. Maxillule not notched stout spine along the cutting edge; mandible with three teeth excluding inferior angle. Measurements of specimen: height of capitulum 9.67 mm, width 5.52 mm, thickness 2.58 mm; length of peduncle 2.79 mm, width 2.29 mm.

Distribution:

East China Sea, Pacific Ocean, Taiwan (Chan et al. 2009b). In this study, *Catherinum rossi* was found at Tanimbar Island, Indonesia.

Type locality:

Stn. 3, Hess Guyot (174°24.8’ W, 17°53.2’ N), 1,692–1,735 m depth (Sigsbee beam trawl); Stn. 1, Allison Guyot (179°36.0’ W, 18°31.0’ N), 1,413–1,645 m depth (otter trawl) (Rao and Newman 1972).

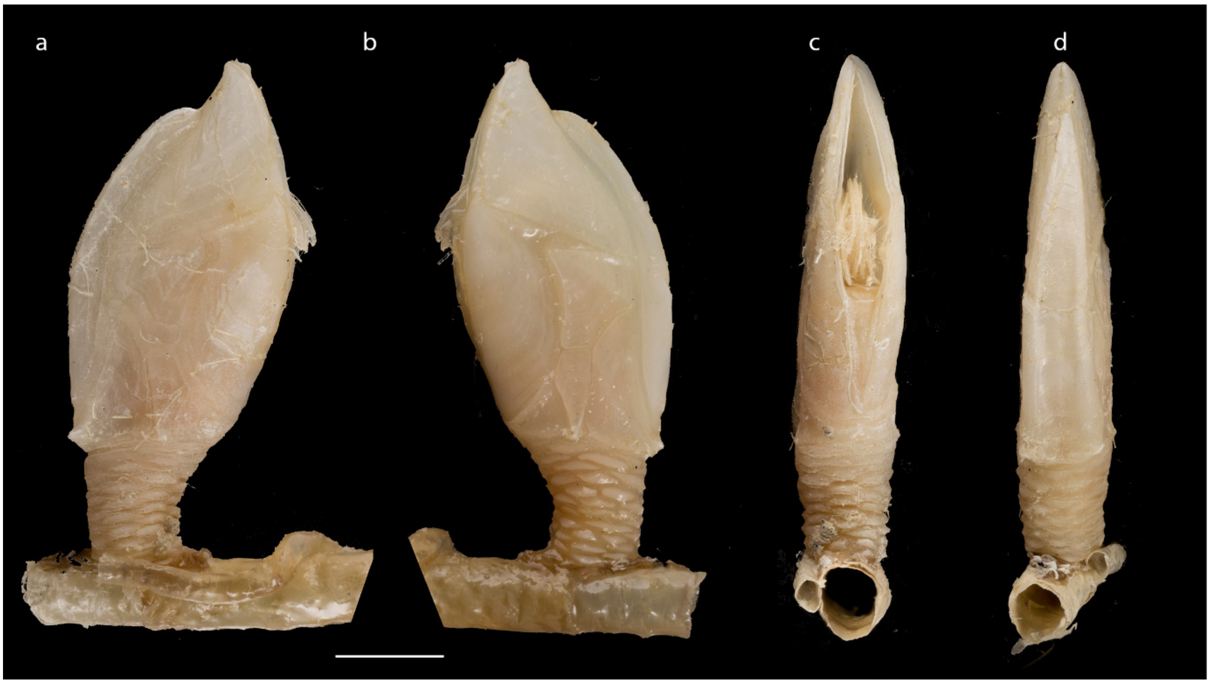

Figure 3.22. *Catherinum rossi* (Rao & Newman, 1972) (MNHN-IU-2019-4933). (**a**) left lateral view showing the capitulum and peduncle, (**b**) right lateral view showing the capitulum and peduncle, (**c**) rostral view showing the capitulum and peduncle, (**d**) carinal view. Scale bars: a–d) 3 mm.

Genus *Planoscalpellum* Zevina, 1978

Arcoscalpellum Hoek, 1907: 85 (part).
Planoscalpellum Zevina, 1978b: 1347.

Diagnosis:

Upper latus with umbo on scutal margin; inframedian latus with umbo apical or sub-basal; carinal latus with umbo on carinal part, may be protruding.

Type species:

Scalpellum planum Hoek, 1883; type locality: 42°42'S, 134°10'E; depth: 4,755 m; bottom temperature: 0.2°C; bottom: red clay.

Planoscalpellum distinctum (Hoek, 1883)

Figure 3.23

Scalpellum distinctum Hoek, 1883: 111–112, pl. VI, figs 10–11. — 1907: 83, pl. VII, fig. 12 — Nilsson-Cantell 1927: 750, text-fig. 4.

Planoscalpellum distinctum. — Zevina 1981: 186–187. — Foster & Buckeridge 1995 a: 360–361, fig. 7(A–C) — Shalaeva & Boxshall 2014: 36, fig. 22.

Material examined:

- Tanimbar Island: 2 specimens, MNHN-IU-2019-4928, Stn. DW 49, 08°00'S, 132°59'E, 206-210 m depth, 29 October 1991.

Diagnosis:

Capitulum with 13 plates separated from each other by distinct chitinous interspaces; scutum almost triangular; upper latus hexagonal, large.

Description:

Capitulum flattened, elongate-oval shape; plates with distinct growth lines, separated from each other by rather broad chitinous interspaces. Scutum triangular, occludent margin arched, umbo of scutum apical, apex slightly turned upwards. Tergum triangular, occludent margin not very long. Carina simply bowed. Upper latus irregularly hexagonal, rostral latus irregularly quadrangular, infra-median latus in the form of wine-glass, carinal latus irregularly quadrangular. Peduncle short, with very small, numerous, calcareous scales. Cirrus I unequal, anterior ramus oval, posterior ramus more slender; cirrus VI with short caudal appendages. Maxillule notched, three stout spines on the upper side; mandible with three teeth, excluding inferior angle. Measurements of two specimens: height of capitulum 6.80–7.90 mm, width 3.68–4.36 mm, thickness 1.24–1.26 mm; length of peduncle 1.39–2.49 mm, width 1.80–2.04 mm.

Distribution:

Pacific, Western Central; known depth range 1,302 to 2,745 m (Shalaeva and Boxshall 2014). In this study, *Planoscalpellum distinctum* was found at Tanimbar Island, Indonesia.

Type locality:
2°33'S, 144°4'E; depth: 1,926 m; bottom temperature: 2.1°C; bottom: Globigerina ooze (Hoek 1883).

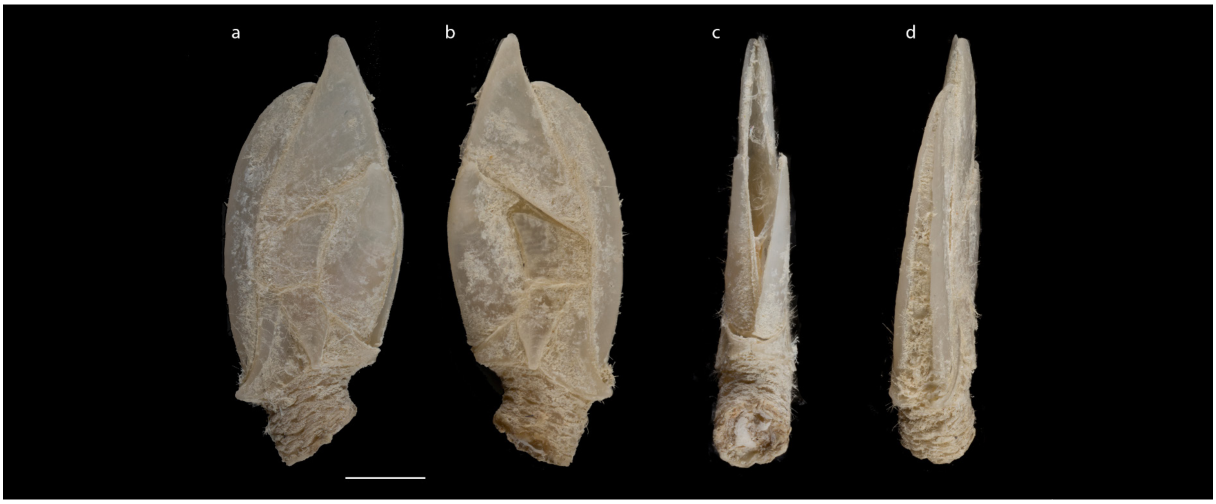

Figure 3.23. *Planoscalpellum distinctum* (Hoek, 1883) (MNHN-IU-2019-4928). (**a**) left lateral view showing the capitulum and peduncle, (**b**) right lateral view showing the capitulum and peduncle, (**c**) rostral view showing the capitulum and peduncle, (**d**) carinal view. Scale bars: a–d) 2 mm.

Genus *Teloscalpellum* Zevina, 1978
Arcoscalpellum Hoek, 1907: 85 (sectio, part.). — Newman & Ross 1971: 42 (part.); Section V. — Pilsbry, 1907: 47 (part.).
Teloscalpellum Zevina, 1978b: 1350. — Liu & Ren 1985: 212. — 2007: 257.

Diagnosis:
Capitulum with 13 or 14 plates; carinal lateral umbo at basi-carinal angle, angle not extending beyond carinal margin; inframedian latus triangular or rod-like-shaped, umbo apical or sub-apical; caudal appendage multi-segmented.

Type species:
Scalpellum spicatum Zevina, 1975.

Teloscalpellum ecaudatum (Calman, 1918)
Figure 3.24

Scalpellum ecaudatum Calman, 1918b: 106, text-fig. 2.
Teloscalpellum ecaudatum. — Zevina, 1981: 365, fig. 282. — Chan 2009: 55, figs 1E, 7.

Material examined:
- Kei Islands: 1 specimen, MNHN-IU-2019-4917, Stn. CP 35, 06°08'S, 132°45'E, 390–502 m depth, 27 October 1991.
- Tanimbar Island: 1 specimen, MNHN-IU-2019-4918, Stn. CP 59, 08°20'S, 132°11'E, 399-405 m depth, 31 October 1991.

Diagnosis:

Capitulum compressed, elongated; 14 plates, sculptured with radiating ribs; inframedian latus triangular; rostro-lateral plates very low; penis and caudal appendages absent.

Description:

Capitulum with all plates strongly ribbed, lines of growth marked by fine, inconspicuous striation. Tergum with occludent margin straight, carinal margin convex, but straight concave near apex. Scutum with occludent margin convex, other margins straight, apex slightly overlapping tergum. Carina evenly curved with flat roof bordered by strong ridges; upper latus quadrangular; rostrum small, triangular, overlapped at sides by rostral latera; inframedian latus very narrow. Peduncle shorter than capitulum, covered with strong scales. Cirrus I with unequal rami (anterior ramus: 11 segmented, posterior ramus: 13 segmented). Maxilla globular with serrulate setae; maxillule not notched; mandible with three major teeth, lower margin with three to four denticles. Measurements of two specimens: height of capitulum 12.07–18.59 mm, width 6.17–11.47 mm, thickness 2.68–5.41 mm; length of peduncle 6.30–8.33 mm, width 3.21–5.41 mm.

Distribution:

Java Sea, Indonesia; Philippines (Chan 2009). In this study, *Teloscalpellum ecaudatum* was found at Kei Islands and Tanimbar Island, Indonesia.

Type locality:

Java Sea; 7°35’S, 114°30’30” E; 132–315 m depth (Calman 1918b).

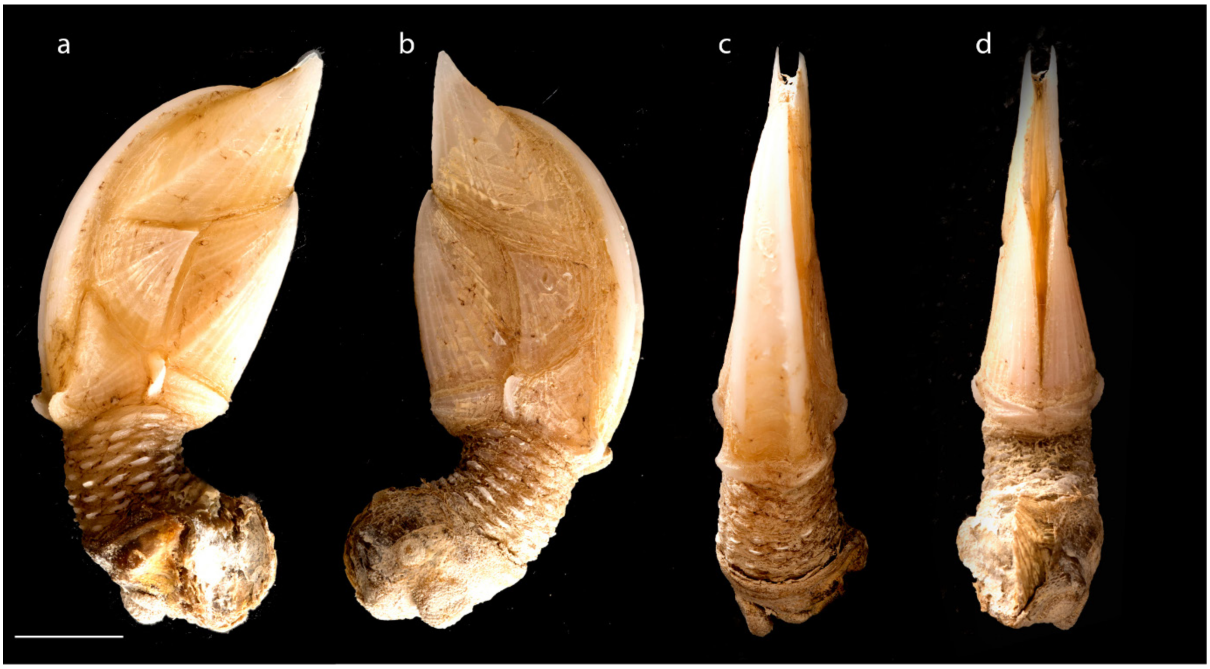

Figure 3.24. *Teloscalpellum ecaudatum* (Calman, 1918) (MNHN-IU-2019-4917). (**a**) left lateral view showing the capitulum and peduncle, (**b**) right lateral view showing the capitulum and peduncle, (**c**) carinal view, (**d**) rostral view showing the capitulum and peduncle. Scale bars: a–d) 5 mm.

Genus *Trianguloscalpellum* Zevina, 1978b

Arcoscalpellum Hoek, 1907: 85 (part). — Pilsbry 1907a: 47. — Newman & Ross 1971: 42 (part).
Trianguloscalpellum Zevina, 1978b: 1349. — Liu & Ren 1985: 205.

Diagnosis:

Capitulum of female or hermaphrodite with 13 or 14 completely calcified plates; tergum and scutum with umbones apical; middle latera triangular, sometimes quadrangular, with apical umbo reaching upper latera; carinolatera triangular or subtriangular with apical umbo; caudal appendages distinctly long.

Type species:

Scalpellum balanoides Hoek, 1883: 129, pl. V, fig. 15, pl. X, fig. 11, pl. XI, figs 1–3; type locality: 5°42’S, 132°25’E; depth: 236 m; bottom: mud; it was found attached to an arm of a Comatula or Pentacrinus.

Trianguloscalpellum balanoides (Hoek, 1883)

Figure 3.25

Scalpellum balanoides Hoek,1883: 129, pl. V, fig. 15, pl. X, fig. 11, pl. XI, figs 1–3. — Broch 1922: 242, fig. 10 — Weltner 1922: 63, taf. II, fig. 7, taf. III, fig. 8. — Nilsson-Cantell 1931: 2. — Hiro 1937b: 42, fig. 33.
Scalpellum gonionotum Pilsbry, 1907b: 360. — Pilsbry 1911: 65, pl. IX, figs 2–4. — Hiro 1937a: 43.
Trianguloscalpellum balanoides. — Zevina 1978b: 1349. — 1981: 294, fig. 221. — Liu & Ren 1985: 210, fig. 16, pl. XI, figs 15–17. — 2007: 256–257, fig. 111. — Rosell 1991: 20–22, fig. 2c–d. — Huang 1994: 517. — 2001: 318. — Jones et al. 2001: 253. —Young 2001: 464, fig. 7. — Jones 2007: 292. — Chan et al. 2009b: 116, figs 95–96. — Shalaeva & Boxshall 2014: 40, fig. 26.

Material examined:

- Kei Islands: 1 specimen, MNHN-IU-2019-4923, Stn. CP 16, 05°17’S, 132°50’E, 330–350 m depth, 24 October 1991, attached to crinoid.
- Tanimbar Island: 2 specimens, MNHN-IU-2019-4924, Stn. CP 86, 09°26’S, 131°13’E, 223–225 m depth, 4 November 1991.

Diagnosis:

Capitulum with 13 fully calcified plates, covered by thin membrane; carina and extremely short, simply bowed without distinct roof; umbo of carina at apex; upper latus triangular; carinal latus almost as high as carina, umbo apical, carinal latus very large, almost similar size to tergum.

Description:

Capitulum flat, narrow at base, same breadth as peduncle. Scutum about twice as long as broad; occludent margin almost straight, umbo at apex. Tergum triangular, the same size as scutum. Carina very short, simply, not very strongly, bowed, umbo at apex. Upper latus triangular, carinal margin absent. Rostral latus quadrangular, umbo at apex of angle formed by rostral and scutal margins. Infra-median latus elongate, triangular, umbo apical. Carinal latus very large, convex, umbo at top of carinal margin. Cirrus I unequal, posterior ramus more slender than anterior ramus; cirrus VI with caudal appendages. Maxillule distinctly notched, two stout spines on upper side; mandible with three teeth excluding inferior angle. Measurements of specimen: height of capitulum 8.20 mm, width 4.40 mm, thickness 1.75 mm; length of peduncle 5.06 mm, width 2.10 mm.

Distribution:

Pacific, Western Central; South and East China Sea; South of Sumatra, Banda Sea, Indonesia; Vietnam; Philippines; Taiwan; South of Japan; attached to crinoids, hydroids; 220–1,097 m depth (Jones et al. 2001; Chan et al. 2009b; Shalaeva and Boxshall 2014). In this study, *Trianguloscalpellum balanoides* was found at Kei Islands and Tanimbar Island, Indonesia.

Type locality:

5°42'S, 132°25'E; depth: 232 m; bottom: mud; attached to arm of a Comatula or Pentacrinus (Hoek 1883).

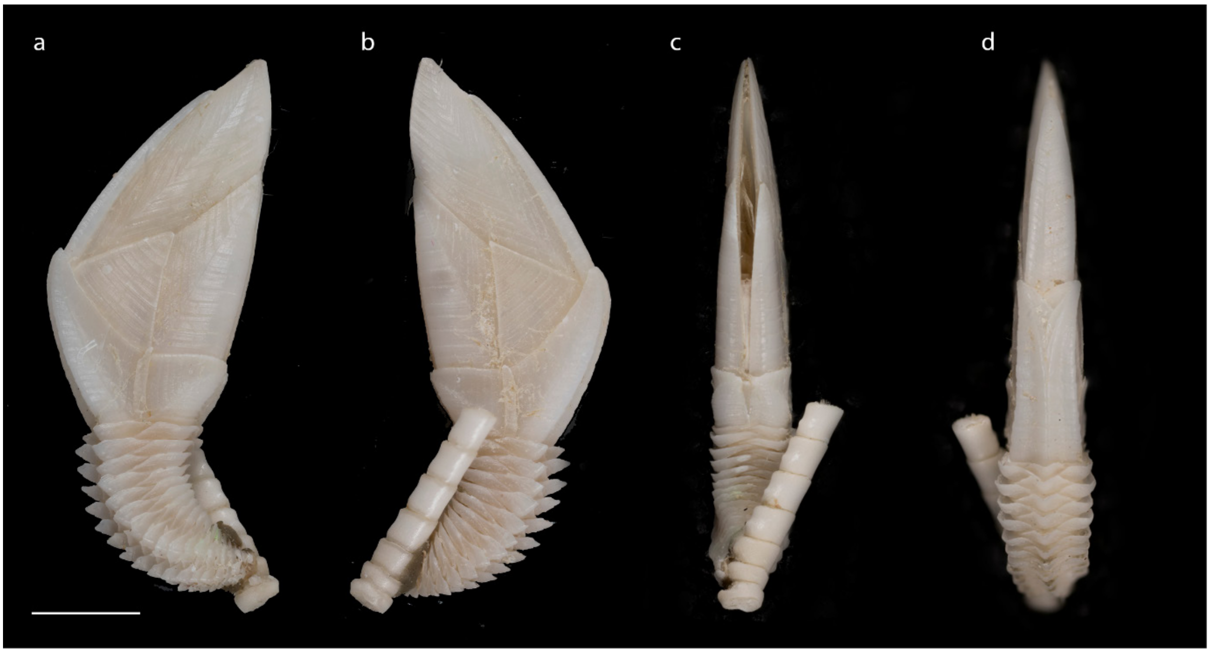

Figure 3.25. *Trianguloscalpellum balanoides* (Hoek, 1883) (MNHN-IU-2019-4923). (**a**) left lateral view showing the capitulum and peduncle, (**b**) right lateral view showing the capitulum and peduncle, (**c**) rostral view showing the capitulum and peduncle, (**d**) carinal view. Scale bars: a–d) 2 mm.

Trianguloscalpellum hirsutum (Hoek, 1883)

Figure 3.26

Scalpellum hirsutum Hoek, 1883: 88, pl. IV, fig. 19. — Gruvel 1905: 66, fig. 74. — Pilsbry 1907a: 25.

Arcoscalpellum hirsutum. — Newman & Ross 1971: 62–64, fig. 28.

Trianguloscalpellum hirsutum. — Zevina 1981: 309, fig. 233. — Chan et al. 2009b: 119–121, figs 100–102. — Chan et al. 2010: 13, figs 1F, 9A–H. — Jones 2012: 371, 376. — Shalaeva & Boxshall 2014: 44, fig. 29.

Material examined:

- Tanimbar Island: 1 specimen, MNHN-IU-2019-4908, Stn. CP 91, 08°44'S, 131°05'E, 884–891 m depth, 5 November 1991.

Diagnosis:

Capitulum with 14 plates covered by membrane, covered by very long hairs; carina simply bowed, umbo at apex, roof flat; upper latus triangular; rostrum very narrow stripe distinctly visible at surface.

Description:

Capitulum small, long hairs covering plates. Scutum elongate, convex, more than twice as long as broad. Tergum large, elongate rhomboid, umbo at apex. Carina simply bowed, roof flat. Upper latus almost triangular, carinal-basal margin arched. Rostrum small, linear-shaped. Rostral latus quadrangular, basal and scutal margins parallel. Infra-median latus triangular, umbo apical. Carinal latus with irregular shape, umbo near apex. Peduncle short. Cirrus I with rami unequal, anterior ramus oval, posterior ramus more slender; cirrus VI with caudal appendages. Maxillule not notched, two stout spines on upper side; mandible with three teeth excluding inferior angle. Measurements of the specimen: height of capitulum 12.18 mm, width 6.50 mm, thickness 3.74 mm; length of peduncle 4.10 mm, width 3.43 mm.

Distribution:

Borneo, Indonesia; Pacific, Western Central and Southeast; Australia; Taiwan; Antarctica; attached to gastropod shells, rocks; 1,502–1,965 m depth (Chan et al. 2010; Jones 2012; Shalaeva and Boxshall 2014). In this study, *Trianguloscalpellum hirsutum* was found at Tanimbar Island, Indonesia.

Type locality:

Pacific, Western Central (Moluccas Sea); 0°48›S, 120°58›E; depth: 252 m; bottom temperature: 2.4°C; bottom: rock (Hoek 1883).

Figure 3.26. *Trianguloscalpellum hirsutum* (Hoek, 1883) (MNHN-IU-2019-4908). (**a**) left lateral view showing the capitulum and peduncle, (**b**) right lateral view showing the capitulum and peduncle, (**c**) carinal view, (**d**) rostral view showing the capitulum and peduncle. Scale bars: a–d) 5 mm.

Genus *Verum* Zevina, 1978

Arcoscalpellum Pilsbry, 1907: 47 (part). — Newman & Ross 1971: 42 (part).
Verum Zevina, 1978b: 1348.

Diagnosis:

Capitulum of female or hermaphrodite, with 13–14 completely calcified plates; tergum with carinal margin straight or slightly to moderately recurving; scutum with or without short apico-lateral arm, umbo apical; carina with apical or subapical umbo, evenly curved or angularly flexed; upper latera sub-triangular or pentagonal, umbo apical or subapical; middle latera narrow, triangular or quadrangular, umbo basal or sub-basal; carinolatera short, umbo basal to sub-basocarinal, usually not or slightly projecting beyond rim of capitulum; caudal appendages short.

Type species:

Scalpellum zenkevichi Zevina, 1972: 44, fig. 3; type locality: Pacific Ocean, 24°27'S, 70°42'E.

Verum australicum (Hoek, 1883)

Figure 3.27

Scalpellum australicum Hoek, 1883: 118, pl. V, fig. 11. — Weltner 1922: 63. — Nilsson-Cantell 1938: 7.
Verum australicum. — Zevina 1981: 223–224, fig. 160. — Jones et al. 1990: 5. — Jones 1992: 156–160, figs 7–8. — Jones 2012: 371, 376. — Shalaeva & Boxshall 2014: 52, fig. 36.

Material examined:

- Tanimbar Island: 1 specimen, MNHN-IU-2019-4930, Stn. CP 86, 09°26'S, 131°13'E, 223–225 m depth, 4 November 1991.

Diagnosis:

Capitulum with 13 plates closely locked together, surface smooth with slightly prominent ridges; carina simply bowed with flat roof; upper latus trapeziform; inframedian latus elongate, narrow; carinal latus with umbo projecting beyond carina.

Description:

Capitulum elongate-oval, flat with distinct ridges and furrow. Scutum slightly convex, umbo apical, occludent margin arched. Tergum triangular, umbo apical, distinctly recurved. Rostral latus irregularly quadrangular; infra median latus narrow, umbo near base; carinal latus quadrangular. Peduncle slightly conical, short, scales near capitulum larger than those near base. Cirrus I unequal, anterior ramus oval, posterior ramus more slender; cirri II to VI very long, rami subequal, segments elongate; cirrus VI with caudal appendages. Maxillule not notched, large spine on upper side, cutting edge almost straight; mandible with three large teeth excluding inferior angle. Measurements of specimen: height of capitulum 10.33 mm, width 6.09 mm, thickness 2.08 mm; length of peduncle 4.62 mm, width 2.24 mm.

Distribution:

Indian Ocean, Western; Pacific Western Central and Southeast; Zanzibar; known depth range 463–2,561 m (Shalaeva and Boxshall 2014). In this study, *Verum australicum* was found at Tanimbar Island, Indonesia.

Type locality:

Between New Guinea and Australia (12°08’S, 145°10’E): Challenger station 184: depth: 2,561 m: bottom temperature: 1.8°C; substrate grey ooze (Hoek 1883).

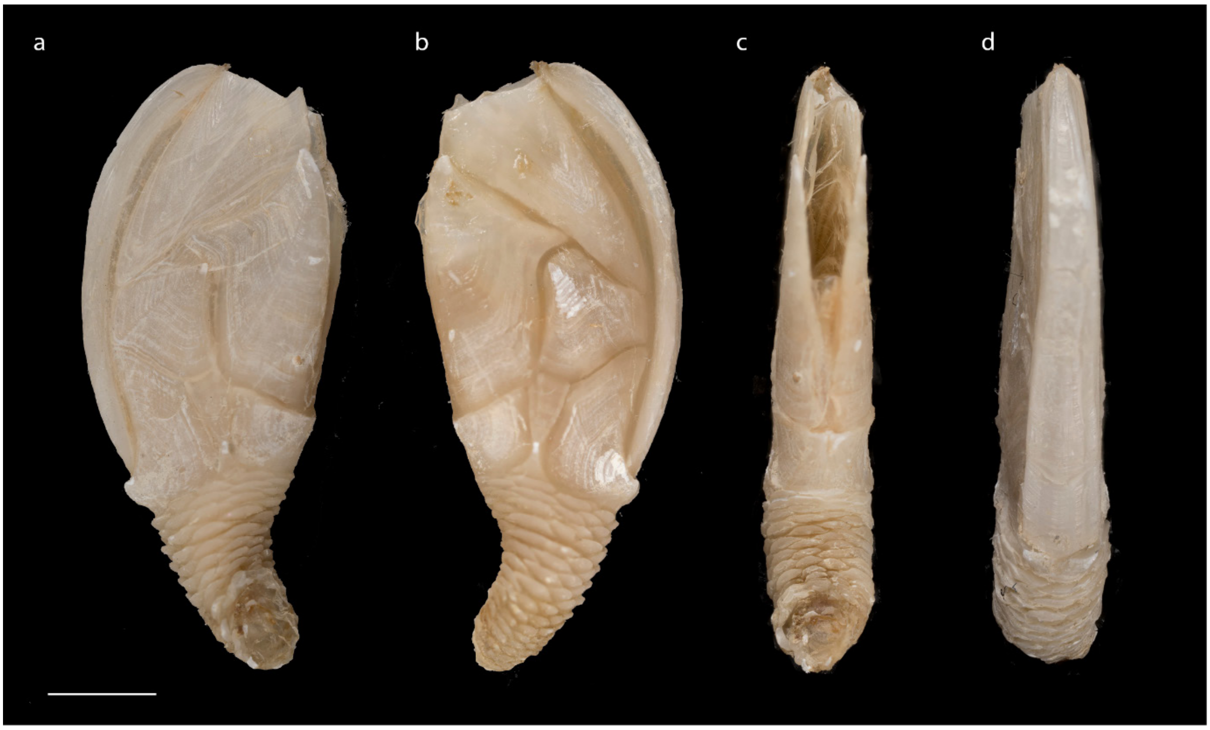

Figure 3.27. *Verum australicum* (Hoek, 1883) (MNHN-IU-2019-4930). (**a**) left lateral view showing the capitulum and peduncle, (**b**) right lateral view showing the capitulum and peduncle, (**c**) rostral view showing the capitulum and peduncle, (**d**) carinal view. Scale bars: a–d) 3 mm.

Verum carinatum (Hoek, 1883)

Figure 3.28

Scalpellum carinatum Hoek, 1883: 76, pl. III, figs 7–8. — Pilsbry 1907a: 53, fig. 18. — Gruvel 1920: 20. — Barnard 1925: 3. — Broch 1953: 7. — Weisbord 1977: 243–244, pl. 27, figs 3–4.

Scalpellum imperfectum Pilsbry, 1907a: 75, fig. 30, pl. IV, figs 15–18. — Annandale 1913: 233. — Barnard 1924: 47. — MacDonald 1929: 537. — Broch, 1953: 9. — Stubbings 1961: 11, text-fig. 2. — 1967: 234.

Meroscalpellum imperfectum. — Newman & Ross 1971: 119, text-fig. 62.

Verum carinatum. — Zevina 1981: 225–226, fig. 163. — Shalaeva & Boxshall 2014: 53, fig. 37.

Material examined:

- Kei Islands: 1 specimen, MNHN-IU-2019-4920, Stn. DW 18, 05°18’S, 133°01’E, 205–212 m depth, 24 October 1991.

Diagnosis:

Capitulum with 14 plates separated by chitinous interspaces, surface smooth; carina bowed, angularly bent, with flat roof; upper latus irregular pentagonal; inframedian latus large, wine-glass-shaped.

Description:

Capitulum elongate, plates covered by thin, chitinous membrane. Scutum elongated, apex pointed, occludent margin very convex. Tergum flat, triangular, apex very recurved, occludent margin very arched. Carina with umbo at top of flat roof. Upper latus flat, irregular pentagonal; rostrum narrow, elongated; rostral lateral convex with rostral margin short; inframedian latus wine-glass-shaped; carinal latus flat, large. Peduncle short, calcareous scales distinct. Cirrus I unequal, anterior ramus broader than posterior ramus; cirri II to VI long, rami equal; cirrus VI with caudal appendages. Maxillule not notched, two large spines on upper side, cutting edge almost straight; mandible with three large teeth excluding inferior angle. Measurements of specimen: height of capitulum 9.14 mm, width 4.53 mm, thickness 1.74 mm; length of peduncle 2.54 mm and width 2.20 mm.

Distribution:

Atlantic, excluding polar areas; Pacific, Southeast. Known depth range 600 to 2,400 m (Shalaeva and Boxshall 2014). In this study, *Verum carinatum* was found at Kei Islands, Indonesia.

Type locality:

Station 135, near the Island of Tristan da Cunha; depth: 1,800 m; bottom: rock, shells (Hoek 1883).

Figure 3.28. *Verum carinatum* (Hoek, 1883) (MNHN-IU-2019-4920). (**a**) left lateral view showing the capitulum and peduncle, (**b**) right lateral view showing the capitulum and peduncle, (**c**) rostral view showing the capitulum and peduncle, (**d**) carinal view. Scale bars: a–d) 3 mm.

Verum novaezelandiae (Hoek, 1883)

Figure 3.29

Scalpellum novae-zelandiae Hoek, 1883: 124, pl. V, figs 7, 8. — 1907: 100, pl. VIII, figs 4, 4a; 1913: 14. — Weltner 1897: 249. — 1922: 71. — Annandale 1905: 83. — 1906b: 389. — 1908: pl. 5, fig. 7. — 1913: 231. — Broch 1927a: 540, fig. 512.

Scalpellum Novae-Zealandiae. — Gruvel 1905: 88, fig. 99.

Scalpellum (*Scalpellum*) *novae-zelandiae*. — Calman 1918b: 123.

Arcoscalpellum novaezelandiae. — Foster 1978: 65, pl. 8D, fig. 39.

non *Scalpellum Novae-Zelandiae*. — Gruvel 1902: 54, pl. 2, figs 12–13, 15. — Gruvel 1912: 346 (= *V. parazelandiae* Young, 1998b).

Verum novaezelandiae. — Zevina 1978b: 1348. — Zevina 1981: 228, fig. 165. — Chan et al. 2009b: 17, figs 1I, 12A–H, 13A–D. — Chan et al. 2010: 17, figs 11–13. — Shalaeva & Boxshall 2014: 53, fig. 39.

Material examined:

- Tanimbar Island: 1 specimen, MNHN-IU-2019-4919, Stn. CP 87, 08°47’S, 130°49’E, 1017–1024 m depth, 5 November 1991.

Diagnosis:

Capitulum with 13 plates covered by very thin, chitinous membrane; carina simply bowed, flat roof with umbo apical; upper latus quadrangular or rather pentagonal, lower edge being truncated; inframedian latus elongate, quadrangular; carinal latus large, elongate, umbo near base; peduncle short.

Description:

Capitulum flatted, elongate, plates separated by narrow, chitinous interspaces. Scutum quadrangular, umbo apical, occludent margin arched. Tergum triangular with umbo slightly produced apex. Carina with bowed, flat roof, increasing little in width from upper to lower. Upper latus irregularly trapeziform; rostral latus with umbo at top of rostral margin; infra-median latus irregular, quadrangular, elongate, narrow; carina latus quadrangular. Cirrus I unequal, anterior ramus broader than posterior ramus; cirrus VI with short caudal appendages. Maxillule slightly notched, two large spines on upper side; mandible with three large teeth excluding inferior angle; labrum slightly convex, with numerous teeth. Measurements of specimen: height of capitulum 13.46 mm, width 6.98 mm, thickness 2.99 mm; length of peduncle 6.02 mm, width 3.23 mm.

Distribution:

Indo-west Pacific: Eastern Africa, Gulf of Aden, eastwards to New Zealand; Philippines; Taiwan; attached to sunken wood, gorgonians, glassy spicule of hexactinellid sponges; 822–4850 m depth (Shalaeva and Boxshall 2014; Jones and Hosie 2016). In this study, *Verum novaezelandiae* was found at Tanimbar Island, Indonesia.

Type locality:

37°34’S, 179°22’E; depth: 1,260 m; bottom temperature: 4.2°C; bottom: grey ooze (Hoek 1883).

Figure 3.29. *Verum novaezelandiae* (Hoek, 1883) (MNHN-IU-2019-4919). (**a**) left lateral view showing the capitulum and peduncle, (**b**) right lateral view showing the capitulum and peduncle, (**c**) carinal view, (**d**) rostral view showing the capitulum and peduncle. Scale bars: a–d) 3 mm.

Order Sessilia Lamarck, 1818

Suborder Verrucomorpha, Pilsbry 1916

Verrucomorpha Pilsbry, 1916: 14. — Newman et al. 1969: 281. — Newman & Ross 1971: 135. — Newman 1987: 8. — 1996: 501. — Buckeridge 1994: 89. — Young, 1998: 74.

Diagnosis:

Shell asymmetrical with four plates (carina, rostrum, tergum and scutum), base membranous or calcareous.

Family Verrucidae Darwin, 1854

Verrucidae Darwin, 1854: 495. — Gruvel 1905: 169. — Withers 1935: 323. — Newman et al. 1969: 281. — Newman & Ross 1971: 135. — Buckeridge 1994: 89. — Young 1998: 74.

Diagnosis:

Scutum and tergum without depressor muscles; movable only on one side; other side immovable, united with rostrum and carina.

Genus *Alteriverruca* Pilsbry, 1916

Verruca Section D *Altiverruca* Pilsbry, 1916: 40.

Altiverruca Pilsbry, 1916: 40 — Newman et al. 1969: 282. — Newman & Ross 1971: 135. — Ren 1984b: 172. — Buckeridge 1994: 92. — Young 1998: 77.

Diagnosis:

Verrucids with erect form; bases of plates not inflected. Operculum close to vertical, myophore absent.

Type species:

Verruca hoeki Pilsbry, 1907.

Altiverruca navicula (Hoek, 1913)

Figure 3.30

Verruca navicula Hoek, 1913: 134, figs 4–6. — Nilsson-Cantell 1927: 778, figs a–f.
Altiverruca navicula. — Buckeridge 1994: 100, fig. 5. — Chan et al. 2009b: 280, figs 245–247. — Chan et al. 2010: 29, figs 2E, 21, 22.

Material examined:

- Tanimbar Island: 3 specimens, MNHN-IU-2019-4941, Stn. CP 91, 08°44'S, 131°05'E, 884–891 m depth, 5 November 1991, attached to peduncle of Alcockianum persona (Annandale, 1916).

Diagnosis:

Shell not depressed; carina and rostrum interlocking with single rib from each plate; movable plates large, scutum with four articular ribs, tergum with six articular ribs, growth lines very distinct; caudal appendages long.

Description:

Shell yellowish. Movable scutum elongately triangular, apex distinctly beaked, projecting freely; surface with numerous articular ridges. Movable tergum large, quadrangular; surface with strongly developed, curved axial articular ridge. Carina and rostrum irregular quadrangular, with carina higher, rostrum broader. Fixed tergum with two parts: (1) triangular portion very narrow at apex, slightly broader in its inferior (2) flat and broad part at a rear portion of shell. Fixed scutum pointed with distinctly beaked apex; composed of broader, nearly flat, triangular portion and narrower inflected portion, only widening towards its inferior. Base of shell elongatedly oval-shaped. Cirrus I with rami very unequal (anterior ramus: 12-segmented, posterior ramus: 28-segmented); cirrus VI with caudal appendages. Maxilla bilobed, fringed with setae, except on the notch; maxillule widely notched, horizontally elongated, two large spines above notch, numerous dense setae at notch; mandible with three teeth excluding inferior angle; labrum slightly concave, conical teeth on cutting margin.

Distribution:

Pacific Ocean (Chan et al. 2010). In this study, *Altiverruca navicula* was found at Tanimbar Island, Indonesia.

Type locality:

(1) 9°3.4'S, 119°56.7'E; depth 959 m; bottom: globigerina ooze. (2) 3° 37.7'S, 131°26'.4E; depth 924 m; bottom: fine grey mud (Hoek 1913).

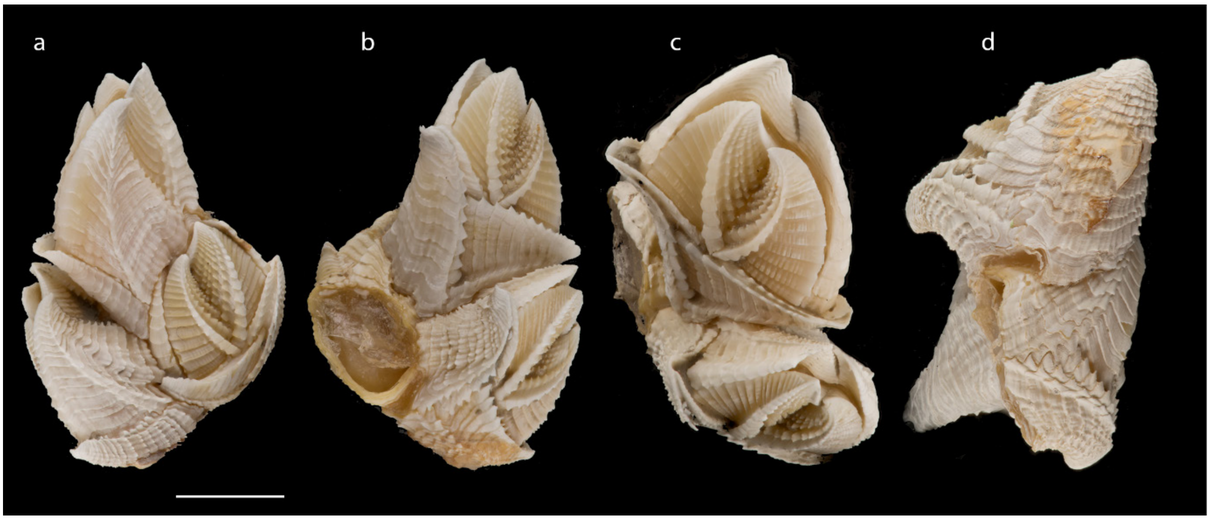

Figure 3.30. *Altiverruca navicula* (Hoek, 1913) (MNHN-IU-2019-4941). (**a**) left lateral view, (**b**) right lateral view, (**c**) upper lateral view, (**d**) lower lateral view. Scale bars: a–d) 7 mm.

Genus *Newmaniverruca* Young, 1998

Verruca Section B: *Verruca*, Group of *Verruca alba* Pilsbry, 1916: 25 (part.).

Verruca Section B: *Verruca*, Group of *Verruca calotheca* Pilsbry, 1916: 30 (part.).

Verruca (*Verruca*): Foster, 1979: 68 (part.). — Zevina 1987: 1812 (part. — Buckeridge 1994: 90 (part.).

Newmaniverruca Young, 1998: 77.

Diagnosis:

Shell with four plates (carina, rostrum, scutum and tergum); operculum parallel to base.

Type species:

Verruca albatrossiana Pilsbry, 1912: 292. — 1916: 47; type locality: East of Luzon, Philippines.

Newmaniverruca albatrossiana (Pilsbry, 1912)

Figure 3.31

Verruca albatrossiana Pilsbry, 1912: 292. — 1916: 47. — Buckeridge, 1994: 91, figs 1a–f. — Buckeridge, 1997: 129.

Verruca grex Hoek, 1913: 142, pl. XI, figs 7–13, pl. XIII, figs 11–13.

Verruca (*Euverruca*) *albatrossiana*. — Broch 1931: 45.

Verruca (*Verruca*) *albatrossiana*. — Ren 1984: 168, fig. 2, pl. 1 (7–11).

Newmaniverruca albatrossiana. — Young 1998: 77. — Chan 2009: 74, figs 2G, 22A–I.

Material examined:

- Kei Islands: 1 specimen, MNHN-IU-2019-4942, Stn. CC 21, 05°14'S, 133°00'E, 688–694 m depth, 25 October 1991, attached to glass rope sponge.

Diagnosis:

Rostrum and fixed scutum with unusual length; rostrum low, fixed scutum larger than fixed tergum.

Description:

Movable plates parallel to base, wall of parietal vertically ribbed; fixed scutum without internal pit. Movable scutum with crescentic ridge and longitudinal striations; movable tergum with articular ribs and diagonal rib. Apices of fixed scutum and tergum contiguous. Carina occupying carino-rostral wall, apices marginal. Cirrus I with rami unequal and serrulate setae; cirrus VI with caudal appendages. Maxilla globular, with fringing setae; maxillule notched, two large setae on upper side; mandible with three teeth excluding inferior angle.

Distribution:

Indo-west Pacific: NW Australia; South China Sea; China; Philippines; attached to cidaroid spines (e.g. *Stereocidaris indica philippinensis* Mortensen, 1928), 345–620 m depth (Jones and Hosie 2016). In this study, *Newmaniverruca albatrossiana* was found at Kei Islands, Indonesia.

Type locality:

East of Luzon, Philippines (Pilsbry 1912).

Figure 3.31. *Newmaniverruca albatrossiana* (Pilsbry, 1912) (MNHN-IU-2019-4942). (**a**) left lateral view, (**b**) right lateral view, (**c**) upper lateral view, (**d**) lower lateral view. Scale bars: a–d) 3 mm.

Suborder Balanomorpha Pilsbry, 1916

Operculata tribe Symetrica Gruvel, 1905: 189.

Balanomorpha Pilsbry, 1916: 47 (Balanidae *sensu* Darwin, 1854).

Diagnosis:

Peduncle absent; shells bilaterally symmetrical on either side of rostrocarinal axis; shell with parietal plates of carina, rostrum and one to three pairs of lateral plates, all separate from one another, variously fused or totally concrescent; base membranous or calcareous; hermaphroditic or with dwarf males.

Family Bathylasmatidae Newman & Ross, 1971

Bathylasmatidae Newman & Ross, 1971: 138 (part.). — Newman & Ross 1976: 37, 45 (part.).
Bathylasmatinae Newman & Ross, 1976: 37, 45. — Buckeridge 1983: 68. — Newman 1996: 502. — Buckeridge 1999: 522. — Jones 2000: 231, tables 1–2.

Diagnosis:

Shell with four or six plates; wall solid or permeated by single row of chitin-filled longitudinal canals; radii absent; one or both rami of cirri I and cirri II sometimes antenniform; labrum without notch in crest.

Subfamily Hexelasminae Newman & Ross, 1976

Hexelasminae Newman & Ross, 1976: 37, 46.

Diagnosis:

Shell with six plates, infiltrated by chitin-filled tubes; basis calcareous; scuta parallel to basis; tergum with distinct spur; cirrus II resembling cirrus I more than cirrus III.

Type genus:

Hexalasma Hoek, 1913.

Genus *Hexelasma* Hoek, 1913

Hexelasma Hoek, 1913: 244 (part.). — Utinomi 1965: 13. — Jones 2000: 240, figs 51, 64, tables 28–30.
Aaptolasma Newman & Ross, 1971: 158.

Diagnosis:

Parietes solid; radii absent; plates with a carina, paired carinolatera and latera and a rostrum without any sign of fusion; caudal appendages absent.

Type species:

Hexelasma velutinum Hoek, 1913: 246 (part.); type locality: Indonesia, 6°08'S, 121°19'E (Siboga Station 105).

Hexelasma arafurae Hoek, 1913

Figure 3.32

Hexelasma arafurae Hoek, 1913: 251, pl. 25, figs 12–16. — Utinomi 1965: 11. — Newman & Ross 1971: 155. — 1976: 46. — Foster 1981: figs 6 F–H. — Jones 2000: 246, fig. 51, tables 28–31.
Aaptolasma arafura. — Foster 1978: 79.

Material examined:

- Kei Islands: 2 specimens, MNHN-IU-2019-4851, Stn. DW 18, 05°18'S, 133°01'E, 205–212 m depth, 24 October 1991.

Diagnosis:

Shell with very wide orifice; alae broadly-triangular with summits oblique; scutum folded longitudinally, articular ridge slightly prominent, deep pit for adductor muscle; tergum beaked, with prominent articular ridge, spur very broadly rounded; inner side of scutum and tergum orange-coloured.

Description:

Shell yellowish, conical, with six plates. Orifice diamond-shaped; scutum triangular elongated with protruding growth-ridges; tergum smaller than scutum, apex beaked, carinal margin rounded, growth-ridges less distinct than on scutum. Cirrus I with unequal rami (anterior ramus: 8-segmented; posterior ramus: 12-segmented), dense long setae on surface areas. Cirrus II with equal rami, dense long setae. Cirri IV–VI with equal rami with numerous segments; segments almost without exception furnished with two pairs very long, stiff, needle-like spines along inner faces. Measurements of specimen: basal length of shell 14.32 mm, orifice length 8.00 mm, carinal height 12.39 mm, orifice width 6.49 mm, basal width 13.76 mm.

Distribution:

Arafura Sea, Indonesia; 205–560 m depth (Jones and Hosie 2016). In this study, *Hexelasma arafurae* was found at Kei Islands, Indonesia.

Type locality:

Indonesia; Siboga stat. 262; 5°54'S, 132°49'E; 560 m depth; bottom: solid bluish-grey mud (Hoek 1913).

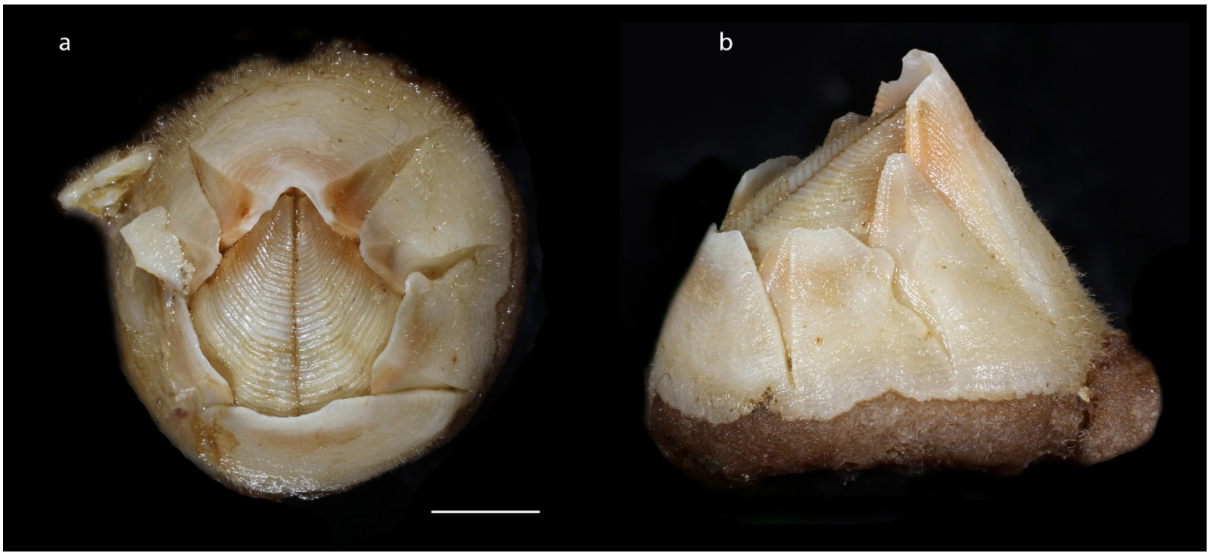

Figure 3.32. *Hexelasma arafurae* Hoek, 1913 (MNHN-IU-2019-4851). (**a**) view from above, (**b**) right lateral view. Scale bars: a, b) 4 mm.

Superfamily Balanoidea Leach, 1817

Balanidae Leach, 1817: 68 — Pilsbry 1916: 48 — Newman et al. 1969: 284 — Newman & Ross 1976: 38, 49 — Newman 1993: 408.
Balaninae — Darwin 1854: 175.
Balanoidea — Newman 1996: 502.

Diagnosis:

Shell wall composed of four or six plates (rostrum, carina and one to three pairs of laterals); parietes solid or tubiferous, when tubiferous rarely secondarily filled; radii solid or tubiferous.

Basis commonly calcareous, solid or permeated by tubes, rarely membranous; when basis calcareous, internal surfaces of compartments commonly with uniform ribs; when calcareous commonly forming complex interdigitations with wall. Opercular plates occlude aperture; articulations between the pairs generally shallow or fused. Cirrus I with rami subequal or grossly unequal; cirri II and III with rami never antenniform; cirrus III resembling II more than IV; caudal appendages absent; penis with basidorsal point. Labrum thin, never bullate; crest with pronounced medial incision; mandible quadri- or quinquedentoid; second and following teeth with one or more subsidiary cusps; fifth tooth often vestigial; inferior angle commonly molariform.

Family Archaeobalanidae Newman & Ross, 1976

Archaeobalanidae Newman & Ross, 1976: 38, 49.

Diagnosis:

Shell with four or sixplates; parietes solid, rarely tubiferous; tubes uniformly or irregularly arranged; radii solid; basis commonly calcareous, rarely tubiferous.

Subfamily Archaeobalaninae Newman & Ross, 1976

Archaeobalaninae Newman & Ross, 1976: 38, 49.

Diagnosis:

Shell with four or six plates; parietes solid or tubiferous; when tubiferous, tubes uniformly arranged in single row; interlaminate figures simple; basis calcareous or membranous, when membranous wall solid.

Type genus:

Archaeobalanus Menesini, 1971: 19.

Genus *Conopea* Say, 1822

Conopea Say, 1822: 323.
Conoplea Gray, 1825: 98, 103.
Balaninus Costa, 1839: 181.
Balanus Section B Darwin, 1854: 216.
Patella-Balanus Hoek, 1913: 160, 162, 221.

Diagnosis:

Shell firm, strong, with six thick compartments; parietes with or without pores; radii solid with summits parallel to basal margin of parietes and denticulated sutural margins; basis calcareous, elongated along carino-rostral axis, boat-shaped; orifice smooth, not dentated; scutum with simple growth ridges; penis with basidorsal point; attached to gorgonians or antipatharians.

Type species:

Conopea elongata Say, 1822; type locality: eastern Florida, USA.

Conopea cymbiformis (Darwin, 1854)

Figure 3.33

Balanus cymbiformis Darwin, 1854: 221, pl. 3, figs 5a, b. — Broch 1931: 85, fig. 29a–b. — Nilsson-Cantell 1938: 55, pl. 2, fig. 3. — Utinomi 1962: 219, fig. 2. — Dong et al. 1982: 103.
Balanus proripiens Hoek, 1913: 228, pl. 24, figs 1–3, pl. 24, figs 1–3. — Nilsson-Cantell 1921: 331, fig. 70 c–d.
Pyrgoma jedani Hoek, 1913: 262, pl. 27, figs 3–8.
Conopea cymbiformis. — Newman & Ross 1976: 55.

Material examined:

- Kei Islands: 9 specimens, MNHN-IU-2019-4823, Stn. DW 30, 05°39'S, 132°56'E, 111–118 m depth, 26 October 1991; 1 specimen, MNHN-IU-2019-4824, Stn. DW 22, 05°22'S, 133°01'E, 82 m depth, 25 October 1991.

Diagnosis:

Shell irregularly conical; orifice oval with swollen border; basis irregularly cup-formed; scutum and tergum triangular, not calcified together; spur of tergum feebly developed.

Description:

Shell yellowish with orange rust-brown in proximal areas. Carina, carinolatera and latera with pale orange-brown and rust red-brown longitudinal stripes, latter may have oblique white spots. Radii with pale orange-brown and rust red-brown horizontal striation. Opercular plates with scutum pink-brown, transparent; tergum transparent white. Shell may appear longer and lower, due to elongation of carina and rostrum or low and comparatively shorter, due to development of rostrum alone or more upright and comparatively higher, with neither carina nor rostrum elongated. Cirrus I with unequal rami (anterior ramus: 7-segmented; posterior ramus: 12-segmented). Cirri II–VI with equal rami, numerous segments. Penis very long, delicate hairs scattered over surface, a few more disposed near tip. Labrum deeply notched, two small teeth on each side of notch. Mandibles with five teeth, inferior angle not distinctly separated from fifth; distance between tips of first and second teeth slightly more than that between those of second and third teeth; third tooth larger; fourth and fifth smaller than others. Maxillule with straight edge and numerous large setae. Measurements of specimen: basal length of shell 7.73 mm, orifice length 4.60 mm, carinal height 8.70 mm, orifice width 3.88 mm, basal width 4.94 mm.

Distribution:

Indo-west Pacific: Indian Ocean; Gulf of Aden, India, east to Fiji and NW to Indonesia, N Australia, Malay Arch.; China; Philippines; S Japan; Fiji Is; attached to coenosarc of gorgonians or antipatharians; littoral–453 m depth (Jones and Hosie 2016). In this study, *Conopea cymbiformis* was found at Kei Islands, Indonesia.

Type locality:
Near Madras, India; attached to a gorgonian (Darwin 1854).

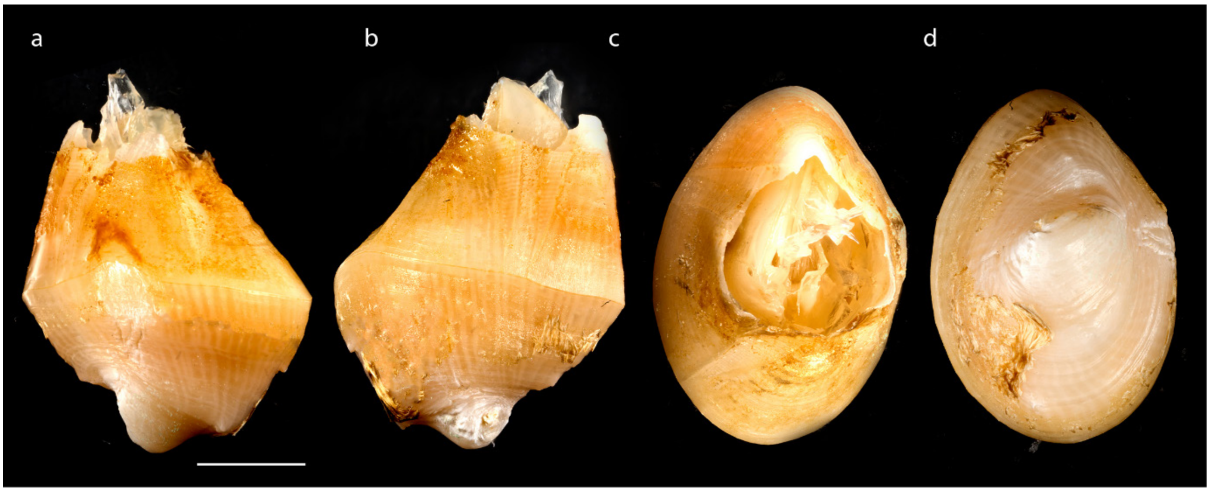

Figure 3.33. *Conopea cymbiformis* (Darwin, 1854) (MNHN-IU-2019-4823). (**a**) left lateral view, (**b**) right lateral view, (**c**) view from above, (**d**) basal view. Scale bars: a–d) 3 mm.

Conopea navicula (Darwin, 1854)
Figure 3.34

Balanus navicula Darwin, 1854: 221, pl. 3, fig. 6a–d. — Hoek 1913: 223, pl. 22, fig. 26, pl. 23, figs 1–3. — Stubbings 1936: 48. — Utinomi 1962: 74, fig 1. — Dong et al. 1982: 103.
Acasta spinitergum Foster, 1982: 209, fig. 4d.
Conopea navicula. — Newman & Ross 1976: 55.

Material examined:
- Tanimbar Island: 12 specimens, MNHN-IU-2019-4821, Stn. CP 82, 09°32'S, 131°02'E, 215–219 m depth, 4 November 1991 attached to gorgonian; 4 specimens, MNHN-IU-2019-4822, Stn. DW 49, 08°00'S, 132°59'E, 206–210 m depth, 29 October 1991, attached to gorgonian.

Diagnosis:
Shell with parietes and basis not porose; carino-lateral compartments very narrow, almost same width from top to bottom; radii with smooth sutural edges; scutum externally striated longitudinally.

Description:
Specimens covered with coenosarc of coral, except orifice. Easily recognisable species due to narrow carino-lateral plate, which is nearly same width at top as bottom; scutum externally longitudinally striated; parietal plates studded with calcareous points. Parietal plates pearly white, solid, superficially appearing to possess longitudinal tubes, growth lines horizontal. Alae moderately developed. Basis calcareous. Size small. Rostrum well developed, concave, lying at angle of ~ 45°. Laterals very well developed. Carino lateral parietes thin, radii and

alae well developed. Carina tall, about half width of rostrum. External surfaces of all parietes with very small, calcareous studs, regularly spaced, arranged along horizontal growth lines. Opercular plates sunk down into orifice. Cirrus I with unequal rami (anterior ramus: 5-segmented; posterior ramus: 7-segmented). Cirrus II with unequal rami (anterior ramus: 6-segmented; posterior ramus: 9-segmented). Cirri III–VI with subequal rami more slender, longer, with segments more elongate. Penis very long, tapering towards tip, bearing few, very minute hairs. Maxilulle with straight edge with numerous large setae. Mandibles with five teeth and inferior angle. Measurements of four specimens: basal length of shell 2.23–4.22 mm, orifice length 1.09–2.02 mm, carinal height 2.04–3.09 mm, orifice width 0.94–1.59 mm, basal width 1.79–2.80 mm.

Distribution:

Indo-west Pacific, from Gulfs of Aden and Persia, India, Malaysia, Indonesia, Gulf of Siam, to southern Japan; 45–220 m depth (Jones and Hosie 2016). In this study, *Conopea navicula* was found at Tanimbar Island, Indonesia.

Type locality:

Madras, India; attached to gorgonian (Darwin 1854).

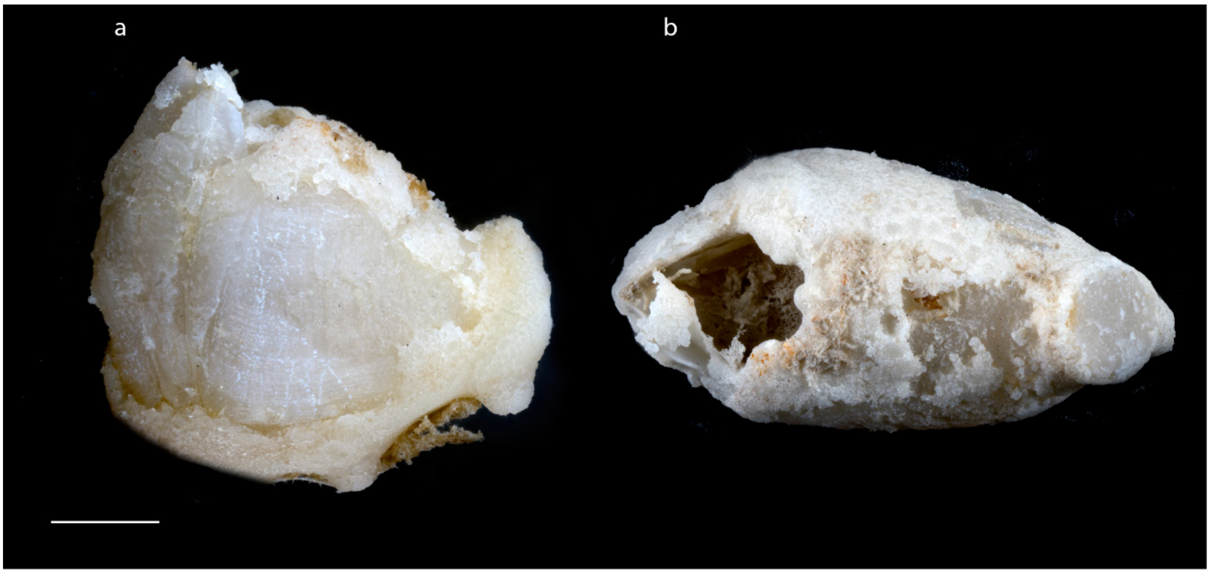

Figure 3.34. *Conopea navicula* (Darwin, 1854) (MNHN-IU-2019-4822). (**a**) left lateral view, (**b**) orifice view. Scale bars: a, b) 1 mm.

Genus *Solidobalanus* Hoek, 1913

Solido–Balanus Hoek, 1913: 159, 192.

Balanus (*Solidobalanus*). — Pilsbry 1916: 220.

Solidobalanus. — Newman & Ross 1976: 23, 50.

Diagnosis:

Shell parietes solid, six plates; radii solid, well developed, with denticulate sutural edges; basis calcareous, solid; complemental male, when present, in pit of rostral plate of hermaphrodite.

Type species:

Balanus auricoma Hoek, 1913: 198, pl. XVIII, figs 20–22, pl. XIX, figs 1–7; type locality: Ternate, Indonesia (Siboga station 136).

Subgenus *Solidobalanus* Hoek, 1913

Solido–Balanus Hoek, 1913: 159, 192.
Balanus (*Solidobalanus*). — Pilsbry 1916: 220.
Solidobalanus. — Newman & Ross 1976: 23, 50.

Diagnosis:

Parietes and radii rather thick, smooth, without pores; basis flat, calcareous; rostrum not very elongated; radii with strongly septate sutural edges; tergal spur narrow; crests for lateral depressor muscles of scutum absent; adductor ridge weak or absent; tergum flat or with shallow furrow without infolded sides; conspicuous teeth on anterior margins of fourth cirri absent.

Type species:

Balanus auricoma Hoek, 1913: 198, pl. XVIII, figs 20–22, pl. XIX, figs 1–7; type locality: Ternate, Indonesia (Siboga station 136).

Solidobalanus auricoma (Hoek, 1913)

Figure 3.35

Balanus (Solidobalanus) auricoma Hoek, 1913: 198, pl. XVIII, figs 20–22, pl. XIX, figs 1–7. — Broch 1922: 323, fig. 62. — 1931: 71. — Foster 1978: 100, fig. 60. — Rosell 1981: 303.
Solidobalanus (Solidobalanus) auricoma. — Newman & Ross 1976: 50.
Solidobalanus auricoma. — Foster 1981: 364, fig. 2G. — Rossel 1991: 38.

Material examined:

- Tanimbar Island: 2 specimens, MNHN-IU-2019-4842, Stn. CP 45, 07°54'S, 132°47'E, 302–305 m depth, 29 October 1991, shell only; 10 specimens, MNHN-IU-2019-4841, Stn. DW 49, 08°00'S, 132°59'E, 206–210 m depth, 29 October 1991, attached to sea urchin spines; 1 specimen, MNHN-IU-2019-4838, Stn. CP 82, 09°32'S, 131°02'E, 215–219 m depth, 4 November 1991, attached to antipatharian; 7 specimens, MNHN-IU-2019-4847, Stn. CP 85, 09°22'S, 131°14'E, 240–245 m depth, 4 November 1991, attached to spines of sea urchin; 63 specimens, MNHN-IU-2019-4850, Stn. CP 86, 09°26'S, 131°13'E, 223–225 m depth, 4 November 1991, attached to spines of sea-urchins.
- Kei Islands: 1 specimen, MNHN-IU-2019-4849, Stn. CP 05, 05°49'S, 132°18'E, 296–299 m depth, 22 October 1991, attached to lateral plate of Chirona tenuis; 1 specimen, MNHN-IU-2019-4844, Stn. CP 12, 05°23'S, 132°37'E, 413–436 m depth, 23 October

1991, attached to antipatharian; 6 specimens, MNHN-IU-2019-4848, Stn. CP 16, 05°17’S, 132°50’E, 330–350 m depth, 24 October 1991, attached to dead gorgonian, spines of sea-urchins, arm of crinoid; 3 specimens, MNHN-IU-2019-4840, Stn. CP 35, 06°08’S, 132°45’E, 390–502 m depth, 27 October 1991; 1 specimen, MNHN-IU-2019-4843, Stn. CP 36, 06°05’S, 132°44’E, 210–268 m depth, 27 October 1991.

Diagnosis:

Shell flatly-conical, colour reddish basally, whitish apically; radii narrow, summits slightly oblique; opercular plates with golden hairs along occludent margins; scutum with articular ridge slightly prominent, adductor ridge absent; tergum narrow, scutal margin distinctly dentated.

Description:

Shell with plates ribbed longitudinally. Shell colour brownish-pink to dull rose-pink, ribs tending to white, colour often faded with specimens appearing uniform white. Parietes of carinolatera very narrow, with single, conspicuous, longitudinal ridge. Scutum with occludent margin straight, surface indistinctly ridged, pit for adductor muscle scarcely visible. Tergum short, narrow, scutal margin straight, unusually distinctly dentated, carinal margin short, convex, depressor muscle crests moderately well developed. Opercular plates with long, golden setae fringing occludent margins, especially distally. Cirri I–II with rami slightly unequal, covered with setae; cirri III–VI longer, more slender, dense setae on inner face. Mandible with four teeth, second to fourth with accessory cusps, lower angle molariform with three blunt cusps in series, lower edge with row of stiff setae. Measurements of five specimens: basal length of shell 6.11–8.18 mm, orifice length 4.18–5.83 mm, carinal height 4.11–6.30 mm, orifice width 2.58–3.19 mm, basal width 4.51–5.96 mm.

Distribution:

Banda Sea (Moluccas, Indonesia); SW Australia; New Zealand; New Caledonia; Philippines to southern Japan; Malaysian water; Gulf of Oman, Persia. 27–502 m depth (Jones and Hosie 2016). In this study, *Solidobalanus auricoma* was found at Kei Islands and Tanimbar Island, Indonesia.

Figure 3.35. *Solidobalanus auricoma* (Hoek, 1913) (MNHN-IU-2019-4850). (**a**) upper lateral view from above, (**b**) left lateral view, (**c**) right lateral view, (**d**) basal view. Scale bars: a–d) 2 mm.

Type locality:

Ternate anchorage; 27 m depth; bottom: mud and stone; numerous specimens on the surface of pieces of rock (Hoek 1913).

Solidobalanus pseudauricoma (Broch, 1931)

Figure 3.36

Balanus (Solidobalanus) pseudauricoma Broch, 1931. — Utinomi 1949: 97, fig. 4.
Solidobalanus (Solidobalanus) pseudauricoma. — Newman & Ross 1976: 51. — Jones 2007: 294.

Material examined:

- Kei Islands: 46 specimens, MNHN-IU-2019-4818, Stn. CP 25, 05°30’S, 132°52’E, 336–346 m depth, 26 October 1991, 30 specimens attached to gorgonian, 16 specimens attached to coral; 6 specimens, MNHN-IU-2019-4825, Stn. CP 27, 05°33’S, 132°51’E, 304–314 m depth, 27 October 1991; 1 specimen, MNHN-IU-2019-4826, Stn. CP 05, 05°49’S, 132°18’E, 296–299 m depth, 22 October 1991, attached to crinoid; 13 specimens, MNHN-IU-2019-4827, Stn. CP 16, 05°17’S, 132°50’E, 330–350 m depth, 24 October 1991; 2 specimens, MNHN-IU-2019-4828, Stn. DW 22, 05°22’S, 133°01’E, 82 m depth, 25 October 1991, 1 specimen attached to gorgonian stem; 8 specimens, MNHN-IU-2019-4830, Stn. CP 05, 05°49’S, 132°18’E, 296–299 m depth, 22 October 1991, 5 specimens attached to gorgonian, 1 specimen attached to crinoid.
- Tanimbar Island: 11 specimens, MNHN-IU-2019-4839, Stn. CP 86, 09°26’S, 131°13’E, 223–225 m depth, 4 November 1991, several specimens attached to spines of sea urchins (associated with Solidobalanus auricoma (Hoek, 1913)).

Diagnosis:

Shell with smooth, glossy white plates, coloured stripes absent; internal plates with thick, solid, finely ribbed longitudinally; base non-porous, radially ribbed.

Description:

Shell plates white, stripes absent. Several specimens with pale pink tinge, one with pale brownish-pink parietes with small, narrow ellipsoidal whitish spots, latter orientated longitudinally producing reticulated effect. Radii whitish, pink tinge along distal borders. Scutal growth lines without longitudinal striations; articular ridge absent; pit for adductor muscle small, round. Tergum with shallow, wide furrow running from apex to base. Cirrus I with unequal (anterior ramus: 7-segmented; posterior ramus: 15-segmented). Cirrus II with rami subequal (anterior ramus: 11-segmented; posterior ramus: 12-segmented). Cirri I and II with very dense, long setae on surface areas. Cirri III–VI with rami slightly subequal, rounded. Penis sturdy, not long. Labrum with very shallow notch, three or four irregularly arranged, blunt teeth on each side. Maxillule with distinct, narrow notch with two large setae on upper side. Mandibles with five teeth, second and third bifid and fifth is rudimentary. Measurements of five specimens: basal length of shell 6.23–12.08 mm, orifice length 4.63–9.62 mm, carinal height 3.48–13.22 mm, orifice width 3.24–6.33 mm, basal width 5.66–9.56 mm.

Distribution:

Manado Bay (Indonesia); Japan (Broch 1931–1932). In this study, *Solidobalanus pseudauricoma* was found at Kei Islands and Tanimbar Island, Indonesia.

Type locality:

Manado Bay, Indonesia (1°31'N, 124°47'E), 500 m depth; Japan (32°25'N, 128°33'E), 400 m depth (Broch 1931–1932).

Remarks:

In the type description, Broch (1931–1932) commented that the specimens were white, without stripes. However, several of the specimens collected by KARUBAR had a pale pink tinge and one specimen (from station DW22) had pale brownish-pink parietes with small, narrow ellipsoidal whitish spots, the latter orientated longitudinally, thus producing a reticulated effect. Radii whitish with pink tinge along distal borders.

Figure 3.36. *Solidobalanus pseudauricoma* (Broch, 1931) (MNHN-IU-2019-4818). (**a**) left lateral view, (**b**) orifice view, (**c**) basal view, (**d**) right lateral view. Scale bars: a–d) 4 mm.

Genus *Striatobalanus* Hoek, 1913

Balanus Section F (part.) Darwin, 1854: 277.
Chirona Gray, 1825: 37. — Pilsbry 1916: 204.
Balanus (*Striato-Balanus*) Hoek, 1913: 159, 179.
Chirona (*Striatobalanus*). — Newman & Ross 1976: 23, 50 (as subgenus).
Striatobalanus. — Jones 2004: 150.

Diagnosis:

Parietes and radii without pores; radii usually narrow; scutum striated longitudinally with adductor ridge; tergum furrow deep; cirrus I with rami very unequal in length.

Type species:

Balanus amaryllis var. (a), var. (b) Darwin, 1854: 279, pl. 7, figs 6a–c.

Type locality:

Unknown.

Striatobalanus amaryllis (Darwin, 1854)

Figure 3.37

Balanus amaryllis var. (a), var. (b) Darwin, 1854: 279, pl. 7, fig. 6a–c. — Hoek 1913: 179, pl. 15, figs 17–21, pl. 16, figs 1–4. — Pilsbry 1916: 217. — Nilsson-Cantell 1925: 329. — Hiro 1936: 624. — 1939c: 243. — Stubbings 1936: 174. — Utinomi 1962: 216. — 1969: 88.

Balanus amaryllis dissimilis Lanchester, 1902: 369, pl. XXXIV, fig. 3–3C, with var. *clarovittata* Lanchester, 1902: 370.

Balanus amaryllis var. *a* (= *Balanus roseus* Lamarck, 1818). — Gruvel 1905: 250, with var. *b* (*niveus*). — Gruvel, 1905: 250 (= *Balanus amaryllis* var. *b* Darwin, 1854: 279)).

Balanus (*Chirona*) *amaryllis.* — Nilsson-Cantell 1921: 329, pl. 3, fig. 9. — Rosell 1981: 302.

Balanus amaryllis forma *euamaryllis.* — Broch, 1922: 321.

Balanus amaryllis forma *laevis* Broch, 1931: 67, fig. 24.

Balanus sp. Dong & Mao, 1956: 290, fig. 8.

Chirona (*Striatobalanus*) *amaryllis.* — Newman & Ross 1976: 50.

Chirona amaryllis. — Foster 1981: 350.

Balanus amaryllis. — Dong et al. 1982: 95.

Balanus amaryllis euamaryllis Dong et al. 1982: 96, figs A–C.

Chirona amaryllis: Zevina et al. 1992: 72, fig. 49.

Striatobalanus amaryllis. — Jones 2004: 150. — Chan et al. 2009b: 222, 190–192.

Material examined:

- Tanimbar Island: 1 specimen (only shell), MNHN-IU-2019-4814, Stn. CP 65, 09°14’S, 132°27’E, 174–176 m depth, 1 November 1991, attached to broken sea urchin shell.

Diagnosis:

Shell conical; orifice large, pentagonal, toothed; shell colour pinkish, lighter transparent stripes run longitudinally over surface; radii very narrow, reddish, upper margins very oblique; alae broader, lighter colour.

Description:

Shell conical; tips of rostrum and carina slightly curved inwards. Orifice large, pentagonal, toothed. Colour yellowish-white, with slightly darker longitudinal lines on main parts of plates. Radii with very oblique summits, broadest a little distance from the orifice, narrower towards basis. Alae broader than radii, summits rounded. Specimen without scutum, tergum and soft parts. Measurements of specimen: basal length of shell 16.76 mm, orifice length 9.13 mm, carinal height 9.89 mm, orifice width 7.24 mm, basal width 15.14 mm.

Distribution:

Arafura Sea, Indonesia. Indo-west Pacific: South and East Africa, Indian Ocean; Australia (N); Singapore; Malay Arch.; Cambodia; Gulf of Thailand; Mouth of Bassac; Vietnam (Bay of Nhatrang; Lien Chien, Tourane; Codor Is); Hong Kong; S China Sea; China; Philippines; Taiwan; Japan (S); attached to rocks, gastropod shells, rusting iron, fouling species; sublittoral, 5–500 m depth (Jones and Hosie 2016). In this study, *Striatobalanus amaryllis* was found at Tanimbar Island, Indonesia.

Type locality:

Unknown.

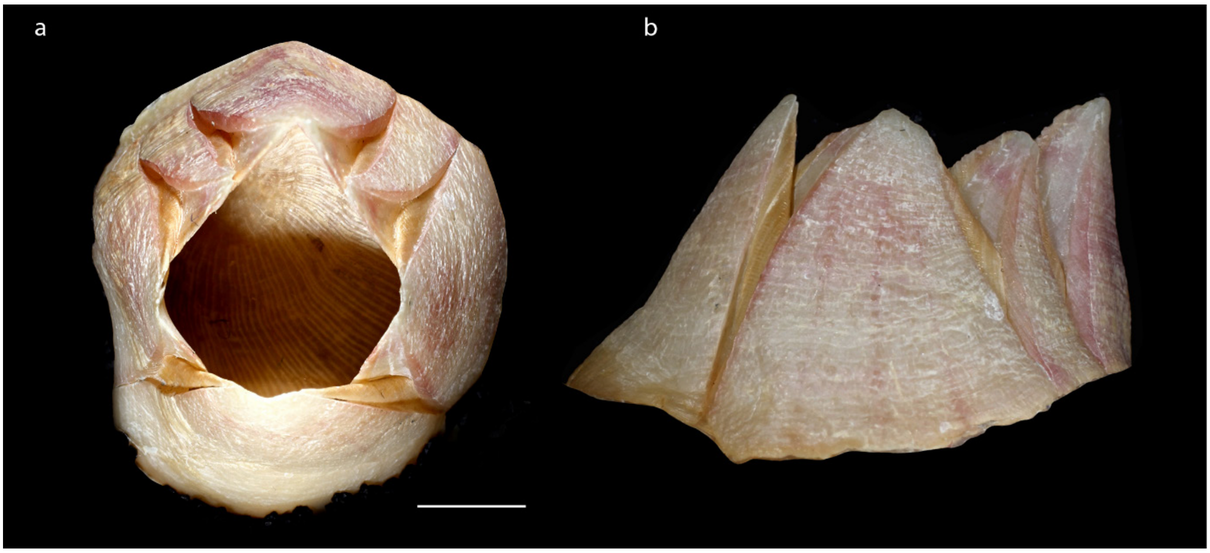

Figure 3.37. *Striatobalanus amaryllis* (Darwin, 1854) (MNHN-IU-2019-4814). (**a**) orifice view, (**b**) right lateral view. Scale bars: a, b) 3 mm.

Striatobalanus tenuis (Hoek, 1883)

Figure 3.38

Balanus tenuis Hoek, 1883: 154, pl. 13, figs 29–33. — 1913: 190, pl. 17, figs 14–19, pl. 18, fig. 1. — Gruvel 1905: 247, fig. 275. — Pilsbry 1916: 216. — Barnard 1924: 74. — Nilsson-Cantell 1925: 34, fig. 13, pl. 1, figs 5–6. — 1927: 785. — 1938: 46. — Broch 1931: 70. — Hiro 1937b: 439, fig. 24. — Utinomi 1962: 216. — 1968: 174. — 1969: 88, fig. 6. — Utinomi & Kikuchi 1966: 6.

Balanus albus Hoek, 1913: 185, pl. 16, figs 12–13, pl. 17, figs 1–6. — Stubbings 1936: 41, fig. 18.

Chirona (Striatobalanus) tenuis. — Newman & Ross 1976: 50. — Rosell 1989: 33, pl. 10g. — 1991: 38.

Balanus (*Chirona*) *tenuis.* — Ren & Liu 1978: 161, fig. 22, pl. 7, figs 6–10. — Nilsson-Cantell 1921: 302.

Balanus tenuis. — Dong et al. 1982: 97, fig. A–C.

Chirona tenuis. — Zevina et al. 1992: 74, fig. 50.

Striatobalanus tenuis. — Jones 2004: 152. — Liu & Ren 2007: 363, fig. 161. — Chan 2009: 74, fig. 2H and fig. 23A–G.

Material examined:

- Kei Islands: 5 specimens, MNHN-IU-2019-4820, Stn. CC 10, 05°21′S, 132°30′E, 329–389 m depth, 23 October 1991; 1 specimen (shell only), MNHN-IU-2019-4835, Stn. CP 16, 05°17′S, 132°50′E, 330–350 m depth, 24 October 1991.
- Tanimbar Island: 1 specimen, MNHN-IU-2019-4832, Stn. DW 49, 08°00′S, 132°59′E, 206–2010 m depth, 29 October 1991; 1 specimen (shell only), MNHN-IU-2019-4833, Stn. CP 65, 09°14′S, 132°27′E, 174–176 m depth, 1 November 1991; 4 specimens (shell only), MNHN-IU-2019-4834, Stn. CP 79, 09°16′S, 131°22′E, 239–250 m, 3 November 1991; 1 specimen (only shell), MNHN-IU-2019-4813, Stn. CP 85, 09°22′S, 131°14′E, 240–245 m, 4 November 1991, attached to shell of gastropod; 2 specimens, MNHN-IU-2019-4819, Stn. CP 86, 09°26′S, 131°13′E, 223–225 m depth, 4 November 1991, attached to gastropod shells.

Diagnosis:

Shell colour whitish to yellowish; surface smooth, glossy; orifice pentagonal shaped, deeply toothed; radii narrow, summits very oblique, slightly concave; basis solid; scutum with longitudinal striations; tergum with short, rather broad spur.

Description:

Shell with six plates, conical; orifice large, distinctly toothed; radii well-developed; basis thin, ribbed, solid. Scutum triangular, not elongated, with longitudinal striations; tergum slightly beaked, exhibiting traces of longitudinal striations, spur short, slightly narrow, depressor crests distinctly developed. Cirri I to VI with rami slightly equal in length, transparent and orange-coloured. Penis rather long, sparse, minute hairs on the surface, tapering towards tip, distinctly hairy at tip. Maxillule with edge slightly straight, all the setae similar sized. Mandibles with five teeth, fourth and fifth small. Measurements of five specimens basal length of shell 18.92–28.30 mm, orifice length 13.78–16.29 mm, carinal height 18.02–20.24 mm, orifice width 10.15–13.70 mm, basal width 20.51–28.03 mm.

Distribution:

Arafura Sea, Indonesia; Indo-west Pacific: S Africa; Persian Gulf; Indian Ocean; Australia (N); Singapore; Malay Arch.; Vietnam; Hong Kong; S China Sea; E China Sea; Philippines; Taiwan; Japan (S); W Pacific; attached to crabs, gastropod, bivalve, shells solitary coral, bark of coconut, gorgonians, antipatharians, stones; 7–551 m depth (Jones and Hosie 2016). In this study, *Striatobalanus tenuis* was found at Kei Islands and Tanimbar Island, Indonesia.

Type locality:

West of Mindoro, Philippines; 6°8'N, 121°19'E; depth: 275 m, at coral-bottom (Hoek 1913).

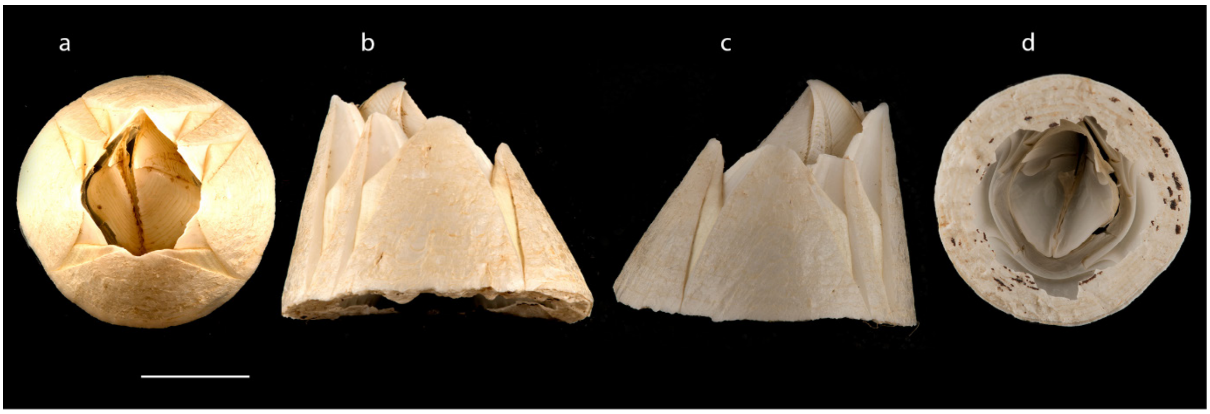

Figure 3.38. *Striatobalanus tenuis* (Hoek, 1883) (MNHN-IU-2019-4820). (**a**) orifice view, (**b**) left lateral view, (**c**) right lateral view, (**d**) basal view. Scale bars: a–d) 10 mm.

Family Pyrgomatidae Gray, 1825

Balanidae Leach, 1817: 68 (part.). — Darwin 1854: 33 (part.).

Balaninae. — Nilsson-Cantell 1921: 306 (part.).

Pyrgomatidae Gray, 1825: 102. — Newman 1996: 503.

Pyrgomatinae. — Ross & Newman 1973: 149.

Diagnosis:

Wall of four plates wholly concrescent; parietes solid or tubiferous; when tubiferous, tubes occur between outer lamina and sheath or between external ribs of wall; interlaminate figures complex, essentially arborescent; radii solid; basis calcareous, rarely tubiferous, membranous in *Pyrgopsella*.

Subfamily Megatrematinae Holthuis, 1982

Bosciinae Newman & Ross, 1976: 59.

Megatrematinae Holthuis, 1982: 319.

Diagnosis:

Wall of four plates wholly concrescent; opercular valves normal; tergum with weakly developed lateral depressor muscle crests or crests lacking; when shell concrescent, sheath with paired sulci.

Type genus:

Megatrema Sowerby, 1823, by original designation (Holthuis 1982).

Tribe Pyrgomini Ross & Pitombo, 2002

Pyrgominini Ross & Pitombo, 2002: 58.

Type genus:

Pyrgomina Baluk & Radwanski, 1967.

Genus *Pyrgomina* Baluk and Radwanski, 1967

Pyrgomina Baluk and Radwanski, 1967b: 691, pl. 1–2.

Type species:

Pyrgomina seguenzai Baluk and Radwanski, 1967a: 485.

Type locality:

Pliocene (Piacenzian Stage); Gournes, Iraklion nomarchia, Island of Crete, Greece, 35°06’N, 25°47’E; host coral unknown (Ross and Pitombo 2002).

Pyrgomina sp.

Figure 3.39

Material examined:

- Tanimbar Island: 1 specimen, MNHN-IU-2019-4817, Stn. CP 86, 09°26’S, 131°13’E, 223–225 m depth, 4 November 1991, attached to coral.

Diagnosis:

Shell purple-pinkish, tall, conical; oriface oval; base permeated by pores, expanded out of the coral; tergum and scutum subtriangular.

Description:

Shell stands exserted on the coral, externally furnished with ribs, lower part rounded with radiating ribs; oriface oval, small and narrow. Scutum triangular, basal margin curved; tergum triangular with narrow spur. Cirrus I with rami unequal (anterior ramus: 10-segmented; posterior ramus: 15-segmented); posterior ramus of cirrus IV without spines. Maxilla globular; maxillule not notched, eight large setae on straight cutting edge; mandible with five major teeth. Measurements of specimen: basal length of shell 7.46 mm, orifice length 2.42 mm, carinal height 10.45 mm, orifice width 1.41 mm, basal width 6.15 mm.

Distribution:

Pyrgomina sp. was found at Tanimbar Island, Indonesia.

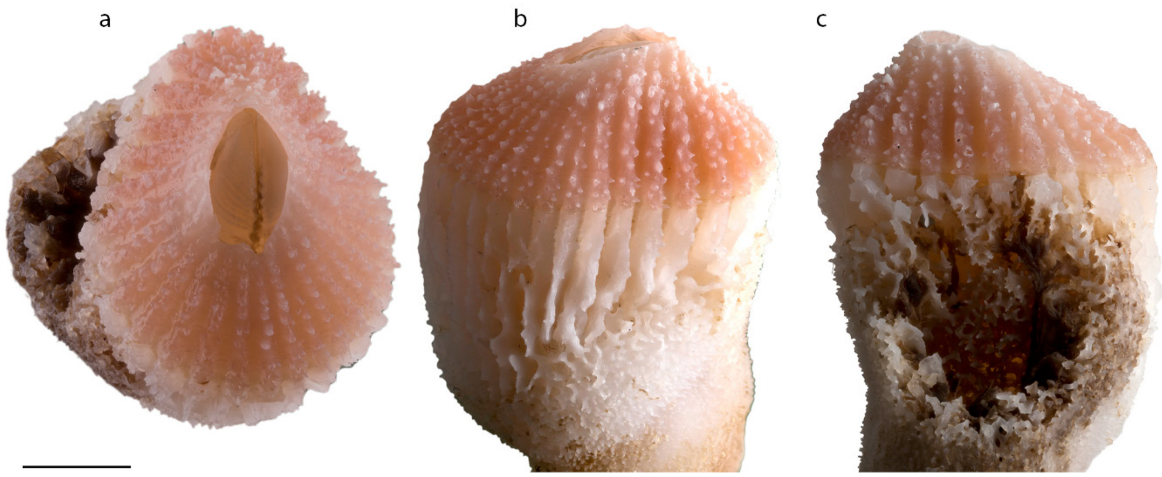

Figure 3.39. *Pyrgomina* sp. (MNHN-UI-2019-4817). (**a**) orifice view, (**b**) left lateral view, (**c**) right lateral view. Scale bars: a–c) 2 mm.

Family Balanidae Leach, 1817

Balanidae Leach, 1817: 68. — Gray 1825: 104. — Darwin 1854: 33 (part.). — Pilsbry 1916: 48. — Nilsson-Cantel 1921: 306. — Newman & Ross, 1976: 59. — Foster 1978: 95. — Buckeridge 1983: 103. — Newman 1996: 503. — Pitombo 2004: 262. — Chan et al. 2009b: 229.

Diagnosis:

Shell with four or six plates; parietes tubiferous; tubes arranged in single uniform row formed between inner and outer lamina, supplementary tubes may form basally; interlaminate figures complex, arborescent; radii solid or tubiferous, more-or-less developed; basis calcareous, commonly tubiferous; caudal appendages absent; penis commonly with basidorsal point.

Subfamily Amphibalaninae Pitombo, 2004

Amphibalaninae Pitombo, 2004: 263.

Diagnosis:

Shell with four or six plates; parietal tubes with one or more rows, commonly transverse septa; radii with transverse teeth on sutural edge with denticles on lower side only; alae not cleft; basis with single tubiferous; scutum with conspicuous adductor ridge; tergum with well-developed depressor muscle crests, growth lines in tergum spur display an obvious change in direction; second maxilla with smooth anterior margin of distal lobe, acuminate setae with enlarged, modified tips.

Genus *Amphibalanus* Pitombo, 2004

Amphibalanus Pitombo, 2004: 263.

Diagnosis:

Shell with four or six plates; parietal tubes with one or more rows, commonly transverse septa; radii with transverse teeth on sutural edge, with denticles on lower side only; alae not cleft; basis with single tubiferous; scutum with conspicuous adductor ridge; tergum with well-developed depressor muscle crests, growth lines in tergum spur display an obvious change in direction; second maxilla with smooth anterior margin of distal lobe, acuminate setae with enlarged, modified tips. Cirrus III with inner face of endopod with pinnate setae, rarely bifurcate (complex) setae.

Type species:

Balanus amphitrite Darwin, 1854: 240 (part.), pl. 5, figs 2a–d, i–k, m–o; type locality: Natal, South Africa.

Amphibalanus amphitrite (Darwin, 1854)

Figure 3.40

Balanus amphitrite Darwin, 1854: 240 (part.), pl. 5, figs 2a-d, i-k, m-o. — Weltner 1897: 264. — Hoek 1913: 167. — Pilsbry 1916: 89. — Zevina et al. 1992: 89, fig. 61. — Puspasari et al. 2001: 7.
Balanus amphitrite var. (1) *communis* Darwin, 1854: 240, pl. 5, fig. 2e, h, l.
Balanus amphitrite communis. — Nilsson-Cantell 1921: 311, fig. 64.
Balanus amphitrite forma *hawaiiensis* Broch, 1922: 314, fig. 56 (part.).
Balanus amphitrite forma *denticulata* Broch, 1927b: 133, fig. 14 (part.).
Balanus amphitrite hawaiiensis. — Hiro 1937c: 432, figs 20, 21.
Balanus amphitrite cochinensis Nilsson-Cantell, 1938b: 43, fig. 11a–e.
Balanus amphitrite var. *fluminensis* Oliveira, 1941: 21, pl. 4, fig. 4, pl. 5, figs 1, 2, pl. 8, figs 1–5.
Balanus amphitrite var. *aeratus* Oliveira, 1941: 22, pl. 4, fig. 5, pl. 9, figs 1–4.
Balanus amphitrite herzi Rogers, 1949: 28, pl. 1, figs 6, 12–15.
Balanus amphitrite franciscanus Rogers, 1949: 29, pl. 1, figs 5, 7, 16–19.
Balanus amphitrite var. *columnarius* Tarasov & Zevina, 1957: 179, 184, fig. 68 a–e.
Balanus amphitrite denticulata Henry, 1959: 192, pl. 1, fig. 5, pl. 3, fig. 7, upper row right.
Balanus amphitrite amphitrite. — Harding 1962: 274, pl. 1a–g, pl. 2a–k. — Dong et al. 1982: 90, fig. A-E. — Rosell 1981: 302.
Balanus amphitrite var. *Hawaiiensis.* — Stubbings 1963b: 15.
Amphibalanus amphitrite. — Pitombo 2004: 263, 274, figs 2A, B, 7A, B, 8C. — Chan et al. 2009b: 241. — Chen et al. 2014: 1071. — Pochai et al. 2017: 27, fig. 9. — Pitriana et al. 2020a: 42, fig. 21.

Material examined:

- Tanimbar Island: 4 specimens, MNHN-IU-2019-4815, Stn. CP 52, 08°03’S, 131°48’E, 1244–1266 m depth, 30 October 1991.

Diagnosis:

Primary parietal tubes with transverse septa; exterior of shell with longitudinal purple striations, horizontal striations absent; tergum short with wide spur; cirri III–VI with erect teeth below posterior angles of distal; cirrus III without complex setae.

Description:

Shell six-plated, conical, round; externally smooth, white with groups of well-spaced, dark purple vertical stripes; horizontal striations on shell surface absent. Interior of paries with single row of tubes; radii solid, wide; alae with summits moderately oblique; basis porose, calcareous. Scutum externally striped, occludent margin toothed, lateral depressor muscle pit small. Tergum with spur wider than long, less than its own width from basi-scutal angle. Cirrus I with unequal rami (anterior ramus: 10-segmented; posterior ramus: 16-segmented). Cirrus II with slightly equal rami (anterior ramus: 10-segemented; posterior ramus: 12-segmented). Cirrus III with rami subequal (anterior ramus: 12-segmented; posterior ramus: 13-segmented. Cirri IV–VI with rami subequal, longer, more slender. Penis moderately long, tapering distally, sparse, minute hairs on surface, distinctly hairy distally. Labrum deeply notched, numerous teeth on each side. Maxilla without notch below upper pair of spines, nine spines between upper and lower pairs, few short spines on inferior angle; lower pair of spines usually on slight prominence, which may be sometimes moderately strong or strong. Mandible with five teeth, inferior angle with second tooth bifid. Measurements of four specimens: basal length of shell 5.27–12.10 mm, orifice length 3.81–7.89 mm, carinal height 3.64–5.65 mm, orifice width 2.72–5.22 mm, basal width 4.62–12.03 mm.

Distribution:

Cosmopolitan in tropical and subtropical waters. Bermuda & SE USA to Brazil; England and West Europe to South coast of Africa Red, Black and Mediterranean Seas; Suez Canal; SE Africa; Indian Ocean; Australia; Singapore; Malaysia; Réam (Cambodia); Gulf of Siam; Vietnam; Condor Island; Tang Trien (South Annam); Cauda Nhatrang; Hongay, Tonkin; S China Sea; Hong Kong; China; Bohai Sea; Taiwan; Philippines; Japan; South Honsyu, Kyusyu & Ryukyu Island; Vladivostok; Hawaii; central California to SW Mexico; fouling species; lower littoral to sublittoral (Jones and Hosie 2016). Recently, also recorded from Ambon Island and Saparua Island, Indonesia (Pitriana et al. 2020a). In this study, *Amphibalanus amphitrite* was found at Tanimbar Island, Indonesia.

Type Locality:

Natal, on a piece of bamboo (Darwin 1854).

Remarks:

Known as an important fouling species of ships and marine installations. The suggestion of anti-fouling paint on the bases of the specimens examined suggests that these specimens were probably knocked off the ship during trawling operations, explaining the great depth at which these specimens were collected, as the normal depth range is 0–9 m.

Figure 3.40. *Amphibalanus amphitrite* (Darwin, 1854) (MNHN-IU-2019-4815). (**a**) orifice view, (**b**) right lateral view, (**c**) basal view. Scale bars: a–c) 4 mm.

3.5 Discussion

Prior to the *Karubar* expedition, 24 species of barnacles had been collected from the Kei Islands and Aru Island by the *Siboga* expedition (Hoek 1913). Other pertinent reference works to the barnacles from these islands are Jones et al. (2001) and Jones and Hosie (2016), who recorded 15 species from the Kei Islands and Aru Island.

In addition to the works of Hoek (1913), Jones et al. (2001) and Jones and Hosie (2016), Broch (1931–1932) reported on 67 species of barnacles collected by the Danish expedition to the Kei Islands (1922) and deposited in the Zoological Museum of Copenhagen University. In his report, only four species, *Euscalpellum rostratum* (Darwin, 1851), *Lepas (Anatifa) anatifera* Linnaeus, 1758, *Conchoderma virgatum* Spengler, 1789 and *Acasta dentifer* (Broch, 1922), were explicitly collected in the Kei Islands. The other barnacle species recorded were collected at other places along the route of this expedition, such as Lampung Bay, Krakatau, Java Sea, Sunda Strait, Makassar Strait, Tual, Banda Neira, Ambon and Saparua Bay.

The lists of Hoek (1913), Broch (1931–1932), Jones et al. (2001) and Jones and Hosie (2016) record a total of 25 species from the Kei Islands, Aru Island and Tanimbar Island. The results currently recorded herein reveal that 40 species are now recorded from these Islands.

Of the 40 species herein, ten are recorded in previous studies: *Megalasma striatum* Hoek, 1883 (listed in Hoek (1913)); *Scalpellum stearnsi* Pilsbry, 1890 (listed in Hoek (1913)); *Annandaleum japonicum* (Hoek, 1883) (listed in Hoek (1913)); *Annandaleum laccadivicum* (Annandale, 1906) (listed in Hoek (1913)); *Regioscalpellum moluccanum* (Hoek, 1883) (listed in Hoek (1913)); *Altiverruca navicula* (Hoek, 1913) (listed in Hoek (1913) and Buckeridge (1994)); *Newmaniverruca albatrossiana* (Pilsbry, 1912) (listed in Hoek (1913) and Buckeridge (1994)); *Hexelasma arafurae* Hoek, 1913 (listed in Hoek (1913) and Jones & Hosie (2016)); *Solidobalanus auricoma* (Hoek, 1913) (listed in Hoek (1913) and Jones et al. (2001)); *Striatobalanus tenuis* (Hoek, 1883) (listed in Hoek (1913) and Jones and Hosie (2016)).The remaining 30 species can, therefore, be considered as new records for the Kei Islands and Tanimbar Island.

The present study and previous works on the barnacles of the Kei Islands, Aru Island and Tanimbar Island, especially the works of Hoek (1883, 1907, 1913), Broch (1922, 1931–1932), Buckeridge (1994, 1997), Jones et al. (2001) and Jones and Hosie (2016), enrich our knowledge of the barnacle fauna of these islands. This study demonstrates once more the value of museum collections as a resource in biodiversity science.

The result of this study also strengthens the statement of Hoeksema (2007) that the Indo-Malayan region (which extends from East Indonesia to the Philippines and the Solomon Islands) is a centre of maximum marine biodiversity. Darwin (1854) demonstrated that this area had greater species richness than elsewhere in the world at the time. He named it the East Indian Archipelago (including the Philippines, Borneo, New Guinea, Sumatra, Java, Malacca and the eastern coast of India) and categorised it as his third province of barnacles. In this province, he found 37 barnacle species, the largest number known at that time, compared with the other provinces.

Regarding the biodiversity of barnacles, the Indo-Malayan region as the centre of benthic biodiversity has not been replaced by other areas. In recent times, many studies and expeditions have been conducted in this area, revealing many more species of barnacles. For example, three expeditions have been undertaken within Philippine waters from 1976 until 1985 through MUSORSTOM Cruises and the collections the U.P. Marine Biological Laboratory at Puerto Galera, Oriental Mindoro (Rosell 1991; Chan 2009). Overall, the three of scientific cruises of MUSORSTOM collected 78 species of barnacles, 43 of which are new records and 12 species are new to science (Rosell 1991). Through the Philippine Panglao expedition (2005), Chan (2009) has also increased the number of barnacles from the Philippines, reporting 20 barnacle species with two new to science.

Similar to the Philippine waters, eastern Indonesian waters also have a high diversity of barnacles. Recently, it has been revealed that the Moluccan Islands in eastern Indonesia have 97 species of barnacles, 23 of which are new records and two species are still awaiting their species descriptions (Pitriana et al. 2020a). Furthermore, this number will increase with the results of the study of the barnacles from Karubar expedition (1991) that have revealed 40 species of barnacles.

The results of the studies of barnacles from the Philippines and eastern Indonesian waters reconfirm the Indo-Malayan region as the epicentre of marine biodiversity.

3.6 Acknowledgements

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CHAPTER 4

Exploring sponge-inhabiting barnacles of eastern Indonesia using micro-CT scanning

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4.1 Abstract

We present a morphological study of Indonesian sponge-inhabiting barnacles using standard light microscopy in combination with micro-CT scanning and computer-aided 3D-reconstruction of the external shell morphology. A taxonomic analysis of the material detected four different genera of sponges inhabited by five different species of balanomorph barnacles, two of which are undescribed. Together with conventional morphological examination by dissection, we provide modern non-destructive imaging methods, using micro-CT scanning to enhance our knowledge of the morphological characters of sponge-inhabiting barnacles from eastern Indonesia. Although there were some methodological limitations regarding the contrast-enhancing technique, this study demonstrates micro-CT as a useful non-destructive technique of integrative taxonomy, for the examination of sponge-inhabiting barnacles.

4.2 Introduction

Barnacles (Cirripedia) are sessile crustaceans where the adult forms are structurally and biologically diverse, and permanently attached to hard substrata or to other living organisms (Newman & Abbott, 1980; Høeg et al*.,* 2015). It comprises three orders, the Thoracica or 'true barnacles' (including Sessilia and Pedunculata), the Acrothoracica (burrowing barnacles), and the Rhizocephala (parasitic barnacles) (Høeg et al*.,* 2015). Some members of the suborder Balanomorpha selectively choose invertebrates or vertebrates as their hosts, ranging from sponges to whales (Foster, 1978). Many epizoic barnacles burrow into, or are overgrown, by the host's tissue (Anderson, 1994). Members of subfamily Acastinae and genus *Membranobalanus* are examples of epibiotic barnacles. Acastinae are obligate symbionts of Porifera and Cnidaria, but also be found in association with gorgonians, alcyonarians, or antipatharians; while *Membranobalanus* are obligate symbiont of Porifera (Kolbasov, 1993; Van Syoc et al*.,* 2015; Yu et al*.,* 2017).

Most species of Acastinae have spines or projections of various lengths on the external surface of the parietes, penetrating as anchors into the sponge tissue (Kolbasov, 1993). In addition, according to Van Syoc et al. (2015) the Acastinae with membranous bases may often be distinguished from *Membranobalanus* spp. by the presence of these calcareous projections on the shell wall. These calcareous projections can be used to differentiate members of the Acastinae and *Membranobalanus*. However, the spines often break away from the shell wall when specimens are removed from their host sponge, leaving only “pores” in the shell wall marking the site of attachment (Van Syoc et al., 2015).

The Acastinae of eastern Indonesia have been studied by Hoek (1913) and Broch (1931–1932) and both noted calcareous projections on the surface of the shell wall. For *Acasta conica,* Hoek (1913: 235) stated “the surface of the parietes is smooth in the lower half, covered in the upper half with rounded scale-like patches, the exact nature of which I have not been able to discover”, and likewise Broch (1931–1932: 98) for *Acasta foraminifera*, “the white shell is anchored in the sponge tissue by rather large spines; it is, however, almost absolutely impossible to prepare away the tissue of the sponge without removing also every such spine, so intimate is the connection with the extremely hard tissue of the sponge”.

Modern non-destructive imaging methods, such as X-ray micro-computed tomography (micro-CT), are particularly well suited to overcome the problems of traditional challenges associated with the size and fragility of small invertebrates (Faulwetter et al., 2013; Semple et al., 2018). Studies on invertebrates utilising 3D-imaging tools now encompass a wide range of applications, including for comparative, developmental and functional morphological research (Metscher, 2009a; Semple et al., 2018). However, the widespread application of micro-CT imaging has only been used in a few studies of barnacles to date. For example, Noever et al. (2015) studied the rhizocephalan root system of parasitic barnacles in their crusteacan host. Hosie et al. (2019) described a new species of sponge-inhabiting barnacle (*Membranobalanus porphyrophilus*) from Australia and presented an interactive, 3D micro-CT derived volume reconstruction of the designated holotype.

In this study, we present the use of micro-CT scanning and 3D reconstruction as a non-destructive method to visualize and count sponge-inhabiting barnacles inside their host. Secondly, we provide a conventional morphological study of the same barnacle specimens extracted from their host, using light microscopy. Our aim is to demonstrate the potentials use of micro-CT imaging in barnacle research, and to develop an approach for a practicable combination of different morphological techniques.

4.3 Material and Methods

4.3.1 Material

Sponge and barnacle specimens examined in this study were collected by the first author between April 2016 and September 2017 at Saparua Island and South East Sulawesi, Indonesia (Table 1). All sponges were photographed using a digital camera (DSLR Nikon D200).

Specimens were then fixed and stored in 96% ethanol and transferred into 75% ethanol for long-term preservation. In total, 14 lots containing four genera of sponge inhabiting barnacles were collected from seven localities.

4.3.2 Specimen preparation, micro-CT, and 3D reconstruction

Specimen preparation

To prepare the samples for micro-CT scanning, sponge specimens were removed from the ethanol and put into dry containers. To avoid movement, the sponges were held in place using cotton. The cotton was soaked in a small amount of ethanol to prevent specimens from drying and thereby shrinkage, which can occur if wet objects are left in a dry environment for a certain amount of time (Metscher, 2009b; Buytaert et al., 2014).

Staining method to enhanced micro-CT imaging of soft body of barnacles

We used Lugol's solution (one part iodine and two parts potassium iodide in an aqueous solution) to stain the soft body of barnacle specimens. To produce a concentration of 0.3%, 0.1% (w/v) iodine and 0.2% (w/v) potassium iodide were dissolved in double-distilled water (Heimel et al., 2019). To scan the soft body, one barnacle for each species was removed from the host sponge. Barnacle specimens were soaked in Lugol's solution for seven days. After seven days, the barnacles were thoroughly rinsed in tap water and put into a dry tube for the scanning process.

Micro computer tomography (micro-CT)

Complete sponge specimens (one sponge for each species) were scanned using X-ray imaging at the Museum für Naturkunde Berlin, Germany, with the Scanner FF35 (Yxlon, Hamburg). Raw files were produced with the help of the software VGStudio Max (Volume Graphics, Heidelberg, Germany). Scanning occurred with the following parameters: 80 kV, 15 W, 16 µm voxel size, 2000 projections/turn helical CT.

3D reconstruction of barnacles inside the sponges

The software Amira 6.0.0 was used for the 3D reconstruction of the raw files. After creating a new project, the raw files were imported into the workspace. To visualize the dataset, the "Volren" tool was applied, which is a volume renderer. In the segmentation mode, the magic wand tool was used to segment the barnacles located inside the sponges. Subsequently, every segmented barnacle was assigned a different "label", making it possible to differentiate between single barnacles by assigning different colours to individual labels. Switching back to project mode and using the "Volren" volume renderer, the opacity of the surrounding medium was adjusted, so that the barnacles are clearly visible. For better visualization purposes, "Specular" was used for shading and the "Ortho" tool was applied to crop the volume and remove part of the plastic container and surrounding matrix.

4.3.3 Specimen direct morphological examination

After specimens were scanned using micro-CT, one to three barnacle specimens were removed from each sponge. Based on the overview scans showing all barnacle specimens situated in each sponge, we could estimate which parts of the sponge to dissect to obtain a specific barnacle specimen. Morphological characters of the hard body parts (parietes and opercular plates) and soft body parts (mouthparts, six pairs of cirri, and penis) were examined as in Pitriana et al. (2020a). Species were identified based on Lamarck (1818), Darwin (1854), Krüger (1911), Hoek (1913), Broch (1931), Rosell (1991), and Kolbasov (1993).

Hard body parts were separated from soft body parts using a scalpel. Shell plates were separated and cleaned with a bleach solution to remove any organic material, rinsed with fresh water, dried and observed under a stereo microscope (Leica M125) and photographed with a digital camera (Leica Microsystems M205C).

Mouthparts (labrum, palps, maxillae, maxillules, and mandible) were dissected using a scalpel, each was mounted on a glass slide and examined under a light microscope (Carl Zeiss Axioskop 20). The cirri were separated into couples of cirri I-VI and the penis, before being mounted on glass slides. The anatomy of these soft body parts was studied under the same light microscope.

4. 4 Results

We found species of four different genera of sponges inhabited by five different species of barnacles, two of them yet undescribed (Table 4. 1). Only the host sponge *Axynissa* sp. was inhabited by two barnacle species, the others only by one barnacle species. Four of the sponge barnacles had a calcareous basis and spines or projections calcareous on the external surface of the parietes. Only the barnacle species *Membranobalanus longirostrum* had a membranous basis and external surface of the parietes without spines or projections calcareous. The number of specimens found in each host sponge varied between a minimum of six (*Acasta* sp. 1 in *Axynissa* sp.) and a maximum of 23 barnacle specimens (*Membranobalanus longirostrum* in *Agelas* sp.) (Table 4. 1).

Table 4.1. Barnacle species and the host sponges from eastern Indonesia

Barnacle species	Host sponge species	**Locality**
Acasta sp. 1	*Axynissa* sp.	Pantai Marina (Southeast Sulawesi)
Acasta sp. 2	*Cinacyrella* sp.	Desa Pia (Saparua Island)
Acasta sulcata Lamarck, 1818	*Spongia* sp.	Porto, Kulur, and Ihamahu (Saparua Island)
Euacasta dofleini (Krüger, 1911)	*Axynissa* sp.	Teluk Haria, Porto, and Desa Ihamahu (Saparua Island)
Membranobalanus longirostrum (Hoek, 1913)	*Agelas* sp.	Teluk Haria (Saparua Island)

Acasta sp. 1

The sponge *Axynissa* sp. found at South East Sulawesi Island (Table 4.1) was inhabited by barnacle *Acasta* sp. 1 (Fig. 4.1a, b). In the micro-CT overview scan of *Axynissa* sp. we found six specimens of barnacle inside the sponge. Barnacles were located near the surface layer of their sponge hosts (Fig. 4.1c). The operculum looming high over the parietes (Fig. 4.1d).

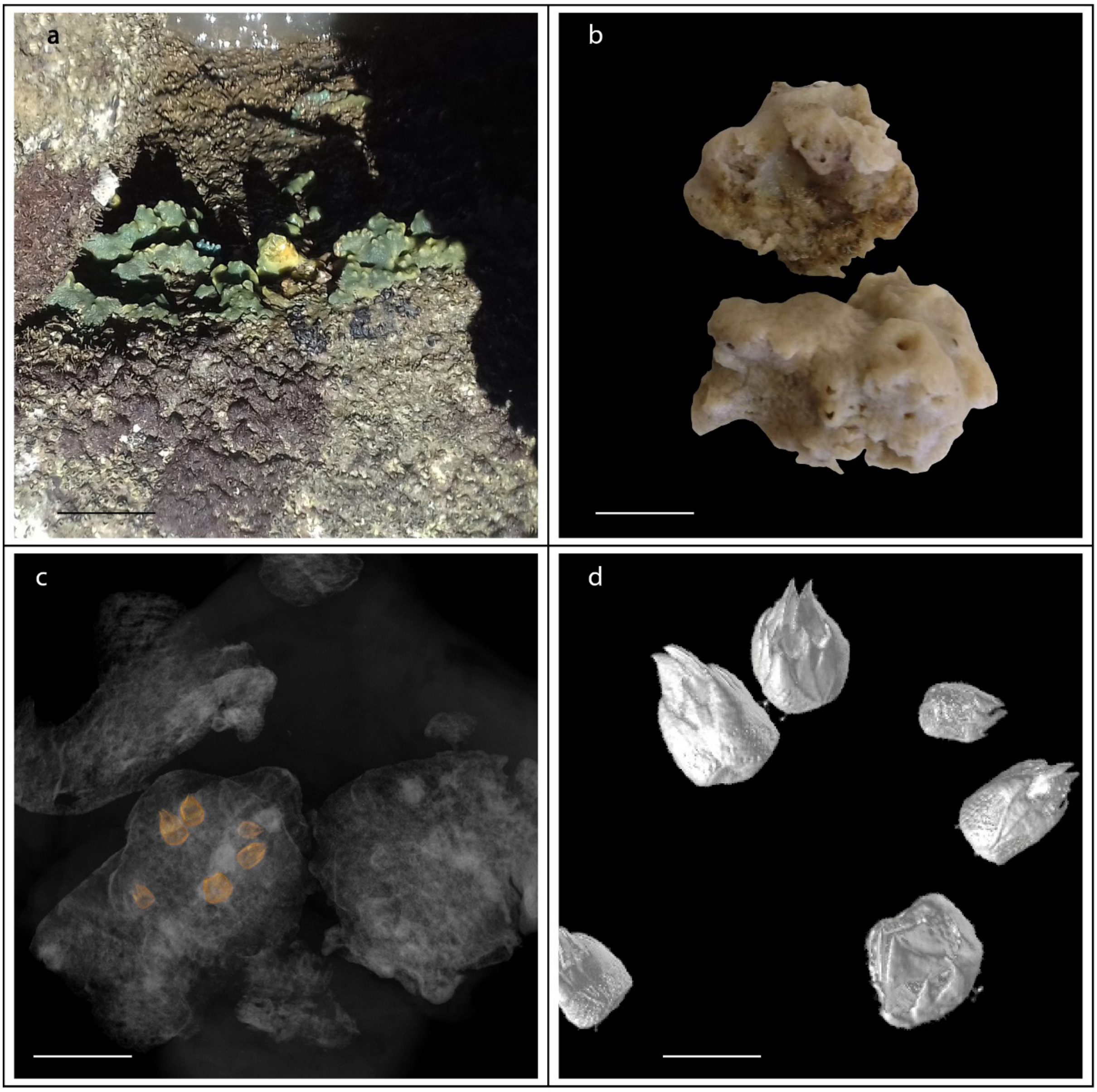

Figure 4.1. *Acasta* sp. 1. (MZB Cru Cir 183) and its host sponge **a)** sponge of *Agelas* sp. **b)** close-up of sponge *Agelas* sp **c)** position of *Acasta* sp. 1 in the host sponge **d)** shell view of *Acasta* sp. 1 Scale bars: 5 cm (**a**); 1 cm (**b**); 1 mm (**c–d**).

The color of the shell was yellowish with operculum soar almost as high as the parietes; orifice was wide; plates externally with lots of calcareous spines (Fig. 4.2a–i). The basis was quadrangular with horizontal growth ridges and the basal rim was crenated (Fig. 4.2e–g). Furthermore, we disassemble the shell to observe each plate in detail. Scutum with horizontal growth ridges and occludental margin was toothed (Fig. 4.2h, i). Tergum apex was beaked, with horizontal growth ridges was present, and the spur was broad (Fig. 4.2h, i).

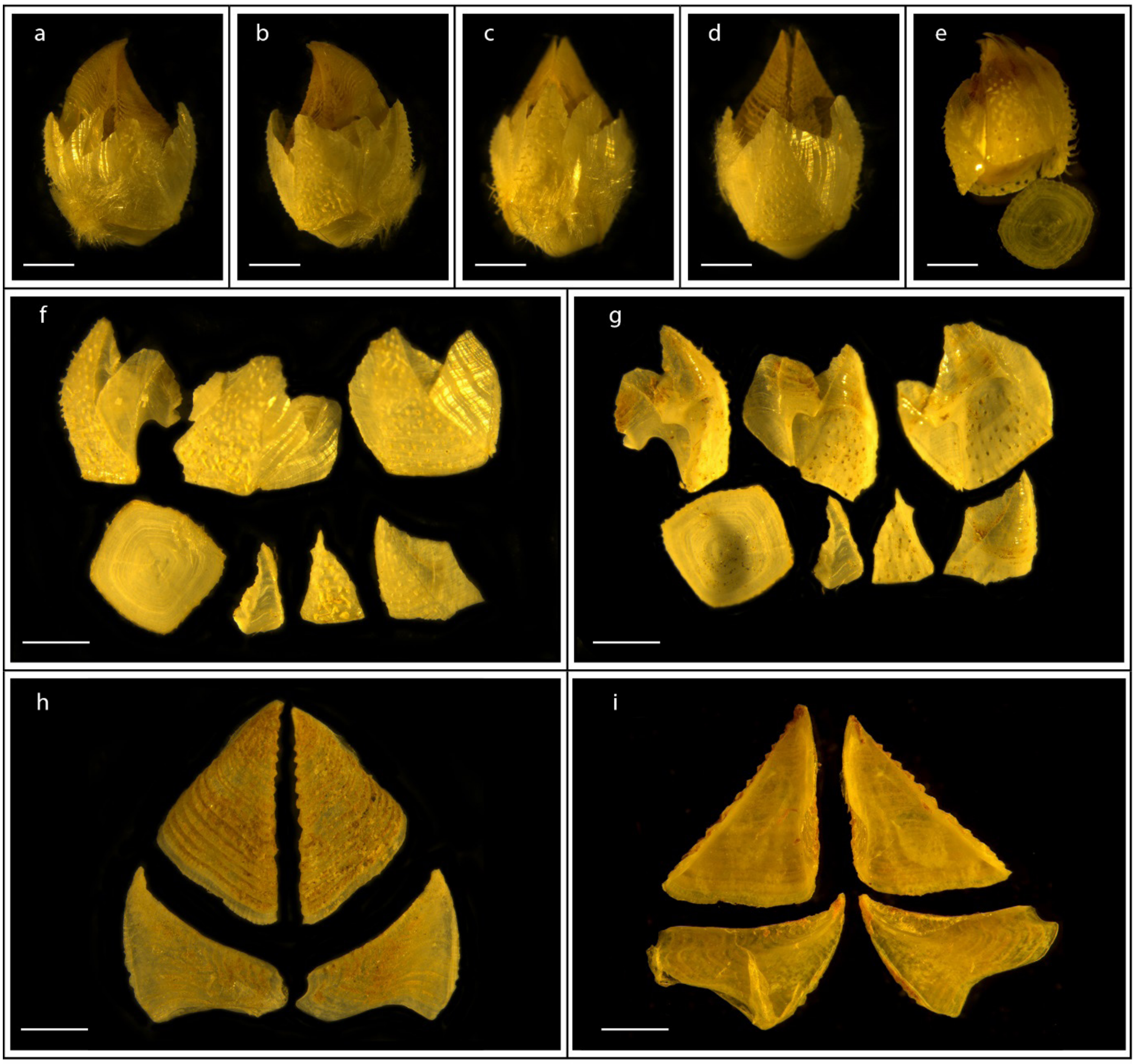

Figure 4.2. Hard body of *Acasta* sp. 1 **a)** shell, right lateral view **b)** shell, left lateral view **c)** carinal view **d)** rostral view **e)** basal view **f)** external view of plates **g)** internal view of plates **h)** external view of scutum and tergum **i)** internal view of scutum and tergum. Scale bars: 1 mm (**a–e**); 0.5 mm (**f–g**); 0.25 mm (**h–i**).

We dissected the soft part of the barnacle to observe the mouthparts, six pairs of cirri, and penis in detail. Cirrus I with rami very unequal in length, posterior margin with serrulate and plumose setae, distal margins of terminal segments of anterior and posterior rami with serrulate and bifid setae (Fig. 4.3a). Cirrus II with rami slightly unequal in length; the posterodistal angle of segments of both rami with serrulate setae; distal margins of terminal segments of anterior and posterior rami with serrulate and bifid setae (Fig. 4.3b). Cirrus IV with rami unequal in length, hooks were present on the frontal margin of the segments of the anterior ramus and basipod (Fig. 4.3c-e). Cirrus V with three small teeth at the frontal edge of proximal segments of the anterior ramus (Fig. 4.3f, g). Cirrus VI was long and slender with equal rami in length (Fig. 4.3h). Penis was annulate and gradually tapering to the tip (Fig. 4.3i). Maxillule cutting edge was straight without a notch, upper and lower margin with two big stout simple setae (Fig. 4.3j); mandible with five teeth, inferior angle with five denticles, lower margin of lateral angle with simple stout setae (Fig. 4.3k); labrum with V-shaped notch and three teeth on each side of the crest (Fig. 4.3l).

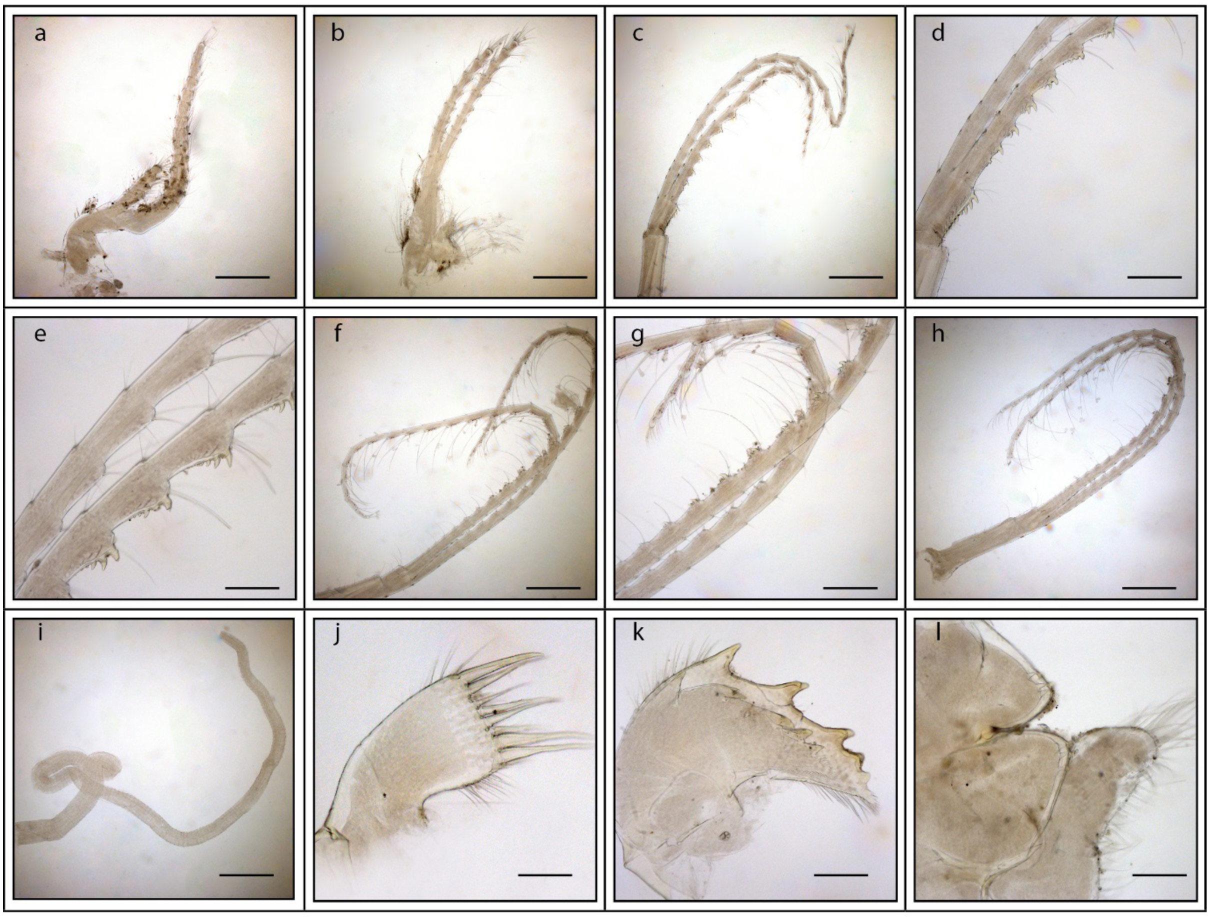

Figure 4.3. Soft body of *Acasta* sp. 1 a) cirrus I **b)** cirrus II **c)** cirrus IV **d)** close-up view of cirrus IV **e)** close-up view of hooks of cirrus IV **f)** cirrus V **g)** close-up view of cirrus V **h)** cirrus VI **i)** penis **j)** maxillule **k)** mandible **l)** labrum. Scale bars: 200 µm (**a–c, f, h, i**); 100 µm (**d, e, g, j–l**).

Acasta sp. 2.

The sponge *Cinacyrella* sp. found at Saparua Island was inhabited by barnacle *Acasta* sp. 2 (Fig. 4.4a). In the micro-CT overview scan of *Cynacyrella* sp. we found nine specimens of barnacle inside the sponge. The barnacle *Acasta* sp. 2 lived in a group near the surface layer of their sponge host with orifice facing the same direction to the surface of the host sponge (Fig. 4.4b, c). The barnacle with hole pattern all over the parietes, except on the operculum (Fig. 4.4d). The operculum plates with slightly horizontal growth ridges (Fig. 4.4e).

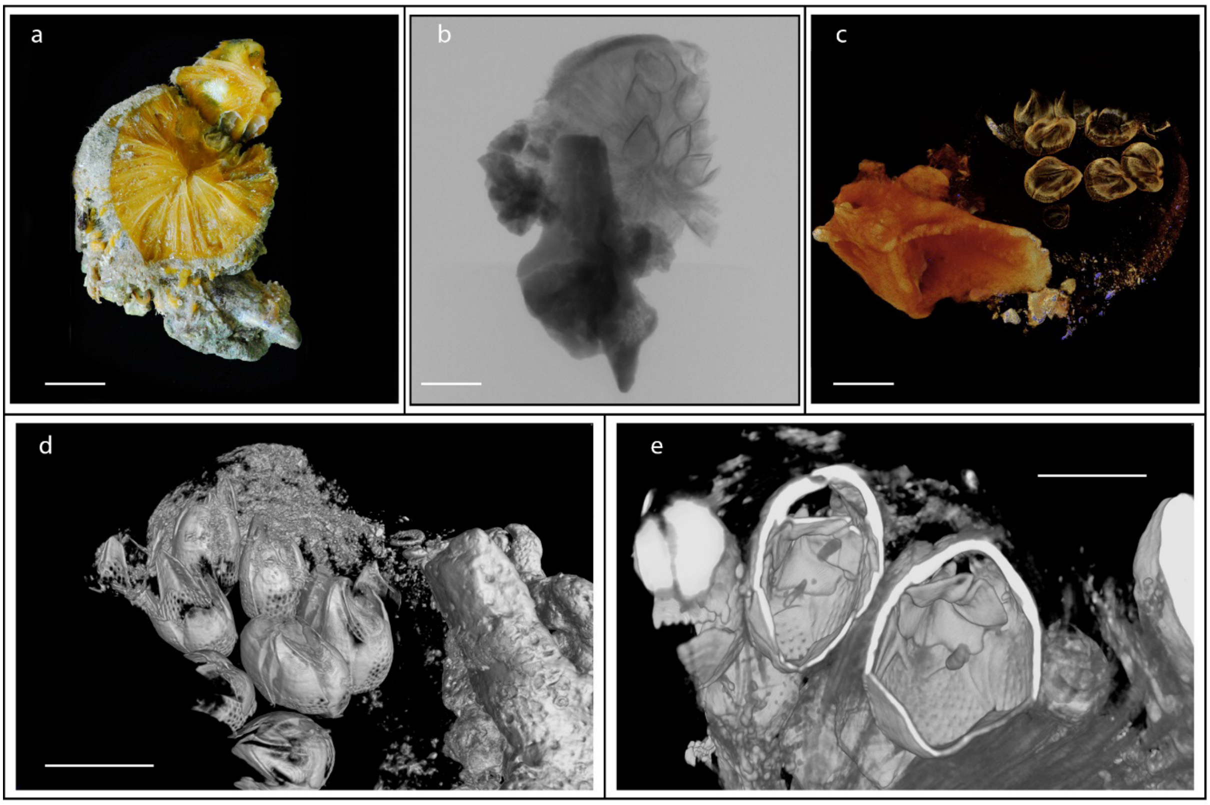

Figure 4.4. *Acasta* sp. 2. (MZB Cru Cir 184) and its host sponge **a)** sponge of *Cinacyrella* sp. **b)** position of *Acasta* sp. 2 in the host sponge **c)** orifice facing the same direction in the host sponge **d)** shell view of *Acasta* sp. 2 **e)** internal view of the plates and operculum. Scale bars: 2 cm (**a**); 1 cm (**b, c**); 1 mm (**d, e**).

After the scanning process, we carefully tried to remove the barnacle from the host and dissected it to verify the species of barnacle. However, we found the barnacle strongly inherent in the sponge and make it very difficult to separate the barnacle with the sponge host without breaking it. After trying several times, finally, we could separate barnacle from the sponge host but with a lot of sponge tissue still attached to the shell of barnacle (Fig. 4.5a). We found the basis consists of four separate plates (Fig. 4.5b). We immersed the barnacle in 2% bleach to completely digest the sponge tissue, but we discovered that the bleach also destroyed the shell of the barnacle (Fig. 4.5c). We immediately rinsed the barnacle with tap water five times and air-dried it for species identification. The basis plates with horizontal growth ridges and shallow radial furrows (Fig. 4.5d, e), and were crenate at the basal rim (Fig. 4.5f). Parietes externally with many holes as marks of attachment of the calcareous spines; internally with longitudinal internal ribs extending from upper to lower part; radii and alae with horizontal ridges (Fig. 4.5g, h). Scutum was semi-transparent and tinged with reddish color at the upper part, horizontal growth ridges were present, occludental margin was slightly toothed (Fig. 4.5i, j). Tergum was semi-transparent with horizontal growth ridges, the apex was beaked and tinged with reddish color (Fig. 4.5i, j).

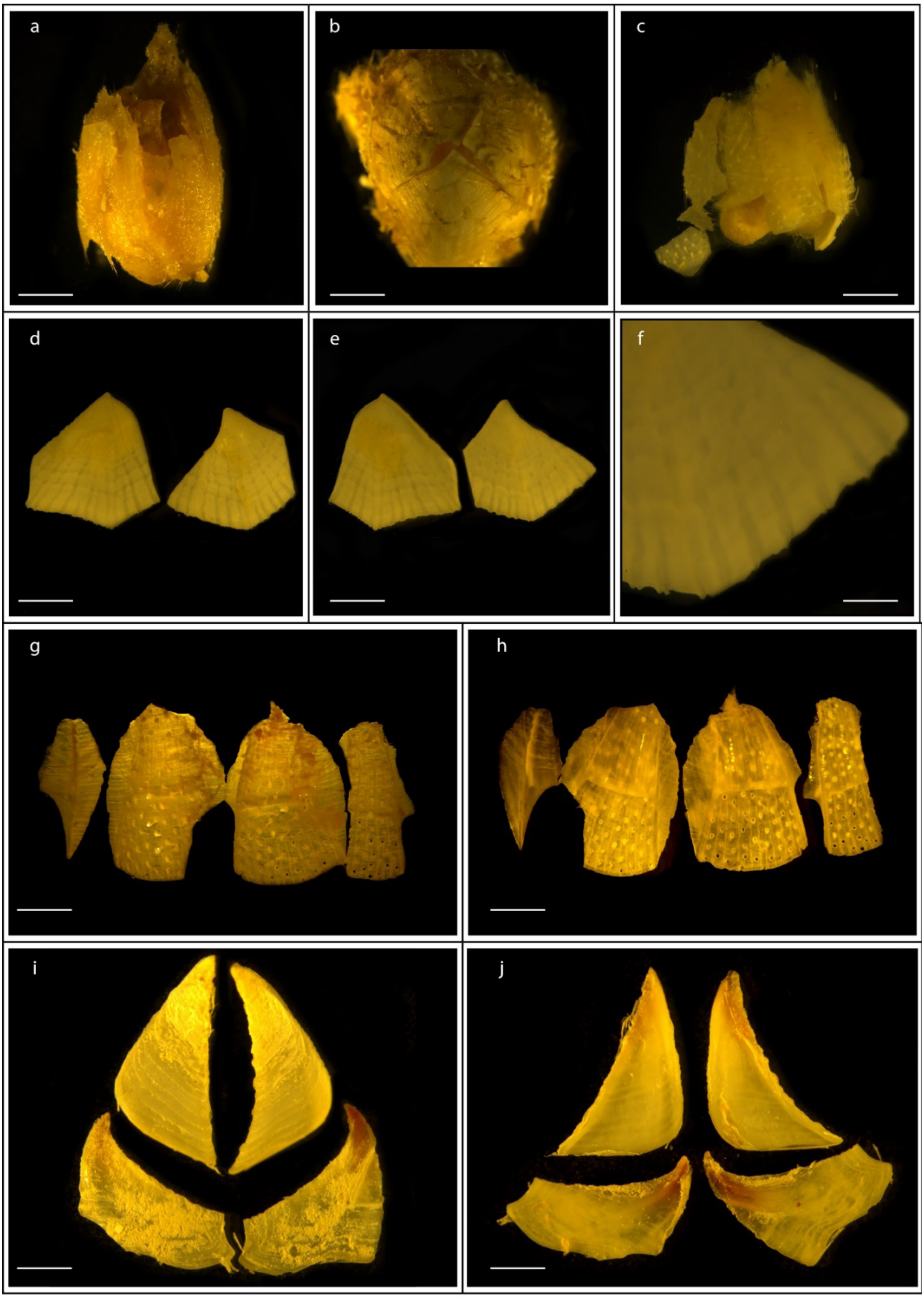

Figure 4.5. Hard body of *Acasta* sp. 2 **a)** shell, lateral view **b)** shell, basal view **c)** shell view after immersed in 2% bleach **d)** external view of the base plates **e)** internal view of the base plates **f)** close-up view of basal rim **g)** external view of plates **h)** internal view of plates **i)** external view of scutum and tergum **j)** internal view of scutum and tergum. Scale bars: 1 mm (**a–c**); 0.5 mm (**d, e, g–h**); 0.25 mm (**f**, **i–l**).

We dissected the soft part of the barnacle to observe the mouthparts, six pairs of cirri, and penis in detail. Cirrus I with rami very unequal in length, anterior and posterior margin with thick serrulate and plumose setae, distal margin of terminal segments of both rami with serrulate setae (Fig. 4.6a). Cirrus II with rami unequal in length, the posterodistal angle of segments of both rami with serrulate setae, the distal margin of terminal segments of both rami with serrulate and bifid setae (Fig. 4.6b). Cirrus III with rami slightly unequal in length, similar to cirrus II, but slender and longer (Fig. 4.6c). Cirrus IV with hooks on the frontal margin of the segments of the anterior rami and basipod; and two small teeth at the frontal edge of proximal segments of the anterior ramus (Fig. 4.6d, e). Penis was annulate with sparse hair distally, and it gradually tapering to the tip (Fig. 4.6f). Maxillule cutting edge was straight without a notch, the upper and lower margin with two big stout simple setae (Fig. 4.6g); mandible with five teeth, inferior angle with two stout denticles, lower margin of lateral angle with simple setae (Fig. 4.6h); mandibular palp with dense setae on the upper region (Fig. 4.6i); labrum with V-shaped notch and two small teeth on each side of the crest (Fig. 4.6j).

Figure 4.6. Soft body of *Acasta* sp. 2 a) cirrus I **b)** cirrus II **c)** cirrus III **d)** cirrus IV **e)** close-up view of hooks of cirrus IV **f)** cirrus V **g)** maxillule **k)** mandible **i)** mandibular palp **j)** labrum. Scale bars: 200 µm (**a–d, f)**; 100 µm (**e, g–j**).

Acasta sulcata Lamarck, 1818

The sponge *Spongia* sp. (Fig. 4.7a, b) found at Saparua Island was inhabited by the barnacle species *Acasta sulcata* (Fig. 4.7c-e). In the micro-CT overview scan of *Spongia* sp. we found 13 barnacle specimens inside the sponge. Barnacles were located near the surface layer of their sponge hosts (Fig. 4.7c), a video of *Acasta sulcata* in *Spongia* sp. was published in the MfN Data Repository Berlin (shown in subchapter 4.7) (Pitriana et al., 2020b). The parietes were externally smooth with calcareous spines attached in some areas (Fig. 4.7d) and ribbed internally (Fig. 4.7d, e). The basis was cup-shaped and pointed at the central umbo (Fig. 4.7e).

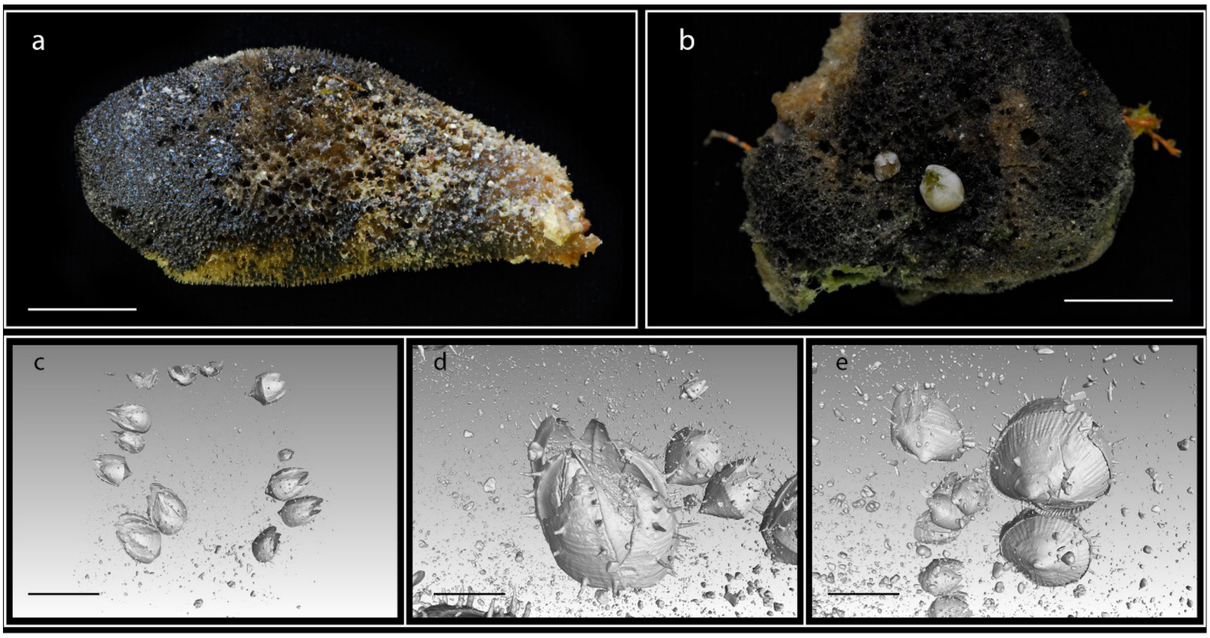

Figure 4.7. *Acasta sulcata* Lamarck, 1818 (MZB Cru Cir 185) and its host sponge **a)** sponge of *Spongia* sp., **b)** *Spongia* sp. inhabited by *Acasta sulcata*, **c)** position of *Acasta sulcata* in the host sponge, **d)** calcareous projections in the external surface parietes of *Acasta sulcata*, **e)** base of *Acasta sulcata*. Scale bars: 2 cm (**a**); 1 cm (**b, c**); 1 mm (**d, e**).

The color of the shell was whitish to yellowish with reddish patches towards the apex; orifice was small and toothed (Fig. 4.8a–l). Parietes externally were smooth, with horizontal growth ridges and calcareous spines; internally, at under sheath, with longitudinal ribs; radii and alae with horizontal ridges (Fig. 4.8a–e). The basis was cup-shaped with basal rim crenated; shallow radial furrows extending from center to the crenate basal rim (Fig. 4.8f). Furthermore, we disassemble the shell to observe each plate in detail (Fig. 4.8g, h). We found scutum with horizontal growth ridges, basal margin slightly concave in middle, occludental margin toothed with tooth size increasing gradually from apex to base (Fig. 4.8i, j). Tergum was semitransparent, apex beaked tinged with reddish color, internally scutal margin also with reddish patches in the upper part, depressor muscle crests was absent, spur was broad, spur furrow was shallow, and carinal margin was perpendicular to basal margin (Fig. 4.8k, l).

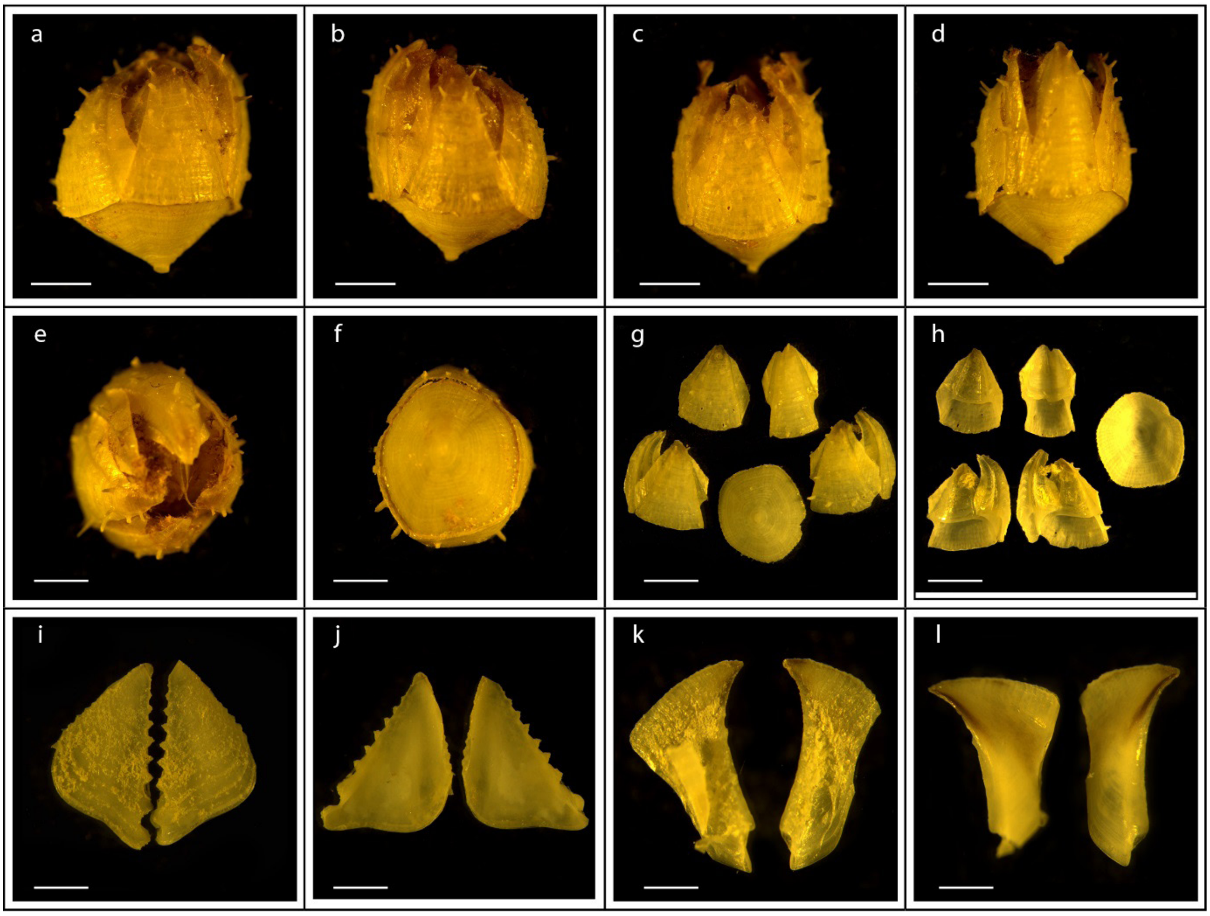

Figure 4.8. Hard body of *Acasta sulcata* **a)** right side view **b)** left side view **c)** rostral view **d)** carinal view **e)** upper view **f)** lower view **g)** external view of plates **h)** internal view of plates **i)** external view of scutum **j)** internal view of scutum **k)** external view of tergum **l)** internal view of tergum. Scale bars: 1 mm (**a–f**); 0.5 mm (**g–h**); 0.25 mm (**i–l**).

We dissected the soft part of the barnacle to observe the mouthparts, six pairs of cirri, and penis in detail. Cirrus I with outer ramus 80% of inner ramus in length; posterior margin with serrulate and plumose setae; distal margins of the terminal segment of anterior and posterior rami with serrulate and bifid setae (Fig. 4.9a). Cirrus II with rami unequal in length; posterodistal angle of segments of both rami with thick serrulate setae; distal margins of the terminal segment of anterior and posterior rami with serrulate and bifid setae (Fig. 4.9b). Cirrus IV with rami unequal in length; there were hooks on the frontal margins of the segments of the anterior rami and basipod (Fig. 4.9c). Cirrus V with two small teeth at the frontal edge of proximal segments of the anterior ramus (Fig. 4.9d). Cirri V and VI with rami subequal in length, terminal segments of anterior and posterior rami with serrulate setae. Maxillule cutting edge was straight without a notch, upper and lower margin with numerous simple setae (Fig. 4.9e); mandible with five teeth, the second to fourth tooth were bifid, inferior angle with six denticles and stout simple setae, upper margin of lateral angle with stout simple setae (Fig. 4.9f); labrum was bilobed, separated by V-shaped notch with three small teeth on each side of the crest (Fig. 4.9g).

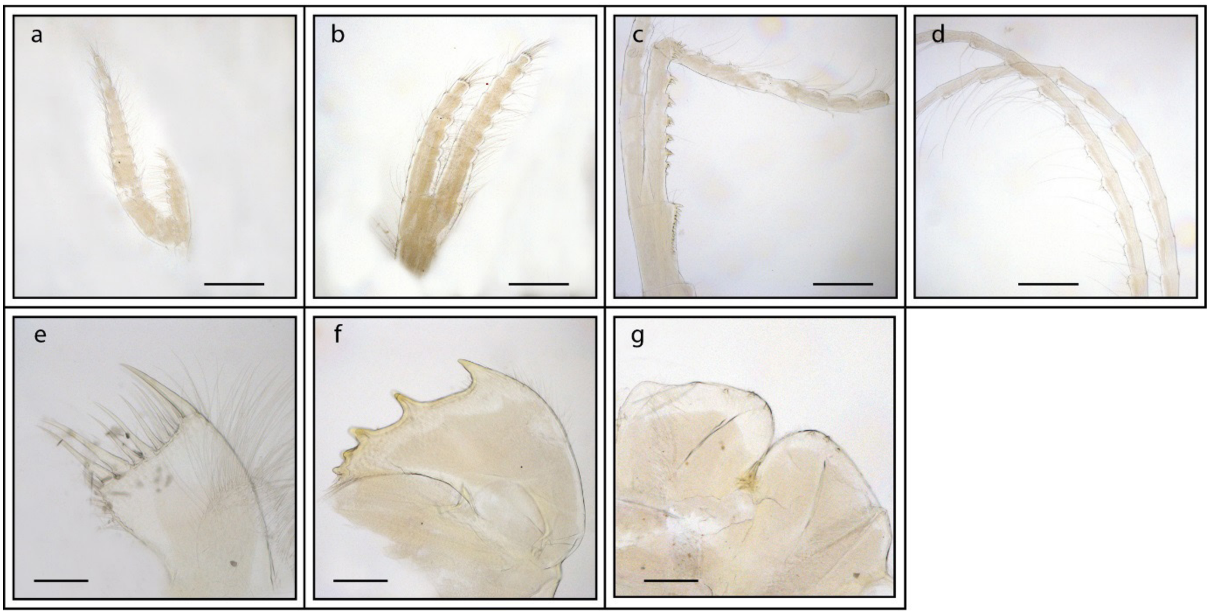

Figure 4.9. Soft body of *Acasta sulcata* **a)** cirrus I **b)** cirrus II **c)** cirrus IV **d)** cirrus V **e)** maxillule **f)** mandible **g)** labrum. Scale bars: 200 µm (**a–d)**; 100 µm (**e–g**).

Euacasta dofleini (Krüger, 1911)

The sponge *Axynissa* sp. (Fig. 4.10a) found at Saparua Island (Table 4.1) was inhabited by the barnacle species *Euacasta dofleini* (Krüger, 1911) (Fig. 4.10a). In the micro-CT overview scan of *Axynissa* sp. we found 12 specimens with their opercula facing the same direction to the surface of their sponge hosts (Fig. 4.10b). The shape of the shell base was quadrangular with four indistinct and shallow radial furrows extending from the center to the crenate basal rim (Fig. 4.10c, d). The calcareous spines were attached on the external surface of plates (Fig. 4.10d, e).

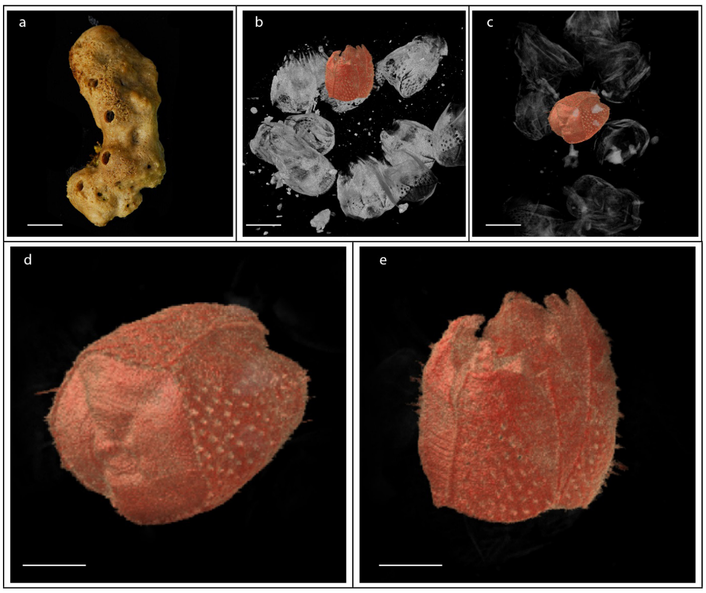

Figure 4.10. *Euacasta dofleini* (Krüger, 1911) (MZB Cru Cir 186) and its host sponge **a)** sponge of *Axynissa* sp. **b)** position of *Euacasta dofleini* in the host sponge **c)** base of *Euacasta dofleini* **d)** close-up of the base **e)** parietes with calcareous projections on the external surface. Scale bars: 3 cm (**a**); 1 mm (**b–e**).

The color of the shell was yellowish with orifice toothed; wall plates have long and worm-shaped calcareous projections on its external surface; the basis was saucer-shaped with basal rim crenated (Fig. 4.11a–f). Furthermore, we disassemble the shell to observe each plate in detail. Scutum with radial striae and occludental margin toothed; tergum was beaked and the apex tinged with pinkish (Fig. 4.11g–j). Carinolaterals have rudimentary parietes, because of a narrow strip separating radii from ala (Fig. 4.11k, l).

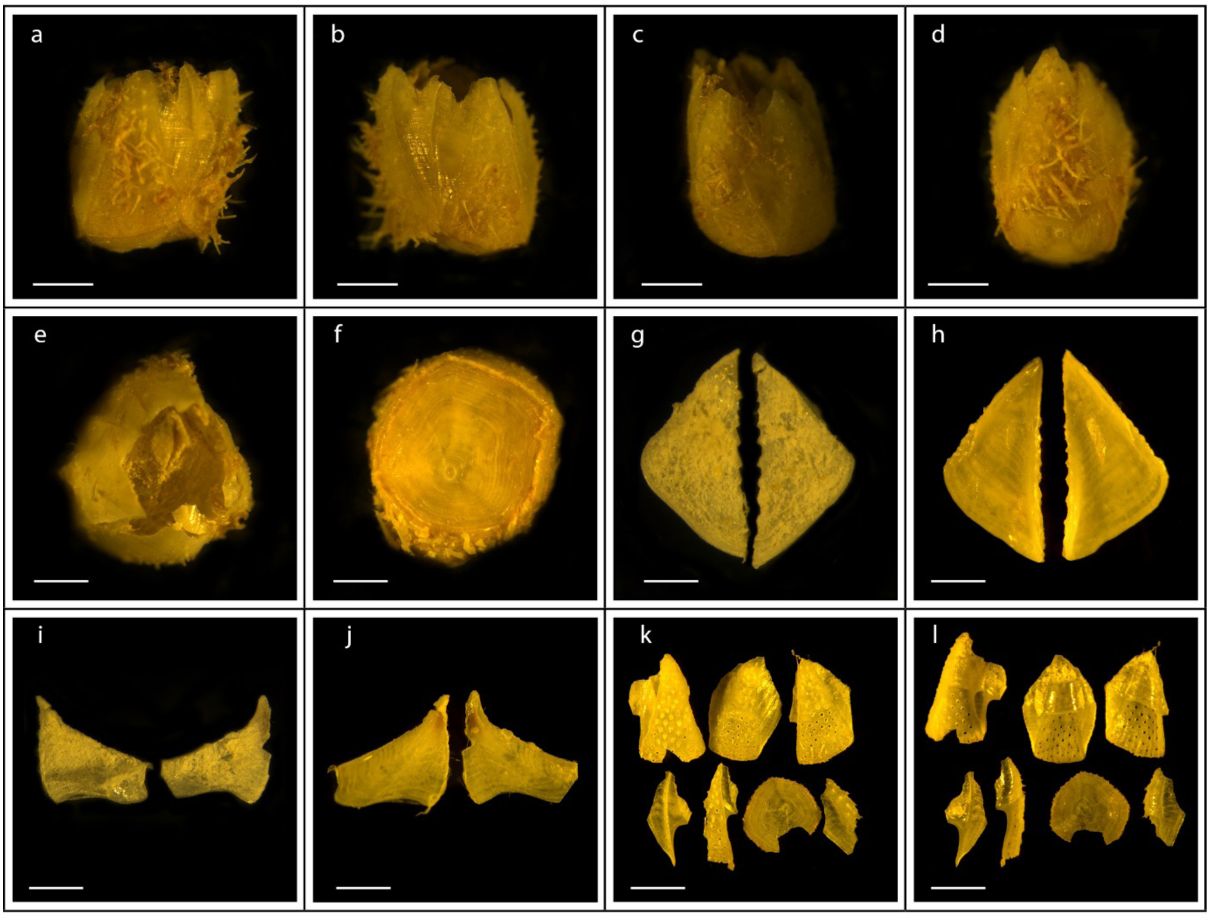

Figure 4.11. Hard body of *Euacasta dofleini* a) right side view **b)** left side view **c)** lateral plates view **d)** rostral view **e)** upper view **f)** lower view **g)** external view of scutum **h)** internal view of scutum **i)** external view of tergum **j)** internal view of tergum **k)** external view of plates **l)** internal view of plates. Scale bars: 1 mm (**a–f**); 0.25 mm (**g–h**); 0.50 mm (**i–l**).

We dissected the soft part of the barnacle to observe the mouthparts, six pairs of cirri, and penis in detail. Cirrus I with rami unequal in length, posterior margin with serrulate and plumose setae (Fig. 4.12a). Cirrus II with rami unequal in length, terminal segments of anterior and posterior rami with bifid setae (Fig. 4.12b). Cirral armature of cirrus IV was well developed with curved hooks on the frontal margin of the segments of the anterior rami and basipod (Fig. 4.12c). Cirrus V and VI were long and slender with equal rami in length (Fig. 4.12d, e). Penis was annulate, without a basidorsal point, and gradually tapering to the tip (Fig. 4.12f). Maxillule has nine large cuspidate setae with upper and lower pairs were the largest; and cutting margin was straight, without a notch (Fig. 4.12g). Mandible with five teeth, the second was bifid, inferior angle with three denticles and stout setae, lower margin bearing simple setae (Fig. 4.12h). Labrum bilobed with deep, V-shaped notch, and three teeth on each crest (Fig. 4.12i).

Figure 4.12. Soft body of *Euacasta dofleini* **a)** cirrus I **b)** cirrus II **c)** cirrus IV **d)** cirrus V **e)** cirrus VI **f)** penis **g)** maxillule **h)** mandible **i)** labrum. Scale bars: 200 µm (**a–b, d–f**); 100 µm (**c**, **g–i**).

Membranobalanus longirostrum (Hoek, 1913)

The sponge *Agelas* sp. found at Saparua Island was inhabited by barnacle *Membranobalanus longirostrum* (Fig. 4.13a, b). In the micro-CT overview scan of *Agelas* sp. we found 23 specimens of barnacle inside the sponge. We discovered only hard parts of the shell can be seen through micro-CT scan (Fig. 4.13c, d).

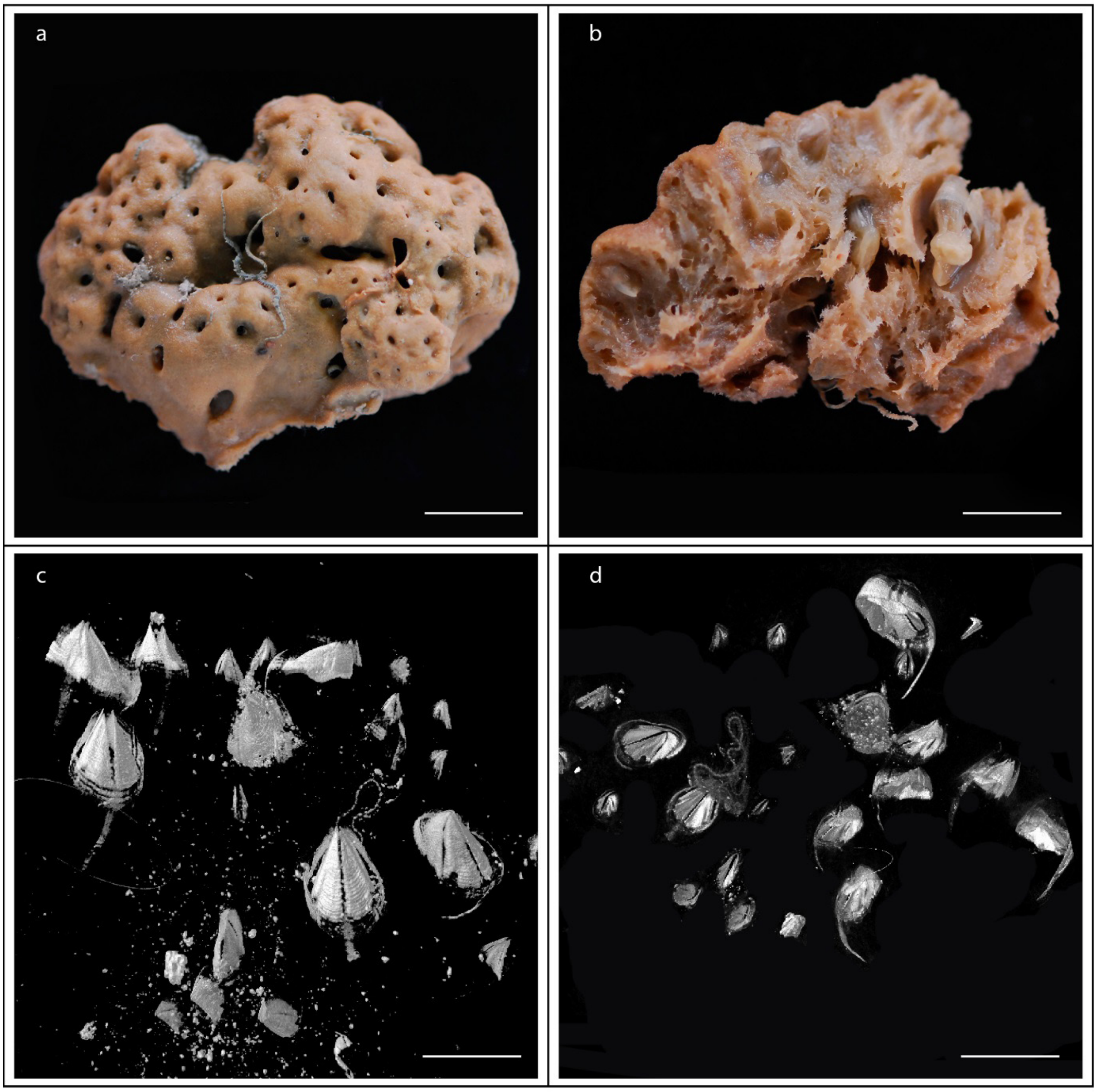

Figure 4.13. *Membranobalanus longirostrum* (Hoek, 1913) (MZB Cru Cir 187) and its host sponge **a)** sponge of *Agelas* sp. **b)** *Membranobalanus longirostrum* in the host sponge **c)** orifice view of *Membranobalanus longirostrum* **d)** rostral view of *Membranobalanus longirostrum.* Scale bars: 2 cm (**a–b,**); 1 mm (**c–d**).

The shell of the barnacle was thin, very brittle, and smooth without calcareous spines; orifice was large and irregularly toothed; the basis was membranous (Fig. 4.14a–e). Furthermore, we disassemble the shell to observe each plate in detail. Scutum with horizontal growth ridges, occludental margin toothed at the lower part, adductor ridge was absent (Fig. 4.14b, c). Tergum was beaked, with horizontal growth ridges; spur was moderately wide and close to the basi-scutal angle (Fig. 4.14b, c). The carina and rostrum were bowed; rostrum was the longest plate, with the basal part extending far beyond the basal margin of the other compartments (Fig. 4.14d, e).

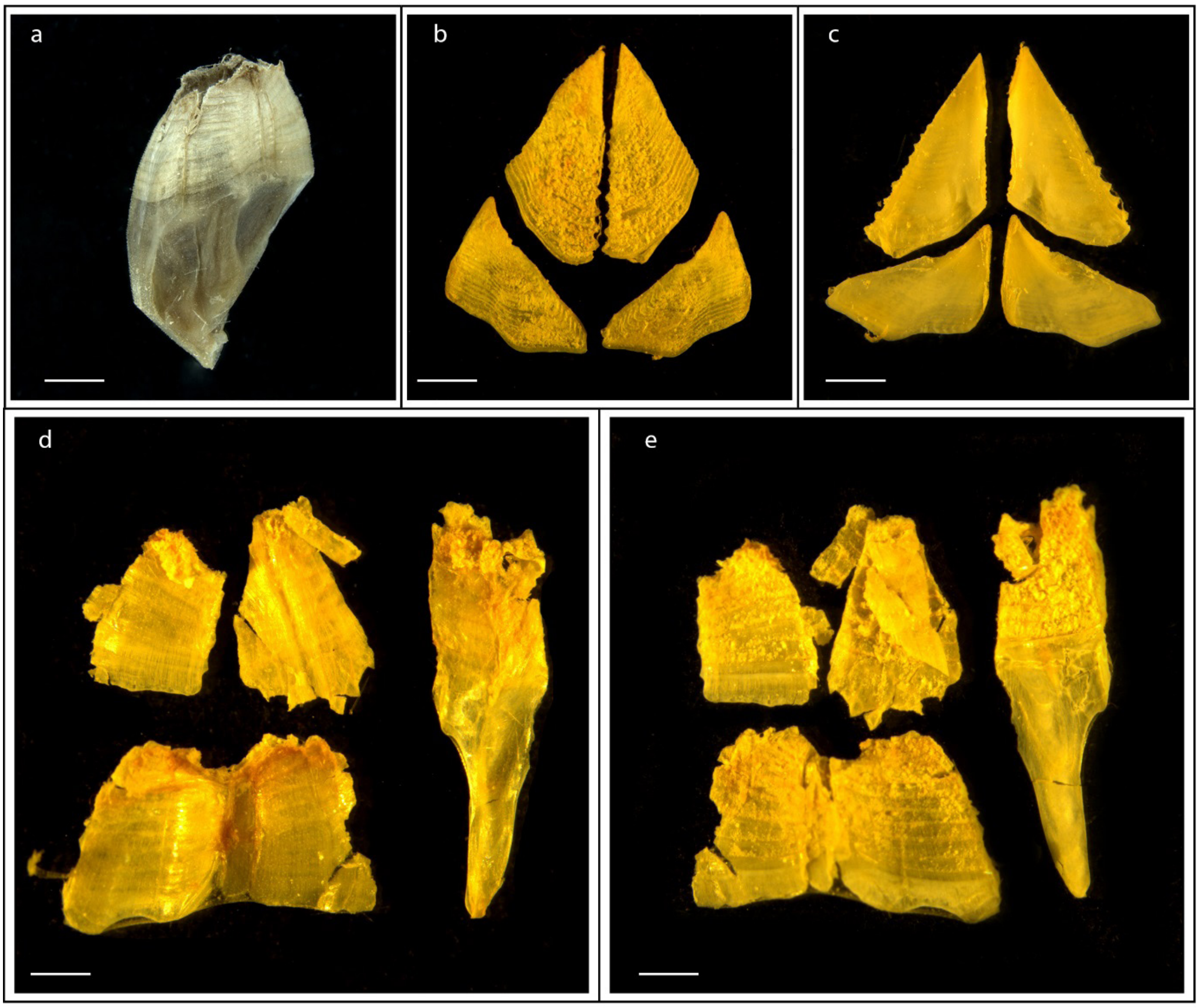

Figure 4.14. Hard body of *Membranobalanus longirostrum* a) shell, lateral view **b)** external view of scutum and tergum **c)** internal view of scutum and tergum **d)** internal view of plates **e)** external view of plates. Scale bars: 1 mm (**a–f**); 0.25 mm (**g–h**); 0.50 mm (**i–l**).

We dissected the soft part of the barnacle to observe the mouthparts, six pairs of cirri, and penis in detail. Cirrus I with outer ramus 80% of inner ramus in length, terminal segments of anterior and posterior rami with bifid setae (Fig. 4.15a). Cirrus II rami slightly unequal in length, with plumose and serrulate setae; the distal segment of posterior ramus with serrulate setae (Fig. 4.15b). Cirrus III with equal rami in length (Fig. 4.15c). Rami of cirrus IV slightly unequal in length, with triangular spine-like teeth, form transverse comb-like rows and were disposed on both segments of the pedicel (Fig. 4.15d). Cirrus V and VI were long and slender (Fig. 4.15e, f). Penis was very long, much longer than the cirri (Fig. 4.15g). Maxillule cutting margin was straight without a notch, with 11 large cuspidate setae, the lower pairs were the largest (Fig. 4.15h). Mandible with five teeth, the second was bifid, the third was small; inferior angle with three denticles and stout setae, lower margin bearing simple setae (Fig. 4.15i). Labrum with a wide notch but not very deep; the shape was bilobed with two teeth on each crest (Fig. 4.15j).

Figure 4.15. Soft body of *Membranobalanus longirostrum* a) cirrus I **b)** cirrus II **c)** cirrus III **d)** cirrus IV **e)** cirrus V **f)** cirrus VI **g)** penis **h)** maxillule **i)** mandible **j)** labrum. Scale bars: 200 µm (**a–g)**; 100 µm (**h–j**).

4.5 Discussion

The results from this morphological study using an innovative approach with micro-CT scanning and 3D reconstruction supports the results from Anderson (1994) who found out that epizoic balanoid adaptations are related to the problem of overgrowth and burial, a reason why the barnacles have to maintain its orifice at the surface of the sponge host. In our study, all barnacle specimens were facing the surface of their sponge hosts. Ilan et al. (1999) also stated that a sponge-inhabiting barnacle settles on the location of the opening to avoid overgrowth. They also found that barnacles *Neoacasta laevigata* had a clumped distribution on its host sponge *Carteriospongia foliascens*. According to Lewis (1992), this clump distribution related to their adaptation for reproduction, since they are sessile organism so the key factor in the pattern distribution of barnacles on a substrate is the distance from the nearest neighbor.

Yu et al. (2020) observed that the arrangement of barnacles in sponges are not random, but mostly accumulate on the inhalant side to make it easier for capturing food. Sponges are important benthic suspension feeders and are believed to slow the water flow and raise the water turbulence, resulting in an increased residence time of possible nutrient particles (Gili

& Coma, 1998). Barnacle as epibionts that can take advantage of the slowed water currents caused by sponges (Nagler et al., 2017). All the statements above might explain the reason why in this study the majority of barnacles found were arranged in groups near the surface of the host sponge.

In this study, barnacle Acastinae were found inhabiting sponge *Spongia* sp., *Axynissa* sp., and *Cynacyrella* sp., which have also previously been reported from the studies of sponge barnacle of America, Red Sea, Indonesia, and worldwide (Van Syoc & Winther, 1999; Ilan et al., 1999; Wibowo et al., 2011; Sulistiono et al., 2014; Van Syoc et al., 2015). While for *Membranobalanus*, according to van Syoc (1988) and Hosie et al. (2019) they were restricted to inhabiting sponges species of the Clionaidae. Additionally in this study, we found the species *Membranobalanus longirostrum* inhabiting the sponge *Agelas* sp. of the family Agelasidae.

By using micro-CT we can see the pattern of calcareous projections on the surface of the shell wall by looking at the pattern of circular holes on the shell, as these holes are the site of attachment of the spines. These calcareous projections or spines are believed to function as an anchor into the surrounding sponge tissue which is well developed in species that inhabit crumbly sponges, but are reduced among species hosted by elastic sponges (Kolbasov, 1993). These features also can be used to distinguish Acastinae from members of the genus *Membranobalanus* (Van Syoc et al., 2015). Because of this important role, it may be that the pattern of these circular holes could also be used as an important character for species identification in future. This study also confirms the advantage of using micro-CT imaging when we examined *Acasta* sp. 2 which was anchored so tightly in the sponge tissue that removing the specimen turned out to be impossible without breaking it.

Invertebrate studies utilising micro-CT scanning provide new ways of looking at the external and internal morphology of organisms of microscopic size (Friedrich & Beutel, 2008). Although micro-CT scanning has great potential in biodiversity research of barnacles by enhancing the visualization of external and internal anatomy, this study also had some methodological limitations. In *Membranobalanus longirostrum*, the contrast in the 3D images was too low to see the membranous basis. This problem could have been caused because the membrane was tightly embedded in the sponge tissue, resulting in a low level of contrast between the membrane and the surrounding host tissue. Although we applied a staining method to visualize the membrane and soft body parts, the contrast of the images was generally too low and we could not fully reconstruct the soft body parts. According to Metscher (2009a), by using a few simple contrast stains, micro-CT can provide versatile, high-contrast, quantitative 3D images of animal soft tissues. The methods can be used on a wide variety of animal specimens fixed and preserved by the most common methods. The most broadly used contrast stains tested so far are inorganic iodine and phosphotungstic acid (PTA) (Metscher, 2009b). These staining methods including iodine-based dyes such as Lugol's solution poses a simple, cost-effective, and nontoxic option for contrast enhancement for soft tissues (Heimel et al., 2019). The use of this staining method has a broad range of different concentrations of iodine and staining durations depends on the type of tissue (Gignac et al., 2016). However, marine organisms exhibit a large diversity of tissue types, chemical components and material combinations, making it almost impossible to predict the effect of a certain contrast-enhancing technique (Faulwetter et al., 2013). In a future project we plan to find a better staining agent to find the most appropriate staining method to get a higher and sufficinet resolution of the barnacles' soft body.

In conclusion, this study demonstrates that micro-CT scanning is a very useful modern technique on morphological and taxonomical examination of the sponge-inhabiting barnacles.

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4.7 Non-invasive 3D visualization of the sponge-inhabiting barnacle *Acasta sulcata* (Crustacea: Cirripedia: Balanomorpha) from the Moluccas, Indonesia. [Dataset].

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Abstract

We present a digital reconstruction (video) of non-invasive microCT scans of barnacle specimens (*Acasta sulcata*) embedded in their sponge host (*Spongia* sp.) from the Indonesian island Saparua, Moluccas.

The sponge specimen, which was supposed to host barnacles, was subjected to micro-tomographic analysis at the Museum für Naturkunde Berlin, using a Phoenix nanotom X-rays tube at 90 kV and 150 µA, generating 1440 projections. The specimen was fixed with foam in a sealed plastic tube in an ethanol-saturated atmosphere. Cone beam reconstruction was performed using the phoenix/x-ray datos/x version 2.3.3 software (GE Sensing and Inspection Technologies GmbH). Effective voxel size, i.e. resolution in three-dimensional space, is 13.33 µm.

Data were visualized in VG Studio Max, version 3.1. Barnacles are shown as an isosurface in red color, the surrounding sponge tissue as volume rendering in grey color (length of sponge host approx. 11 cm; size of barnacles approx. 2.5 mm).

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Chapter 5

General conclusion and outlook

5.1 General conclusion

This doctoral thesis was composed of three major works with four questions. The first question dealt with the number of species of Moluccan barnacles collect from recent fieldwork, including the species known to science, the number of new records, and the number of new species. These questions are adressed in manuscripts 1 and 3, which deal with recent field sampling activities. The resulting checklist of barnacles (Crustacea, Cirripedia) from the Moluccas, East Indonesia, in the first manuscript lists twenty-five species of barnacles collected from recent fieldwork, including twenty-three new records in the Moluccas and two that are still awaiting description. Meanwhile, the checklist in manuscript 3 lists four barnacles from Saparua Island, including one that is proposed as a new species.

The second quenstion is how many cryptic species are hidden in the collected material of morphologically similar, can be answered with checklist of biodiversity discovery of barnacles (Crustacea, Cirripedia) from the Moluccas, East Indonesia. Molecular analysis was conducted to confirm the molecular taxonomic identity of the barnacles from the Moluccas with sequences published in GenBank to examine whether they cluster near congeneric or conspecific accessions. In total, 120 new sequences (COI = 62 sequences, 18S = 58 sequences) were produced and a total of 172 sequences from GenBank (COI = 84 sequences, 18S = 88 sequences) were included in our analysis. The vast majority of new samples from the Moluccas matched sequences from the same species that were available in GenBank. Two taxa for which we have several sequences did not come up with a name in the BOLD system. The isolated position in our tree leads us to the hypothesis that these taxa are new to science, i.e. *Microeuraphia* sp. and *Amphibalanus* sp.

The third question, regarding the deep-sea barnacles collected from the Moluccas by the Karubar expedition (1991), is discussed in manuscript 2. This collection is housed in the Muséum National d'Histoire Naturelle, Paris and revealed 40 species recorded from the Kei, Aru and Tanimbar Islands, and two of which we propose as new species. Based on comparison with the literature on barnacles from Kei, Aru and Tanimbar Islands, 23 species can be considered new records for these islands. Together with the checklists of all species in manuscript 1 and sponge-dwelling barnacles in manuscript 3, this summary shows that 126 species are recorded in the Moluccas, including 46 new records and 5 proposed new species.

The fourth question, relating to the study of sponge-dwelling barnacles of the Moluccas using a modern non-destructive imaging method, X-ray micro-computed tomography (Micro-CT scanning), is discussed in manuscript 3. Through the use of micro-CT scanning, it can be seen that barnacles generally live in groups near the surface of the host sponge. Using a micro-CT scan, the pattern of calcareous projections on the surface of the shell wall can also be seen by looking at the pattern of circular holes, as these holes are the sites of spinal attachment. This study also confirms the advantage of using micro-CT scan for the examination of sponge barnacles, whose deep roots in sponge tissues make it almost impossible to pull out barnacles without breaking them.

Based on these results, this doctoral thesis concludes that 126 species are recorded from the Moluccas, including 46 new records, and 5 proposed new species. This supports the assumption that the Indo-Malayan region (including the Moluccas Islands) is a centre of high benthic biodiversity. However, a comparison of the number of species previously recorded from the Moluccas with those recorded in this study indicates that species diversity for each island has been heavily underestimated. Molecular results also indicate that the barnacle fauna of the region is understudied. Nonetheless, a modern non-destructive imaging method, X-ray micro-computed tomography (Micro-CT scanning) is proven to be a very useful technique for studying the morphology and taxonomy of barnacles from the Moluccas. When paired with classic morphological examination, this technique has the potential to be an extremely useful tool for understanding the integrative taxonomy of barnacles and helping identify further species of barnacles.

5.2 Outlook

This doctoral thesis has demonstrated that, despite being part of the global epicentre of marine biodiversity, knowledge of the barnacle fauna of the Moluccas is still limited. For example, seven species were previously known from around Ambon Island, compared to the twenty-four species found in this study. For smaller islands, such as Saparua and Pombo, no barnacle species were previously recorded. Given the size of the Moluccan Archipelago, which consists of more than 1,000 islands—many of which, including relatively large islands such as Haruku, Buru, Yamdena or Wetar, have never been sampled—it can be expected that more intensive sampling of these islands would yield a much higher number of species.

The molecular results also indicate that the barnacles of the region are understudied. The generic assignment of some described species is also challenged. For example, *Amphibalanus zhujiangensis* was found to be more closely related to *Megabalanus* than to other *Amphibalanus* species, suggesting the need to conduct in-depth research on this species to clarify its taxonomy. These points all underline again the necessity of a more comprehensive approach to sampling in the region, as well as the need to explore more molecular markers for a truly integrative taxonomy of barnacles, not just in the Moluccas.

Considering that the Moluccas have long been a destination for scientific exploration, having hosted at least fifty scientific expeditions, it is challenging to obtain the specimen data that is deposited in museums around the world. In addition, for most genera of deep-sea barnacles, taxonomic information is limited and reliable taxonomic keys are rare. Many species of barnacles were described based on a single (adult) specimen. Data on morphological changes during larval and post-larval development are mostly lacking. Limited sample sizes, for example from previous research expeditions, do not allow for the assessment of intraspecific variability. The only chance to contribute more taxonomic data on barnacles from such remote areas as the Moluccas is to re-examine the type and other specimens deposited in museum collections. These reasons demonstrate once more the importance of museum collections as a study resource in biodiversity science.

The deep-sea barnacle specimens from the Moluccas deposited in museum collections could be compared with recently collected specimens. Although it is difficult to collect or examine evidence from deep-sea areas, and although these areas seem so far away that it is unimaginable that human activity would affect them, deep-sea barnacles might provide clues how climate change is affecting the deep ocean. They may also provide data regarding whether environmental changes such as global warming could potentially affect the deep oceans, which remain among the most mysterious parts of the world.

Barnacle studies utilising micro-CT scanning provide us new ways of looking at the external and internal morphology of organisms in the millimetre–micrometre size range. However, in this study we experienced a problem with unsatisfactorily low-contrast image of soft body. Even after staining, soft body details could not be seen clearly. As such, various methods must be attempted to determine the staining method that is best suited to examining soft body through micro-CT scanning.

CHAPTER 6

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APPENDIX

7.1 Supplementary material for An annotated checklist and integrative biodiversity discovery of barnacles (Crustacea: Cirripedia) from the Moluccas, East Indonesia

Table 7.1. Table of sample information for DNA samples sequenced for this study.

No.	Species name	Island	Internal code	Specimen voucher	GenBank number	
					COI	18S RNA
1	*Amphibalanus zhujiangensis*	Saparua	Bcl1716PM775	MZB Cru Cir 019-1	MK995334	MK981347
2	*A. zhujiangensis*	Sulawesi	Bcl4517PM1404	Bcl4517PM1404	MK995335	MK981348
3	*A. zhujiangensis*	Saparua	Bcl9016PM1222	MZB Cru Cir 021	MK995336	MK981349
4	*A. zhujiangensis*	Seram	Bcl3317PM1307	MZB Cru Cir 010-3	MK995337	MK981350
5	*A. zhujiangensis*	Sulawesi	Bcl4517PM1406	Bcl4517PM1406	MK995338	MK981351
6	*A. zhujiangensis*	Ambon	Bcl2316PM803	MZB Cru Cir 016-1	MK995339	MK981352
7	*A. zhujiangensis*	Sulawesi	Bcl4517PM1405	Bcl 4517PM1405	MK995340	MK981353
8	*A. zhujiangensis*	Sulawesi	Bcl4517PM1407	Bcl4517PM1407	MK995341	MK981354
9	*Amphibalanus variegatus*	Saparua	Bcl5316PM1004	MZB Cru Cir 013-1	MK995342	-
10	*A. variegatus*	Saparua	X3PM922	MZB Cru Cir 015-2	MK995343	-
11	*A. variegatus*	Saparua	X2PM732	MZB Cru Cir 015-1	MK995344	-
12	*A. variegatus*	Saparua	Bcl4416PM953	MZB Cru Cir 013-2	MK995345	MK981355
13	*A. variegatus*	Sulawesi	Bcl7717PM1874	Bcl7717PM1874	MK995346	-
14	*Amphibalanus amphitrite*	Sulawesi	Bcl6317PM1730	Bcl6317PM1730	MK995347	-
15	*A. amphitrite*	Sulawesi	Bcl6317PM1780	Bcl6317PM1780	MK995348	-
16	*Amphibalanus* sp.	Ambon	Bcl1117PM125	MZB Cru Cir 136	MK995349	MK981356
17	*A.* sp.	Seram	Bcl4117PM1379	MZB Cru Cir 137-2	MK995350	MK981357
18	*A.* sp.	Ambon	Bcl4216PM937	MZB Cru Cir 135	MK995351	MK981358
19	*A.* sp.	Sulawesi	Bcl5217PM1550	Bcl5217PM1550	MK995352	MK981359
20	*A.* sp.	Seram	Bcl4117PM1378	MZB Cru Cir 137-1	MK995353	MK981360
21	*A.* sp.	Sulawesi	Bcl7517PM1857	Bcl7517PM1857	MK995354	MK981361
22	*Acasta* sp.	Sulawesi	Y0117PM1750	Y0117PM1750	-	MK981362
23	*Tetraclita singaporensis*	Sulawesi	Bcl5417PM1640	Bcl5417PM1640	MK995355	MK981363
24	*T. singaporensis*	Sulawesi	Bcl5717PM1663	Bcl5717PM1663	MK995356	MK981364
25	*T. singaporensis*	Sulawesi	Bcl5917PM1699	Bcl5917PM1699	MK995357	MK981365
26	*T. singaporensis*	Sulawesi	Bcl7617PM1867	Bcl7617PM1867	MK995358	MK981366

27	*T. singaporensis*	Sulawesi	Bcl7417PM1847	Bcl7417PM1847	MK995359	MK981367
28	*Tetraclita squamosa*	Saparua	Bcl8416PM1199	MZB Cru Cir 093-1	MK995360	MK981368
29	*T. squamosa*	Ambon	Bcl1517PM291	MZB Cru Cir 081-1	MK995361	MK981369
30	*T. squamosa*	Saparua	Bcl4916PM986	MZB Cru Cir 095-1	MK995362	MK981370
31	*T. squamosa*	Ambon	Bcl1717PM347	MZB Cru Cir 096-1	-	MK981371
32	*T. squamosa*	Ambon	Bcl0917PM120	MZB Cru Cir 092-1	-	MK981372
33	*T. squamosa*	Ambon	Bcl3017PM720	MZB Cru Cir 099-1	-	MK981373
34	*T. squamosa*	Sulawesi	Bcl6517PM1769	Bcl6517PM1769	-	MK981374
35	*Tetraclita kuroshioensis*	Ambon	Bcl0317PM13	MZB Cru Cir 097	MK995363	MK981375
36	*T. kuroshioensis*	Ambon	Bcl0717PM39	MZB Cru Cir 098-1	MK995364	MK981376
37	*T. kuroshioensis*	Sulawesi	Bcl6417PM1740	Bcl6417PM1740	MK995365	MK981377
38	*T. kuroshioensis*	Sulawesi	Bcl4417PM1403	Bcl4417PM1403	MK995366	MK981378
39	*T. kuroshioensis*	Saparua	Bcl7916PM1180	MZB Cru Cir 100	MK995367	MK981379
40	*Newmanella spinosus*	Sulawesi	Bcl4817PM1441	Bcl4817PM1441	MK995368	-
41	*Yamaguchiella coerulescens*	Ambon	Bcl1216PM494	MZB Cru Cir 126-1	-	MK981381
42	*Neonrosella vitiata*	Ambon	X1PM723	MZB Cru Cir 132-1	-	MK981384
43	*Tesseropora rosea*	Ambon	Bcl0216PM27	MZB Cru Cir 075-1	MK995370	-
44	*Dosima fascicularis*	Ambon	Bcl2417PM500	MZB Cru Cir 048-1	MK995371	MK981385
45	*Heteralepas japonica*	Deep sea	Bcl9416PM1911	MZB Cru Cir 050-1	MK995372	MK981386
46	*Lepas anserifera*	Ambon	Bcl2317PM495	MZB Cru Cir 059-1	MK995373	-
47	*L. anserifera*	Seram	Bcl3417PM1322	MZB Cru Cir 061-1	MK995374	MK981387
48	*L. anserifera*	Seram	Bcl3517PM1323	MZB Cru Cir 062-1	MK995375	MK981388
49	*Nesochthamalus intertextus*	Ambon	Bcl2217PM429	MZB Cru Cir 070-1	MK995376	MK981389
50	*Capitulum mitella*	Ambon	Bcl0617PM34	MZB Cru Cir 032-1	-	MK981390
51	*Chthamalus moro*	Ambon	Bcl0417PM14	MZB Cru Cir 039-1	MK995377	MK981391
52	*C. moro*	Saparua	Bcl4116PM902	MZB Cru Cir 046-1	MK995378	-
53	*C. moro*	Saparua	Bcl3316PM872	MZB Cru Cir 045-1	MK995379	MK981392
54	*C. moro*	Ambon	Bcl1417PM289	MZB Cru Cir 036-1	MK995380	-
55	*C. moro*	Pombo	Bcl8816PM1217	MZB Cru Cir 043-1	MK995381	MK981393
56	*C. moro*	Seram	Bcl4317PM1388	MZB Cru Cir 047-1	MK995382	MK981394
57	*C. moro*	Ambon	Bcl1217PM243	MZB Cru Cir 040-1	MK995383	MK981395
58	*C. moro*	Saparua	Bcl5916PM1052	MZB Cru Cir 044-2	MK995384	MK981396
59	*C. moro*	Pombo	Bcl8816PM1218	MZB Cru Cir 043-2	MK995385	MK981397
60	*C. moro*	Saparua	Bcl2116PM787	MZB Cru Cir 044-1	MK995386	MK981398
61	*C. moro*	Ambon	Bcl2717PM613	MZB Cru Cir 041-1	MK995387	MK981399
62	*C. moro*	Seram	Bcl4317PM1389	MZB Cru Cir 047-2	MK995388	MK981400

63	*Microeuraphia* sp.	Seram	Bcl3917PM1358	MZB Cru Cir 138-1	MK995389	MK981401
64	*M.* sp.	Seram	Bcl3917PM1359	MZB Cru Cir 138-2	MK995390	MK981402
65	*M.* sp.	Sulawesi	Bcl4917PM1510	Bcl4917PM1510	MK995391	MK981403
66	*M.* sp.	Sulawesi	Bcl5517PM1641	Bcl5517PM1641	MK995392	MK981404
67	*M.* sp.	Sulawesi	X4PM1494	X4PM1494	MK995393	MK981405
68	*M.* sp.	Sulawesi	Bcl5317PM1625	Bcl5317PM1625	MK995394	-
69	*M.* sp.	Sulawesi	Bcl6217PM1725	Bcl6217PM1725	MK995395	MK981406
70	*M.* sp.	Sulawesi	X5PM1581	X5PM1581	MK995396	MK981407

Table 7.2. Measurements for *Heteralepas japonica* (N = 25).

Parameter	Range (mm)	Mean ± SD (mm)	Median (mm)
A	11.9-18.6	15.1 ± 0.9	14.5
B	8.7-15.3	12.2 ± 2.5	12.2
C	7.7-27.6	16.3 ± 2.7	11.1
D	3.2-9.4	6.5 ± 0.8	4.4
E	2.0-3.0	2.5 ± 0.0	2.0
F	7.0-13.3	9.1 ± 0.2	7.6
G	5.1-10.4	7.3 ± 1.0	7.2
A/B	1.1-1.5	1.2 ± 0.2	1.2
A/C	0.6-1.7	1.0 ± 0.4	1.4
A/D	1.6-3.9	2.5 ± 0.8	3.3
A/E	4.1-9.2	6.3 ± 0.5	7.2
A/F	1.4-2.1	1.7 ± 0.1	1.9
A/G	1.6-2.5	2.1 ± 0.4	2.0
B/C	0.5-1.5	0.7 ± 0.5	1.2
B/D	1.4-3.6	2.0 ± 1.1	2.8
B/E	2.9-6.9	5.1 ± 1.2	6.1
B/F	1.1-1.8	1.4 ± 0.3	1.6
B/G	1.3-2.1	1.7 ± 0.6	1.7
C/D	1.3-4.8	2.7 ± 0.2	2.5
C/E	3.8-12.5	6.5 ± 1.3	5.5
C/F	0.9-3.1	1.8 ± 0.4	1.5
C/G	1.3-3.9	2.2 ± 0.2	1.5
D/E	1.7-4.1	2.7 ± 0.4	2.2
D/F	0.4-1.1	0.7 ± 0.1	0.6
D/G	0.6-1.3	0.9 ± 0.0	0.6
E/F	0.2-0.4	0.3 ± 0.0	0.3
E/G	0.2-0.5	0.4 ± 0.0	0.3
F/G	0.9-1.8	1.3 ± 0.2	1.1

Key to parameters: A = capitulum height; B = capitulum width; C = peduncle length; D = orifice height; E = number of crests; F = capitulum thickness; G = peduncle width.

Table 7.3. Measurements for *Dosima fascicularis* (N = 6).

Parameter	Range (mm)	Mean ± SD (mm)	Median (mm)
TH	11.7-19.5	16.0 ± 0.8	19.0
CH	10.5-17.1	13.7 ± 2.5	15.3
DBC	4.0-6.8	5.5 ± 0.2	6.6
CS	6.5-10.2	8.3 ± 1.2	9.4
LS	8.1-11.1	9.6 ± 0.8	10.6
WS	5.4-7.3	6.9 ± 1.0	8.0
LT	6.2-11.1	8.6 ± 1.6	10.0
WT	2.7-4.4	3.6 ± 0.8	3.8
TH/CH	1.1-1.2	1.2 ± 0.2	1.3
TH/DBC	2.6-3.2	2.9 ± 0.0	2.9
TH/CS	1.8-2.2	1.9 ± 0.2	2.0
TH/LS	1.4-1.9	1.7 ± 0.1	1.8
TH/WS	2.2-2.6	2.3 ± 0.2	2.9
TH/LT	1.7-2.1	1.9 ± 0.2	1.9
TH/WT	2.9-5.7	4.5 ± 0.9	5.1
CH/DBC	2.1-2.7	2.5 ± 0.3	2.3
CH/CS	1.6-1.7	1.6 ± 0.2	1.6
CH/LS	1.3-1.5	1.4 ± 0.1	1.5
CH/WS	1.9-2.1	2.0 ± 0.1	1.9
CH/LT	1.5-1.7	1.6 ± 0.0	1.5
CH/WT	2.6-4.2	3.8 ± 0.2	4.1
DBC/CS	0.6-0.8	0.7 ± 0.1	0.7
DBC/LS	0.5-0.7	0.6 ± 0.0	0.6
DBC/WS	0.7-0.9	0.8 ± 0.1	0.8
DBC/LT	0.6-0.7	0.6 ± 0.1	0.7
DBC/WT	1.0-2.0	1.5 ± 0.3	1.8
CS/LS	0.8-0.9	0.9 ± 0.0	0.9
CS/WS	1.2-1.2	1.2 ± 0.0	1.2
CS/LT	0.9-1.1	1.0 ± 0.0	0.9
CS/WT	1.6-2.7	2.3 ± 0.2	2.5
LS/WS	1.3-1.5	1.4 ± 0.1	1.3
LS/LT	1.0-1.3	1.1 ± 0.1	1.1
LS/WT	2.1-3.1	2.7 ± 0.4	2.8
WS/LT	0.7-0.9	0.8 ± 0.0	0.8
WS/WT	1.3-2.3	1.9 ± 0.2	2.1
LT/WT	1.5-2.8	2.4 ± 0.2	2.6

Key to parameters: TH = total height; CH = capitulum height; DBC = diameter of the base of capitulum; LS = scutum length; WS = scutum width; LT = tergum length; WT = tergum width.

Table 7.4. Measurements for *Lepas anserifera* (N = 25).

Parameter	Range (mm)	Mean ± SD (mm)	Median (mm)
TH	14.2-31.9	21.1 ± 4.0	22.2
CH	8.1-14.8	12.0 ± 1.3	13.0
DBC	2.0-7.2	4.0 ± 0.6	4.0
CS	5.2-12.4	8.1 ± 1.5	8.5
LS	6.3-12.3	9.6 ± 1.3	9.6
WS	4.7-11.3	7.3 ± 1.2	7.7
LT	4.3-9.6	7.7 ± 0.6	7.9
WT	1.6-3.2	2.5 ± 0.2	2.7
TH/CH	1.3-2.5	1.8 ± 0.1	1.7
TH/DBC	2.7-7.2	5.5 ± 0.2	5.6
TH/CS	1.3-3.8	2.6 ± 0.0	2.6
TH/LS	1.3-3.1	2.2 ± 0.1	2.3
TH/WS	1.5-4.1	2.9 ± 0.0	2.9
TH/LT	2.1-5.5	2.8 ± 0.3	2.8
TH/WT	5.8-13.8	8.5 ± 1.0	8.1
CH/DBC	1.7-4.7	3.2 ± 0.1	3.3
CH/CS	1.0-1.7	1.5 ± 0.1	1.5
CH/LS	1.0-1.4	1.3 ± 0.1	1.4
CH/WS	1.1-2.0	1.7 ± 0.1	1.7
CH/LT	1.3-2.2	1.6 ± 0.0	1.7
CH/WT	3.9-5.9	4.8 ± 0.2	4.7
DBC/CS	0.3-0.8	0.5 ± 0.0	0.5
DBC/LS	0.3-0.7	0.4 ± 0.0	0.4
DBC/WS	0.4-0.9	0.6 ± 0.0	0.5
DBC/LT	0.3-0.9	0.5 ± 0.0	0.5
DBC/WT	0.9-3.3	1.6 ± 0.1	1.4
CS/LS	0.7-1.0	0.9 ± 0.0	0.9
CS/WS	1.0-1.2	1.1 ± 0.0	1.1
CS/LT	0.9-1.8	1.1 ± 0.1	1.1
CS/WT	2.4-5.5	3.3 ± 0.4	3.1
LS/WS	1.1-1.8	1.3 ± 0.0	1.3
LS/LT	1.1-2.0	1.3 ± 0.1	1.2
LS/WT	3.6-5.6	3.9 ± 0.3	3.5
WS/LT	0.8-1.6	1.0 ± 0.1	1.0
WS/WT	2.1-5.1	2.9 ± 0.3	2.8
LT/WT	2.4-4.3	3.1 ± 0.1	2.9

Key to parameters: TH = total height; CH = capitulum height; DBC = diameter of the base of capitulum; LS = scutum length; WS = scutum width; LT = tergum length; WT = tergum width.

Table 7.5. Measurements for *Capitulum mitella* (N = 25).

Parameter	Range (mm)	Mean ± SD (mm)	Median (mm)
TH	10.7-7.1	24.7 ± 10.7	26.7
CH	7.0- 4.6	14.9 ± 5.4	16.6
RC	5.8-27.3	15.6 ± 6.3	17.1
RT	5.5-24.2	13.7 ± 5.7	15.2
DBC	4.5-20.4	11.0 ± 10.8	10.6
TH/CH	1.2-2.2	1.6 ± 1.6	1.6
TH/RC	1.0-2.2	1.6 ± 0.3	1.6
TH/RT	1.3-2.5	1.8 ± 0.3	1.8
TH/DBC	1.5-2.9	2.3 ± 0.4	2.3
CH/RC	0.7-1.2	1.0 ± 0.1	1.0
CH/RT	0.8-1.4	1.1 ± 0.1	1.1
CH/DBC	0.9-1.9	1.4 ± 1.4	1.4
RC/RT	0.9-1.3	1.2 ± 1.2	1.2
RC/DBC	1.3-1.7	1.4 ± 0.1	1.4
RT/DBC	1.0-1.5	1.3 ± 0.1	1.2

Key to parameters: TH = total height; CH = capitulum height; RC = distance from rostrum to carina; RT = rostrum height; DBC = capitulum diameter.

Table 7.6. Measurements for *Pseudoctomeris sulcata* (N = 2).

Parameter	Range (mm)	Mean ± SD (mm)	Median (mm)
LB	16.2-16.7	16.4 ± 0.3	16.4
LO	5.5-7.9	6.7 ± 1.8	6.7
H	7.4-7.7	7.6 ± 0.2	7.6
WO	4.3-6.1	5.2 ± 1.3	5.2
WB	11.5-15.0	13.3 ± 2.5	13.3
LB/LO	2.0-3.1	2.5 ± 0.7	2.6
LB/H	2.1-2.2	2.2 ± 0.1	2.2
LB/WO	2.7-3.9	3.3 ± 0.9	3.3
LB/WB	1.1-1.5	1.3 ± 0.3	1.3
LO/H	0.7-1.0	0.9 ± 0.2	0.9
LO/WO	1.3-1.3	1.3 ± 0.0	1.3
LO/WB	0.5-0.5	0.5 ± 0.0	0.5
WO/H	0.6-0.8	0.7 ± 0.2	0.7
WB/H	1.5-1.9	1.8 ± 0.3	1.7
WB/WO	2.5-2.7	2.6 ± 0.2	2.6

Key to parameters: LB = basal lenght; LO = orifice lenght; H = carinal heigth; WO = orifice width; WB = basal width.

Table 7.7. Measurements for *Hexechamaesipho pilsbryi* (N = 10).

Parameter	Range (mm)	Mean ± SD (mm)	Median (mm)
LB	8.9-17.0	14.1 ± 3.4	14.6
LO	4.2-6.9	5.7 ± 0.5	5.4
H	1.0-3.7	1.7 ± 0.1	1.7
WO	3.6-5.6	4.3 ± 0.0	3.7
WB	10.3-16.4	13.4 ± 0.3	12.6
LB/LO	1.7-4.5	2.3 ± 0.4	2.7
LB/H	0.8-1.3	8.4 ± 2.6	8.7
LB/WO	1.4-6.6	3.3 ± 0.9	3.9
LB/WB	0.8-1.4	1.1 ± 0.3	1.2
LO/H	1.4-6.6	3.4 ± 0.5	3.2
LO/WO	1.0-1.7	1.3 ± 0.1	1.5
LO/WB	0.3-0.5	0.4 ± 0.1	0.4
WO/H	1.4-3.9	2.6 ± 0.2	2.2
WB/H	3.1-16.6	8.0 ± 0.3	7.4
WB/WO	2.2-4.3	3.1 ± 0.1	3.4

Key to parameters: LB = basal lenght; LO = orifice lenght; H = carinal heigth; WO = orifice width; WB = basal width.

Table 7.8. Measurements for *Nesochthamalus intertextus* (N = 10).

Parameter	Range (mm)	Mean ± SD (mm)	Median (mm)
LB	8.9-12.1	10.5 ± 0.2	11.0
LO	3.0-4.9	3.8 ± 0.5	4.6
H	1.3-3.1	2.2 ± 0.3	2.2
WO	2.5-3.9	3.3 ± 0.3	3.7
WB	6.9-10.3	9.0 ± 0.4	10.0
LB/LO	2.2-3.5	2.8 ± 0.3	2.4
LB/H	3.5-8.1	5.0 ± 0.6	5.1
LB/WO	2.8-3.9	3.2 ± 0.3	3.0
LB/WB	0.9-1.4	1.2 ± 0.1	1.1
LO/H	1.3-2.3	1.8 ± 0.0	2.1
LO/WO	1.0-1.4	1.2 ± 0.2	1.2
LO/WB	0.4-0.6	0.4 ± 0.1	0.5
WO/H	1.2-2.1	1.5 ± 0.4	1.7
WB/H	2.6-6.0	4.3 ± 0.8	4.7
WB/WO	2.2-3.8	2.8 ± 0.1	2.7

Key to parameters: LB = basal length; LO = orifice length; H = carinal height; WO = orifice width; WB = basal width.

Table 7.9. Measurements for *Euraphia hembeli* (N = 1).

Parameter	Value (mm)
LB	37.4
LO	18.3
H	14.3
WO	15.2
WB	28.6
LB/LO	2.1
LB/H	2.6
LB/WO	2.5
LB/WB	1.3
LO/H	1.3
LO/WO	1.2
LO/WB	0.6
WO/H	1.1
WB/H	2.0
WB/WO	1.9

Key to parameters: LB = basal length; LO = orifice length; H = carinal height; WO = orifice width; WB = basal width.

Table 7.10. Measurements for *Microeuraphia* sp. (N = 2).

Parameter	Range (mm)	Mean ± SD (mm)	Median (mm)
LB	3.6-9.9	6.8 ± 4.4	6.8
LO	1.5-4.5	3.0 ± 2.2	3.0
H	1.2-2.2	1.7 ± 0.8	1.7
WO	0.7-3.6	2.1 ± 2.0	2.1
WB	3.0-9.1	6.0 ± 4.3	6.0
LB/LO	2.2-2.5	2.3 ± 0.2	2.3
LB/H	3.1-4.3	3.7 ± 0.9	3.7
LB/WO	2.8-5.0	3.9 ± 1.5	3.9
LB/WB	1.1-1.2	1.1 ±0.1	1.1
LO/H	1.2-2.0	1.6 ± 0.5	1.6
LO/WO	1.3-2.0	1.6 ± 0.5	1.6
LO/WB	0.4-0.5	0.5 ± 0.0	0.5
WO/H	0.6-1.6	1.1 ± 0.7	1.1
WB/H	2.6-4.0	3.3 ± 1.0	3.3
WB/WO	2.1-4.0	3.3 ± 1.2	3.3

Key to parameters: LB = basal length; LO = orifice length; H = carinal height; WO = orifice width; WB = basal width.

Table 7.11. Measurements for *Chthamalus moro* (N = 25).

Parameter	Range (mm)	Mean ± SD (mm)	Median (mm)
LB	2.4-5.1	3.6 ± 0.8	4.5
LO	1.0-3.4	1.7 ± 1.5	2.4
H	0.8-1.7	1.3 ± 0.0	1.7
WO	0.7-1.7	1.2 ± 0.1	1.1
WB	1.4-4.1	2.8 ± 0.5	3.7
LB/LO	1.4-3.3	2.3 ± 1.0	2.2
LB/H	2.0-4.4	2.9 ± 0.5	2.7
LB/WO	1.7-4.3	3.2 ± 0.4	4.1
LB/WB	1.1-1.7	1.3 ± 0.0	1.2
LO/H	0.8-2.4	1.4 ± 0.9	1.4
LO/WO	0.8-2.9	1.5 ± 1.1	2.1
LO/WB	0.4-1.2	0.6 ± 0.3	0.6
WO/H	0.6-1.4	0.9 ± 0.1	0.7
WB/H	1.2-3.2	2.3 ± 0.3	2.2
WB/WO	1.0-3.5	2.5 ± 0.2	3.4

Key to parameters: LB = basal length; LO = orifice length; H = carinal height; WO = orifice width; WB = basal width.

Table 7.12. Measurements for *Tetraclitella divisa* (N = 1).

Parameter	Value (mm)
LB	11.1
LO	4.9
H	2.4
WO	3.5
WB	9.7
LB/LO	2.3
LB/H	4.7
LB/WO	3.1
LB/WB	1.2
LO/H	2.1
LO/WO	1.4
LO/WB	0.5
WO/H	1.5
WB/H	4.1
WB/WO	2.7

Key to parameters: LB = basal length; LO = orifice length; H = carinal height; WO = orifice width; WB = basal width.

Table 7.13. Measurements for *Tetraclitella karandei* (N = 3).

Parameter	Range (mm)	Mean ± SD (mm)	Median (mm)
LB	10.1-17.4	14.2 ± 3.7	12.7
LO	3.8-5.6	4.5 ± 3.7	4.0
H	0.4-0.7	0.6 ± 0.1	0.7
WO	2.7-5.2	3.8 ± 0.6	3.2
WB	8.2-18.2	13.4 ± 4.0	11.1
LB/LO	2.7-3.6	3.1 ± 0.7	3.1
LB/H	13.6-48.3	29.3 ± 8.7	19.7
LB/WO	3.3-4.3	3.8 ± 0.4	4.0
LB/WB	1.0-1.2	1.1 ± 0.1	1.2
LO/H	5.1-15.4	9.2 ± 1.5	6.2
LO/WO	1.1-1.4	1.2 ± 0.2	1.3
LO/WB	0.3-0.5	0.4 ± 0.1	0.4
WO/H	3.7-14.5	8.1 ± 1.7	4.9
WB/H	11.1-50.5	28.4 ± 8.8	17.3
WB/WO	3.0-3.9	3.5 ± 0.6	3.5

Key to parameters: LB = basal length; LO = orifice length; H = carinal height; WO = orifice width; WB = basal width.

Table 7.14. Measurements for *Tesseropora rosea* (N = 15).

Parameter	Range (mm)	Mean ± SD (mm)	Median (mm)
LB	9.7-25.6	16.6 ± 7.5	19.1
LO	2.9-7.8	6.1 ± 0.1	6.0
H	4.4-13.0	8.4 ± 2.8	9.0
WO	2.3-6.9	5.3 ± 0.5	5.0
WB	9.7-24.5	15.2 ± 10.5	17.1
LB/LO	1.5-4.9	2.8 ± 1.2	3.2
LB/H	1.4-3.6	2.0 ± 0.2	2.1
LB/WO	1.8-5.4	3.3 ± 1.9	3.9
LB/WB	0.8-1.4	1.1 ± 0.3	1.2
LO/H	0.3-1.5	0.8 ± 0.2	0.7
LO/WO	1.1-1.3	1.2 ± 0.2	1.2
LO/WB	0.2-0.8	0.4 ± 0.3	0.4
WO/H	0.3-1.4	0.7 ± 0.3	0.6
WB/H	1.2-4.2	1.9 ± 0.6	1.8
WB/WO	1.7-5.3	3.0 ± 2.5	3.5

Key to parameters: LB = basal length; LO = orifice length; H = carinal height; WO = orifice width; WB = basal width.

Table 7.15. Measurements for *Tetraclita kuroshioensis* (N = 5).

Parameter	Range (mm)	Mean ± SD (mm)	Median (mm)
LB	12.1-21.6	17.2 ± 5.8	16.2
LO	3.2-5.3	3.9 ± 0.2	3.8
H	7.3-10.4	8.4 ± 1.1	8.0
WO	2.4-4.2	2.9 ± 0.3	2.6
WB	18.1-21.8	17.7 ± 5.0	14.5
LB/LO	3.3-5.4	4.5 ± 1.3	4.3
LB/H	1.4-2.8	2.1 ± 1.0	2.1
LB/WO	4.4-8.4	6.0 ± 2.9	6.4
LB/WB	0.8-1.1	1.0 ± 0.0	1.1
LO/H	0.4- 0.5	0.5 ± 0.1	0.5
LO/WO	1.2-1.6	1.3 ± 0.2	1.5
LO/WB	0.2-0.3	0.2 ± 0.1	0.3
WO/H	0.3-0.4	0.4 ± 0.0	0.3
WB/H	1.3-2.5	2.1 ± 0.9	1.9
WB/WO	3.9-7.5	6.1 ± 2.5	5.7

Key to parameters: LB = basal length; LO = orifice length; H = carinal height; WO = orifice width; WB = basal width.

Table 7.16. Measurements for *Tetraclita squamosa* (N = 5).

Parameter	Range (mm)	Mean ± SD (mm)	**Median (mm)**
LB	20.1-30.2	25.4 ± 3.4	27.6
LO	4.4-7.9	6.1 ± 1.7	6.7
H	11.9-14.2	12.9 ± 0.3	12.5
WO	3.4-7.2	5.3 ± 1.4	5.7
WB	19.3-28.3	24.8 ± 0.2	26.0
LB/LO	3.8-4.6	4.2 ± 0.6	4.2
LB/H	1.6-2.4	2.0 ± 0.2	2.2
LB/WO	4.2-5.9	4.9 ± 0.6	4.9
LB/WB	0.9-1.2	1.0 ± 0.1	1.1
LO/H	0.4-0.6	0.5 ± 0.1	0.5
LO/WO	1.0-1.3	1.2 ± 0.0	1.2
LO/WB	0.2-0.3	0.3 ± 0.1	0.3
WO/H	0.3-0.5	0.4 ± 0.1	0.5
WB/H	1.6-2.1	1.9 ± 0.0	2.1
WB/WO	3.9-5.7	4.9 ± 1.1	4.7

Key to parameters: LB = basal length; LO = orifice length; H = carinal height; WO = orifice width; WB = basal width.

Table 7.17. Measurements for *Yamaguchiella coerulescens* (N = 25).

Parameter	Range (mm)	Mean ± SD (mm)	Median (mm)
LB	8.3 – 29.0	19.5 ± 12.6	17.2
LO	4.2 – 11.5	7.1 ± 3.3	6.8
H	5.7 – 17.7	11.0 ± 5.2	9.3
WO	3.2 – 11.8	7.1 ± 4.1	7.4
WB	8.5 – 27.8	19.7 ±12.0	18.6
LB/LO	1.8 – 3.5	2.8 ± 0.7	2.3
LB/H	1.4 – 2.7	1.8 ±0.4	1.7
LB/WO	1.9 – 3.7	2.8 ± 0.5	2.2
LB/WB	0.8 – 1.3	0.1 ± 0.1	0.9
LO/H	0.5 – 1.0	0.7 ± 0.1	0.8
LO/WO	0.9 – 1.3	1.0 ± 0.1	0.9
LO/WB	0.3 – 0.5	0.4 ± 0.1	0.4
WO/H	0.5 – 0.9	0.7 ± 0.0	0.8
WB/H	1.4 – 2.9	1.8 ± 0.2	1.9
WB/WO	2.1 – 3.8	2.8 ± 0.3	2.4

Key to parameters: LB = basal length; LO = orifice length; H = carinal height; WO = orifice width; WB = basal width.

Table 7.18. Measurements for *Neonrosella vitiata* (N = 4).

Parameter	Range (mm)	Mean ± SD (mm)	Median (mm)
LB	15.4-22.8	18.9 ± 5.3	19.1
LO	5.2-6.9	5.9 ± 0.5	5.8
H	5.3-6.9	5.8 ± 0.3	5.5
WO	5.0-5.4	5.1 ± 0.2	5.2
WB	13.8-22.8	18.8 ± 6.3	18.3
LB/LO	2.8-3.7	3.2 ± 0.6	3.3
LB/H	2.9-4.0	3.3 ± 0.8	3.4
LB/WO	3.1-4.3	3.7 ± 0.9	3.7
LB/WB	0.9-1.1	1.0 ± 0.1	1.1
LO/H	1.0-1.1	1.0 ± 0.0	1.0
LO/WO	1.1-1.3	1.2 ± 0.0	1.1
LO/WB	0.3-0.4	0.3 ± 0.1	0.3
WO/H	0.8-0.9	0.9 ± 0.0	0.9
WB/H	2.6-4.0	3.2 ± 1.0	3.3
WB/WO	2.8-4.3	3.7 ± 1.1	3.5

Key to parameters: LB = basal length; LO = orifice length; H = carinal height; WO = orifice width; WB = basal width.

Table 7.19. Measurements for *Newmanella spinosus* (N = 5).

Parameter	Range (mm)	Mean ± SD (mm)	Median (mm)
LB	17.4-21.0	19.3 ± 1.1	18.2
LO	5.3-7.2	6.5 ± 0.7	5.8
H	6.8-8.9	8.1 ± 1.5	7.8
WO	5.0-6.7	5.9 ± 0.2	5.1
WB	15.9-20.5	18.8 ± 2.5	17.6
LB/LO	2.7-3.3	3.0 ± 0.2	3.2
LB/H	2.0-2.8	2.4 ± 0.6	2.4
LB/WO	2.9-3.6	3.3 ± 0.1	3.5
LB/WB	1.0-1.1	1.0 ± 0.1	1.0
LO/H	0.6-0.9	0.8 ± 0.2	0.8
LO/WO	1.0-1.2	1.1 ± 0.1	1.1
LO/WB	0.3-0.4	0.4 ± 0.0	0.3
WO/H	0.6-0.8	0.7 ± 0.2	0.7
WB/H	1.8-2.9	2.4 ± 0.8	2.3
WB/WO	2.9-3.7	3.2 ± 0.4	3.4

Key to parameters: LB = basal length; LO = orifice length; H = carinal height; WO = orifice width; WB = basal width.

Table 7.20. Measurements for *Amphibalanus amphitrite* (N = 15).

Parameter	Range (mm)	Mean ± SD (mm)	Median (mm)
LB	3.1-17.8	10.3 ± 1.2	9.2
LO	1.5-8.1	5.1 ± 1.5	4.0
H	2.1-10.8	5.4 ± 0.4	4.7
WO	1.5-5.4	3.8 ± 1.2	2.9
WB	2.8-17.6	8.6 ± 1.6	6.5
LB/LO	1.4-3.3	2.0 ± 0.7	2.6
LB/H	1.2-5.8	2.0 ± 0.1	2.0
LB/WO	1.7-4.9	2.2 ± 1.2	3.7
LB/WB	0.8-2.7	1.2 ± 0.2	1.5
LO/H	0.6-3.2	1.0 ± 0.3	0.8
LO/WO	0.9-1.6	1.3 ± 0.1	1.4
LO/WB	0.3-1.1	0.6 ± 0.1	0.6
WO/H	0.4-2.0	0.8 ± 0.2	0.6
WB/H	0.6-4.7	1.7 ± 0.2	1.4
WB/WO	1.4-3.5	2.3 ± 0.5	2.5

Key to parameters: LB = basal length; LO = orifice length; H = carinal height; WO = orifice width; WB = basal width.

Table 7.21. Measurements for *Amphibalanus reticulatus* (N = 5).

Parameter	Range (mm)	Mean ± SD (mm)	**Median (mm)**
LB	7.7-16.3	12.1 ± 2.7	10.7
LO	3.5-8.9	6.8 ± 1.2	5.7
H	3.2-10.5	6.9 ± 0.9	5.2
WO	2.5-7.1	4.9 ± 0.8	3.5
WB	2.9-15.5	10.0 ± 2.4	9.6
LB/LO	1.5-2.5	1.8 ± 0.1	1.9
LB/H	1.3-3.2	1.8 ± 0.2	2.0
LB/WO	1.8-3.5	2.5 ± 0.1	3.1
LB/WB	0.9-4.9	1.4 ± 0.0	1.1
LO/H	0.8-1.4	1.0 ± 0.0	1.1
LO/WO	1.1-1.9	1.4 ± 0.1	1.7
LO/WB	0.5-3.0	0.8 ± 0.0	0.7
WO/H	0.5-1.0	0.7 ± 0.0	0.7
WB/H	0.3-2.5	1.5 ± 0.2	1.8
WB/WO	0.4-3.0	2.1 ± 0.1	2.7

Key to parameters: LB = basal length; LO = orifice length; H = carinal height; WO = orifice width; WB = basal width.

Table 7.22. Measurements for *Amphibalanus variegatus* (N = 10).

Parameter	**Range (mm)**	**Mean ± SD (mm)**	**Median (mm)**
LB	8.3-11.8	10.3 ± 1.1	9.3
LO	4.8-8.8	6.4 ± 0.4	5.2
H	4.3-8.4	5.7 ± 0.8	5.1
WO	3.4-5.3	4.2 ± 0.3	3.9
WB	6.9-10.4	9.1 ± 1.4	8.3
LB/LO	1.3-2.0	1.7 ± 0.1	1.8
LB/H	1.4-2.1	1.9 ± 0.1	1.8
LB/WO	2.2-2.8	2.5 ± 0.1	2.4
LB/WB	1.0-1.2	1.1 ± 0.1	1.1
LO/H	0.9-1.4	1.1 ± 0.1	1.0
LO/WO	1.3-1.8	1.5 ± 0.0	1.3
LO/WB	0.6-0.9	0.7 ± 0.1	0.6
WO/H	0.6-0.9	0.8 ± 0.1	0.8
WB/H	1.2-1.9	1.7 ± 0.0	1.6
WB/WO	1.9-2.4	2.2 ± 0.2	2.1

Key to parameters: LB = basal length; LO = orifice length; H = carinal height; WO = orifice width; WB = basal width.

Table 7.23. Measurements for *Amphibalanus zhujiangensis* (N = 11).

Parameter	Range (mm)	Mean ± SD (mm)	Median (mm)
LB	5.8-21.6	12.6 ± 7.9	13.7
LO	3.0-10.0	6.5 ± 3.1	6.1
H	2.8-16.5	8.7 ± 4.1	6.9
WO	2.6-7.6	4.9 ± 1.8	4.8
WB	4.8-19.2	10.5 ± 3.7	8.8
LB/LO	1.2-2.4	1.9 ± 0.2	2.2
LB/H	0.9-2.1	1.5 ± 0.1	2.0
LB/WO	2.0-3.4	2.5 ± 0.7	2.6
LB/WB	1.0-1.7	1.2 ± 0.3	1.4
LO/H	0.5-1.1	0.8 ± 0.1	0.9
LO/WO	1.0-1.7	1.3 ± 0.2	1.2
LO/WB	0.5-0.9	0.7 ± 0.1	0.7
WO/H	0.4-1.1	0.6 ± 0.2	0.8
WB/H	0.7-1.8	1.3 ± 0.4	1.5
WB/WO	1.6-3.1	2.1 ± 0.1	1.8

Key to parameters: LB = basal length; LO = orifice length; H = carinal height; WO = orifice width; WB = basal width.

Table 7.24. Measurements for *Amphibalanus* sp. (N = 4).

Parameter	Range (mm)	Mean ± SD (mm)	Median (mm)
LB	7.4-12.2	10.8 ± 2.3	11.9
LO	3.6-8.3	6.0 ± 1.9	6.9
H	5.5-9.4	7.1 ± 1.6	6.8
WO	2.6-5.9	4.3 ± 1.4	4.3
WB	6.3-11.8	9.4 ± 2.3	9.8
LB/LO	1.4-2.1	1.9 ± 0.3	2.0
LB/H	1.2-1.8	1.5 ± 0.3	1.5
LB/WO	1.9-3.2	2.6 ± 0.5	2.7
LB/WB	1.0-1.3	1.2 ± 0.1	1.2
LO/H	0.7-0.9	0.8 ± 0.1	0.9
LO/WO	1.3-1.6	1.4 ± 0.1	1.4
LO/WB	0.6-0.7	0.6 ± 0.1	0.6
WO/H	0.5-0.7	0.6 ± 0.1	0.6
WB/H	1.1-1.5	1.3 ± 0.1	1.3
WB/WO	2.0-2.6	2.3 ± 0.3	2.2

Key to parameters: LB = basal length; LO = orifice length; H = carinal height; WO = orifice width; WB = basal width.

Table 7.25. Measurements for *Megabalanus tintinnabulum* (N = 4).

Parameter	Range (mm)	Mean ± SD (mm)	Median (mm)
LB	26.0-49.2	37.3 ± 1.1	1.1
LO	13.7-16.3	15.2 ± 0.1	0.1
H	20.1-49.4	39.3 ± 16.5	16.5
WO	10.4-15.9	13.1 ± 3.7	3.7
WB	29.0-43.1	37.4 ± 9.9	10.0
LB/LO	1.6-3.1	2.5 ± 0.1	0.1
LB/H	0.6-1.9	1.1 ± 0.8	0.8
LB/WO	2.3-3.7	2.9 ± 0.9	0.9
LB/WB	0.8-1.3	1.0 ± 0.3	0.3
LO/H	0.3-0.8	0.4 ± 0.3	0.3
LO/WO	0.9-1.4	1.2 ± 0.4	0.4
LO/WB	0.4-0.5	0.4 ± 0.1	0.1
WO/H	0.3-0.5	0.4 ± 0.1	0.1
WB/H	0.8-1.4	1.0 ± 0.3	0.3
WB/WO	2.6-3.1	2.9 ± 0.0	0.0

Key to parameters: LB = basal length; LO = orifice length; H = carinal height; WO = orifice width; WB = basal width.

Table 7.26. Measurements for *Megabalanus zebra* (N = 8).

Parameter	Range (mm)	Mean ± SD (mm)	Median (mm)
LB	5.4-19.0	14.3 ± 5.0	8.9
LO	3.1-7.6	6.2 ± 2.8	5.1
H	4.4-13.1	9.2 ± 5.4	8.2
WO	1.7-6.2	4.4 ± 2.4	3.4
WB	5.0-20.0	13.6 ± 5.6	8.9
LB/LO	1.7-3.0	2.3 ± 0.0	1.7
LB/H	1.0-2.3	1.6 ± 0.1	1.1
LB/WO	2.5-3.9	3.2 ± 0.5	2.8
LB/WB	0.9-1.2	1.1 ± 0.1	1.0
LO/H	0.6-1.1	0.7 ± 0.1	0.7
LO/WO	1.2-1.8	1.5 ± 0.3	1.6
LO/WB	0.4-0.6	0.5 ± 0.1	0.6
WO/H	0.4-0.7	0.5 ± 0.0	0.4
WB/H	1.1-2.3	1.5 ± 0.0	1.1
WB/WO	2.5-3.8	3.1 ± 0.3	2.7

Key to parameters: LB = basal length; LO = orifice length; H = carinal height; WO = orifice width; WB = basal width.

Table 7.27. Kimura 2-parameter (K2P) distances of COI sequences between species

!Title: *Microeuraphia* sp1;

!Format DataType=Distance DataFormat=LowerLeft NTaxa=29;

!Description

Analysis ====================

Analysis = ====================

Scope = Pairs of taxa

Estimate Variance = ====================

Variance Estimation Method = Bootstrap method

No. of Bootstrap Replications = 1000

Substitution Model = ====================

Substitutions Type = Nucleotide

Model/Method = Kimura 2-parameter model

Substitutions to Include = d: Transitions + Transversions

Rates and Patterns = ====================

Rates among Sites = Uniform Rates

Pattern among Lineages = Same (Homogeneous)

Data Subset to Use = ====================

Gaps/Missing Data Treatment = Pairwise deletion

Select Codon Positions = 1st,2nd,3rd,Non-Coding

No. of Sites:641

d:Estimate

S.E:Standard error

[1] #Microeuraphia_sp1_Bcl3917PM1359_{Microeuraphia_sp1}

[2] #Microeuraphia_sp1_Bcl3917PM1358_{Microeuraphia_sp1}

[3] #Microeuraphia_sp2_JX083873.1_{Microeuraphia_sp2}

[4] #Microeuraphia_sp2_Bcl4917PM1510_{Microeuraphia_sp2}

[5] #Microeuraphia_sp2_Bcl5517PM1641_{Microeuraphia_sp2}

[6] #Microeuraphia_sp2_X4PM1494_{Microeuraphia_sp2}

[7] #Microeuraphia_sp2_Bcl6217PM1725_{Microeuraphia_sp2}

[8] #Microeuraphia_sp2_Bcl5317PM1625_{Microeuraphia_sp2}

[9] #Microeuraphia_sp2_X5PM1581_{Microeuraphia_sp2}

[10] #Chthamalus_moro_Bcl2116PM787_{Chthamalus_moro}

[11] #Chthamalus_moro_Bcl4317PM1388_{Chthamalus_moro}

[12] #Chthamalus_moro_Bcl4116PM902_{Chthamalus_moro}

[13] #Chthamalus_moro_Bcl0417PM14_{Chthamalus_moro}

[14] #Chthamalus_moro_Bcl1417PM289_{Chthamalus_moro}

[15] #Chthamalus_moro_Bcl3316PM872_{Chthamalus_moro}

[16] #Chthamalus_moro_Bcl8816PM1217_{Chthamalus_moro}

[17] #Chthamalus_moro_Bcl1217PM243_{Chthamalus_moro}

[18] #Chthamalus_moro_KJ010437.1_{Chthamalus_moro}

[19] #Chthamalus_moro_KJ010460.1_{Chthamalus_moro}

[20] #Chthamalus_moro_Bcl2717PM613_{Chthamalus_moro}

[21] #Chthamalus_moro_Bcl4317PM1389_{Chthamalus_moro}

[22] #Chthamalus_moro_Bcl5916PM1052_{Chthamalus_moro}

[23] #Chthamalus_moro_Bcl8816PM1218_{Chthamalus_moro}

[24] #Chthamalus_malayensis_EU304446.1_{Chthamalus_malayensis}

[25] #Chthamalus_malayensis_EU304427.1_{Chthamalus_malayensis}

[26] #Pseudoctomeris_sulcata_KC138504.1_{Pseudoctomeris_sulcata}

[27] #Pseudoctomeris_sulcata_KC138503.1_{Pseudoctomeris_sulcata}

[28] #Hexechamaesipho_pilbryi_KC896285.1_{Hexechamaesipho_pilsbry}

[29] #Hexechamaesipho_pilbryi_KC896196.1_{Hexechamaesipho_pilsbry}

[1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17
18 19 20 21 22 23 24 25 26 27 28 29

[1]

[2] 0.01741

[3] 0.11657 0.11824

[4] 0.10524 0.11066 0.10892

[5] 0.10143 0.10682 0.10321 0.00628

[6] 0.09957 0.10494 0.10135 0.00786 0.00156

[7] 0.10847 0.11391 0.11219 0.01262 0.00942 0.00942

[8] 0.11078 0.11625 0.11070 0.01262 0.00944 0.00944 0.00628

[9] 0.10506 0.11047 0.10873 0.01103 0.00785 0.00785 0.00784 0.00470

[10] 0.18576 0.18549 0.20097 0.16661 0.16669 0.16669 0.17069 0.17088 0.17088

[11] 0.17655 0.17837 0.19770 0.16001 0.16008 0.16008 0.16590 0.16606 0.16414 0.02269

[12] 0.18663 0.18845 0.19734 0.16398 0.16377 0.16377 0.16962 0.17010 0.16787 0.02436 0.01266

[13] 0.18037 0.18635 0.19521 0.16199 0.16178 0.16178 0.16761 0.16808 0.16586 0.02436 0.01106 0.00470

[14] 0.18037 0.18219 0.19734 0.16001 0.15980 0.15980 0.16561 0.16606 0.16386 0.02269 0.01266 0.01264 0.01104

[15] 0.18453 0.18635 0.19734 0.16799 0.16778 0.16778 0.17366 0.17416 0.17192 0.02269 0.00946 0.00945 0.00786 0.00945

[16] 0.18245 0.18427 0.19521 0.16199 0.16178 0.16178 0.16962 0.17010 0.16787 0.01939 0.00946 0.00945 0.00786 0.00628 0.00628

[17] 0.19313 0.19282 0.19322 0.16808 0.16787 0.16787 0.17579 0.17427 0.17203 0.01772 0.03056 0.03383 0.03217 0.02886 0.03051 0.02721

[18] 0.18419 0.18152 0.19693 0.16432 0.16648 0.16648 0.17357 0.17171 0.16902 0.00774 0.02317 0.02908 0.02709 0.02510 0.02510 0.02116 0.02112

[19] 0.17917 0.17653 0.19437 0.16192 0.16166 0.16166 0.16871 0.16927 0.16417 0.00774 0.02317 0.02709 0.02510 0.02313 0.02313 0.01920 0.01916 0.00951

[20] 0.18663 0.18635 0.19948 0.16598 0.16577 0.16577 0.17164 0.17212 0.16989 0.00638 0.01911 0.02233 0.02070 0.02233 0.01908 0.01908 0.01744 0.00951 0.00759

[21] 0.18663 0.18635 0.19734 0.16598 0.16577 0.16577 0.17164 0.17212 0.16989 0.00478 0.02074 0.02397 0.02233 0.02070 0.02070 0.01746 0.01583 0.00759 0.00568 0.00470

[22] 0.18453 0.18427 0.19734 0.16799 0.16778 0.16778 0.17366 0.17416 0.17192 0.01284 0.02565 0.02890 0.02725 0.02561 0.02561 0.02233 0.01103 0.01530 0.01336 0.01264 0.01104

[23] 0.18873 0.19056 0.20163 0.16799 0.16778 0.16778 0.17366 0.17416 0.17192 0.01122 0.02074 0.02397 0.02233 0.02070 0.02070 0.01746 0.01262 0.01530 0.01336 0.01104 0.00945 0.00786

[24] 0.16067 0.15864 0.14139 0.14065 0.14068 0.13873 0.14844 0.14653 0.14653 0.14783 0.15481 0.15481 0.15481 0.15888 0.16092 0.15481 0.15489 0.14955 0.14718 0.15078 0.14878 0.15279 0.15481

[25] 0.19383 0.19145 0.17812 0.18701 0.18498 0.18710 0.19108 0.19126 0.18701 0.17194 0.18325 0.17903 0.17903 0.17903 0.18537 0.17903 0.18953 0.17079 0.17079 0.17693 0.17693 0.17693 0.18325 0.12208

[26] 0.22366 0.22552 0.22039 0.21550 0.20647 0.20429 0.21455 0.21754 0.21511 0.21094 0.22280 0.22018 0.21798 0.22018 0.22018 0.22239 0.22478 0.21882 0.22416 0.21360 0.21798 0.21360 0.22239 0.22431 0.20447

[27] 0.22798 0.22984 0.22470 0.21310 0.20849 0.20630 0.21659 0.21958 0.21714 0.20451 0.21633 0.21375 0.21157 0.21375 0.21375 0.21593 0.21829 0.20849 0.21372 0.20724 0.21157 0.20724 0.21593 0.22220 0.20434 0.01266

[28] 0.21973 0.22442 0.20993 0.21598 0.21341 0.21109 0.22207 0.22285 0.22025 0.21070 0.21634 0.21827 0.21592 0.21358 0.22299 0.21592 0.22320 0.21187 0.20923 0.21827 0.21827 0.22062 0.22299 0.19075 0.20642 0.20163 0.19951

[29] 0.21341 0.21076 0.21460 0.22582 0.22320 0.22082 0.23194 0.23283 0.23017 0.20402 0.20738 0.21395 0.21162 0.20929 0.20929 0.21162 0.21887 0.20944 0.20680 0.20929 0.20929 0.21162 0.21395 0.18828 0.20182 0.20911 0.20698 0.05390

Estimates of Evolutionary Divergence between Sequences

The number of base substitutions per site from between sequences are shown. Standard error estimate(s) are shown above the diagonal and were obtained by a bootstrap procedure (1000 replicates). Analyses were conducted using the Kimura 2-parameter model [1]. This analysis involved 30 nucleotide sequences. Codon positions included were 1st+2nd+3rd+Noncoding. All ambiguous positions were removed for each sequence pair (pairwise deletion option). There was a total of 641 positions in the final dataset. Evolutionary analyses were conducted in MEGA X [2] The presence of n/c in the results denotes cases in which it was not possible to estimate evolutionary distances.

Table 7.28. Kimura 2-parameter (K2P) distances of COI sequences between species

Title: *Amphibalanus* sp. with Balanidae COI

Description

Analysis ====================

Analysis = ====================

Scope = Pairs of taxa

Estimate Variance = ====================

Variance Estimation Method = Bootstrap method

No. of Bootstrap Replications = 1000

Substitution Model = ====================

Substitutions Type = Nucleotide

Model/Method = Kimura 2-parameter model

Substitutions to Include = d: Transitions + Transversions

Rates and Patterns = ====================

Rates among Sites = Uniform Rates

Pattern among Lineages = Same (Homogeneous)

Data Subset to Use = ====================

Gaps/Missing Data Treatment = Pairwise deletion

Select Codon Positions = 1st,2nd,3rd,Non-Coding

No. of Sites:641

d:Estimate

S.E:Standard error

[1] #Amphibalanus_sp_Bcl4117PM1378_{Amphibalanus_sp}

[2] #Amphibalanus_sp_Bcl4117PM1379_{Amphibalanus_sp}

[3] #Amphibalanus_sp_Bcl4216PM937_{Amphibalanus_sp}

[4] #Amphibalanus_sp_Bcl5217PM1550_{Amphibalanus_sp}

[5] #Amphibalanus_sp_Bcl1117PM125_{Amphibalanus_sp}

[6] #Amphibalanus_amphitrite_Bcl6717PM1780_{Amphibalanus_amphitrite}

[7] #Amphibalanus_amphitrite_KM211494.1_{Amphibalanus_amphitrite}

[8] #Amphibalanus_amphitrite_JQ035517.1_{Amphibalanus_amphitrite}

[9] #Amphibalanus_amphitrite_Bcl6317PM1730_{Amphibalanus_amphitrite}

[10] #Amphibalanus_variegatus_X3PM922_{Amphibalanus_variegatus}

[11] #Amphibalanus_variegatus_Bcl7717PM1874_{Amphibalanus_variegatus}

[12] #Amphibalanus_variegatus_Bcl4416PM953_{Amphibalanus_variegatus}

[13] #Amphibalanus_variegatus_X2PM732_{Amphibalanus_variegatus}

[14] #Amphibalanus_variegatus_Bcl5316PM1004_{Amphibalanus_variegatus}

[15] #Amphibalanus_variegatus_KC138446.1_{Amphibalanus_variegatus}

[16] #Amphibalanus_variegatus_JQ035521.1_{Amphibalanus_variegatus}

[17] #Amphibalanus_zhujiangensis_Bcl4517PM1405_{Amphibalanus_zhujiangensis}

[18] #Amphibalanus_zhujiangensis_Bcl2316PM803_{Amphibalanus_zhujiangensis}

[19] #Amphibalanus_zhujiangensis_Bcl4517PM1407_{Amphibalanus_zhujiangensis}

[20] #Amphibalanus_zhujiangensis_KC138448.1_{Amphibalanus_zhujiangensis}

[21] #Amphibalanus_zhujiangensis_Bcl4517PM1406_{Amphibalanus_zhujiangensis}

[22] #Amphibalanus_zhujiangensis_Bcl1716PM775_{Amphibalanus_zhujiangensis}

[23] #Amphibalanus_zhujiangensis_Bcl3317PM1307_{Amphibalanus_zhujiangensis}

[24] #Amphibalanus_zhujiangensis_Bcl9016PM1222_{Amphibalanus_zhujiangensis}

[25] #Amphibalanus_zhujiangensis_Bcl4517PM1404_{Amphibalanus_zhujiangensis}

[26] #Megabalanus_tintinnabulum_KC138488.1_{Megabalanus_tintinnabulum}

[27] #Megabalanus_tintinnabulum_KC138487.1_{Megabalanus_tintinnabulum}

[28] #Megabalanus_zebra_KX538962.1_{Megabalnus_zebra}

[29] #Megabalanus_zebra_KC138491.1_{Megabalnus_zebra}

[30] #Balanus_trigonus_KU204234.1_{Balanus_trigonus}

[31] #Balanus_trigonus_KU204228.1_{Balanus_trigonus}

[1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22 23 24 25 26 27 28 29 30 31]

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[2] 0.0046966974 [0.0000000000][0.0000000000][0.0016551544][0.0164387962][0.0169862196][0.0164481263][0.0164158272][0.0151328766][0.0149621674][0.0150276614][0.0150461009][0.0150276614][0.0156716558][0.0150885071][0.0193328954][0.0194806599][0.0194821695][0.0190560821][0.0193209599][0.0192014184][0.0194247013][0.0192014184][0.0192014184][0.0194291114][0.0197770490][0.0177400219][0.0173374427][0.0178503279][0.0180220074]

[3] 0.0046966974 0.0000000000 [0.0000000000][0.0016551544][0.0164387962][0.0169862196][0.0164481263][0.0164158272][0.0151328766][0.0149621674][0.0150276614][0.0150461009][0.0150276614][0.0156716558][0.0150885071][0.0193328954][0.0194806599][0.0194821695][0.0190560821][0.0193209599][0.0192014184][0.0194247013][0.0192014184][0.0192014184][0.0194291114][0.0197770490][0.0177400219][0.0173374427][0.0178503279][0.0180220074]

[4] 0.0046966974 0.0000000000 0.0000000000 [0.0016551544][0.0164387962][0.0169862196][0.0164481263][0.0164158272][0.0151328766][0.0149621674] [0.0150276614][0.0150461009][0.0150276614][0.0156716558][0.0150885071] [0.0193328954][0.0194806599][0.0194821695][0.0190560821][0.0193209599] [0.0192014184][0.0194247013][0.0192014184][0.0192014184][0.0194291114] [0.0197770490][0.0177400219][0.0173374427][0.0178503279][0.0180220074]

[5] 0.0031268374 0.0015625013 0.0015625013 0.0015625013 [0.0164637380][0.0169629271][0.0164430821][0.0164164018][0.0150978453][0.0149141680] [0.0149908357][0.0150103882][0.0149908357][0.0156408747][0.0150796726] [0.0193032739][0.0194372170][0.0194505723][0.0190154763][0.0192937268] [0.0191685932][0.0193957002][0.0191685932][0.0191685932][0.0193721487] [0.0197394879][0.0176753478][0.0172907304][0.0177869289][0.0179527814]

[6] 0.1481065093 0.1499921937 0.1499921937 0.1499921937 0.1480542068 [0.0094555782][0.0086465512][0.0078733224][0.0166872899][0.0164196824] [0.0163928960][0.0165801745][0.0165508226][0.0164086139][0.0159750893] [0.0195555574][0.0197214971][0.0197999103][0.0195089180][0.0196034112] [0.0198198088][0.0197999103][0.0196034112][0.0196034112][0.0197458871] [0.0201601852][0.0198404902][0.0198949386][0.0175754589][0.0173187862]

[7] 0.1540002534 0.1539343061 0.1539343061 0.1539343061 0.1518893134 0.0476872705 [0.0040746599][0.0045095804][0.0173190035][0.0171670193][0.0170978367][0.0172487556][0.0172487556][0.0181083253][0.0176084539] [0.0205799638][0.0205903308][0.0206962059][0.0203055526][0.0204793653] [0.0206655608][0.0206962059][0.0204793653][0.0204793653][0.0204954790] [0.0211430233][0.0196465331][0.0197028965][0.0187935937][0.0186730238]

[8] 0.1506313451 0.1505695796 0.1505695796 0.1505695796 0.1486202594 0.0421422092 0.0098870053 [0.0027910836][0.0164774660][0.0163106626][0.0162759696][0.0164360045][0.0164127935][0.0170803427][0.0166382471] [0.0200469158][0.0200961733][0.0201848617][0.0198396763][0.0199964494] [0.0202036648][0.0201848617][0.0199964494][0.0199964494][0.0200061706] [0.0205834516][0.0197164000][0.0192197126][0.0180767109][0.0180859806]

[9] 0.1501760779 0.1501095597 0.1501095597 0.1501095597 0.1481640320 0.0370236881 0.0115707643 0.0047114497 [0.0164340532][0.0161942379][0.0161660278][0.0163294162][0.0163047465][0.0165756112][0.0161373645] [0.0200310676][0.0200749267][0.0201536609][0.0198916473][0.0199612211] [0.0201643822][0.0201536609][0.0199612211][0.0199612211][0.0194711483] [0.0200600794][0.0194321009][0.0190463534][0.0178133503][0.0176562801]

[10] 0.1320893711 0.1339470093 0.1339470093 0.1339470093 0.1320386100 0.1454147087 0.1526468513 0.1434116583 0.1415311940 [0.0034725341][0.0015096842][0.0000000000][0.0000000000][0.0055528015][0.0054583057][0.0194580020][0.0196559067][0.0195424522][0.0190785481][0.0193308308][0.0191754862][0.0193691996][0.0191754862][0.0191754862][0.0172386246][0.0174469355][0.0196200705][0.0175034845][0.0162798411][0.0165089449]

[11] 0.1294040438 0.1312415920 0.1312415920 0.1312415920 0.1293476504 0.1424806507 0.1500426640 0.1409893246 0.1386418603 0.0078940078 [0.0030738622][0.0034565516][0.0034511954][0.0057197866][0.0057835924][0.0192876854][0.0195525360][0.0194038630][0.0190127787][0.0191897770][0.0190329633][0.0192205475][0.0190329633][0.0190329633][0.0174788509][0.0176988018][0.0188068238][0.0175412856][0.0162419618][0.0161106137]

[12] 0.1311865825 0.1330305084 0.1330305084 0.1330305084 0.1311365668 0.1424806507 0.1500426640 0.1409893246 0.1386418603 0.0015723283 0.0062671794 [0.0015024289][0.0015003460][0.0053290060][0.0052307562][0.0190534077][0.0192637659][0.0191486927][0.0187893214][0.0189473717][0.0187980671][0.0189911976][0.0187980671][0.0187980671][0.0173853952][0.0175926718][0.0191776279][0.0175962334][0.0163314003][0.0162034047]

[13] 0.1314111174 0.1332584523 0.1332584523 0.1332584523 0.1313609168 0.1446607380 0.1520918472 0.1431634535 0.1407997149 0.0000000000 0.0078567944 0.0015649465 [0.0000000000][0.0055424034][0.0054493397][0.0193080947][0.0195059609][0.0193907698][0.0190336370][0.0191927165][0.0190371555][0.0192282884][0.0190371555][0.0190371555][0.0172228685][0.0174361602][0.0194705398][0.0174781079][0.0161780995][0.0164093396]

[14] 0.1311865825 0.1330305084 0.1330305084 0.1330305084 0.1311365668 0.1444111551 0.1520918472 0.1429161093 0.1405575714 0.0000000000 0.0078444677 0.0015625013 0.0000000000 [0.0055345819][0.0054407380][0.0192799757][0.0194774941][0.0193636825][0.0190058227][0.0191669382][0.0190111561][0.0192022511][0.0190111561][0.0190111561][0.0171889803][0.0173995404][0.0194705398][0.0174477435][0.0161499297][0.0163799183]

[15] 0.1393695352 0.1412336481 0.1412336481 0.1412336481 0.1392994097 0.1411012193 0.1582902736 0.1468567159 0.1411012193 0.0175475102 0.0190665065 0.0158761879 0.0175195597 0.0174916982 [0.0030743056][0.0190327479][0.0192450920][0.0190979381][0.0187311393][0.0189354614][0.0187991886][0.0189802020][0.0187991886][0.0187991886][0.0175879378][0.0177665301][0.0185879866][0.0181830432][0.0165038111][0.0163001310]

[16] 0.1317522722 0.1336002405 0.1336002405 0.1336002405 0.1316918412 0.1373112915 0.1521708290 0.1411012193 0.1353955803 0.0175251242 0.0190492388 0.0158565501 0.0174972452 0.0174694547 0.0062912298 [0.0188867678][0.0191192123][0.0189650208][0.0185984057][0.0187848052][0.0186586884] [0.0188550660][0.0186586884][0.0186586884][0.0175932934][0.0176645435] [0.0185402687][0.0179568123][0.0161893364][0.0159697234]

[17] 0.1818428275 0.1817388880 0.1817388880 0.1817388880 0.1796854970 0.1958726603 0.2026672331 0.2009364512 0.2003390586 0.1832552970 0.1819523093 0.1798904508 0.1822763051 0.1819523093 0.1804250026 0.1764158181 [0.0040851228][0.0035857935][0.0035597855][0.0038230480][0.0039098076][0.0039071329] [0.0035506240][0.0035506240][0.0195997074][0.0195510828][0.0194240002] [0.0183544702][0.0196728011][0.0192437511]

[18] 0.1839089462 0.1838007466 0.1838007466 0.1838007466 0.1817388880 0.2000920946 0.2026672331 0.2009364512 0.2003390586 0.1853429827 0.1840227057 0.1819523093 0.1843509969 0.1840227057 0.1824911212 0.1784692091 0.0094491001 [0.0035707469][0.0035525551][0.0038279762][0.0039251395][0.0039225783] [0.0035607254][0.0035607254][0.0192823004][0.0192125343][0.0194462417] [0.0180351736][0.0195758351][0.0192164712]

[19] 0.1818428275 0.1817388880 0.1817388880 0.1817388880 0.1796854970 0.2000920946 0.2026672331 0.2009364512 0.2003390586 0.1811762919 0.1798904508 0.1778370598 0.1802101864 0.1798904508 0.1783673865 0.1743708255 0.0078617972 0.0078617972 [0.0031606720][0.0034766762][0.0035136677][0.0027265842][0.0031599672][0.0031599672][0.0194732433][0.0194144965][0.0191465966] [0.0183114693][0.0196521468][0.0192756694]

[20] 0.1763182033 0.1762261216 0.1762261216 0.1762261216 0.1741894589 0.1965775720 0.1982128607 0.1966901412 0.1968084919 0.1770440370 0.1764158181 0.1743708255 0.1767293661 0.1764158181 0.1742773842 0.1703057625 0.0078865988 0.0078865988 0.0062992959 [0.0027359803][0.0028424893][0.0028259279][0.0022944165][0.0022944165][0.0191311237][0.0190851324][0.0185852402] [0.0178969899][0.0195837810][0.0191799545]

[21] 0.1818428275 0.1817388880 0.1817388880 0.1817388880 0.1796854970 0.1979779265 0.2004350866 0.1988087885 0.1982159132 0.1791058956 0.1778370598 0.1757920672 0.1781525704 0.1778370598 0.1763182033 0.1723341628 0.0094491001 0.0094491001 0.0078617972 0.0047170161 [0.0021691738][0.0021744601][0.0014562994][0.0014562994][0.0193744726][0.0193340828][0.0188955785] [0.0181880834][0.0194529169][0.0190603609]

[22] 0.1797852114 0.1796854970 0.1796854970 0.1796854970 0.1776405044 0.2000920946 0.2026672331 0.2009364512 0.2003390586 0.1770440370 0.1757920672 0.1737554045 0.1761033872 0.1757920672 0.1742773842 0.1703057625 0.0094491001 0.0094491001 0.0078617972 0.0047170161 0.0031299007 [0.0022126512][0.0015891449][0.0015891449][0.0193138669][0.0192624396][0.0189971992][0.0181461927][0.0193437138][0.0189529137]

[23] 0.1818428275 0.1817388880 0.1817388880 0.1817388880 0.1796854970 0.2000920946 0.2026672331 0.2009364512 0.2003390586 0.1791058956 0.1778370598 0.1757920672 0.1781525704 0.1778370598 0.1763182033 0.1723341628 0.0094491001 0.0094491001 0.0047022290 0.0047170161 0.0031299007 0.0031299007 [0.0016375586][0.0016375586][0.0194732433][0.0194144965][0.0192293861][0.0183744474][0.0196206270][0.0192451575]

[24] 0.1797852114 0.1796854970 0.1796854970 0.1796854970 0.1776405044 0.1979779265 0.2004350866 0.1988087885 0.1982159132 0.1770440370 0.1757920672 0.1737554045 0.1761033872 0.1757920672 0.1742773842 0.1703057625 0.0078617972 0.0078617972 0.0062795174 0.0031397277 0.0015625013 0.0015625013 0.0015625013 [0.0000000000][0.0193138669][0.0192624396][0.0189971992][0.0181461927][0.0193437138][0.0189529137]

[25] 0.1797852114 0.1796854970 0.1796854970 0.1796854970 0.1776405044 0.1979779265 0.2004350866 0.1988087885 0.1982159132 0.1770440370 0.1757920672 0.1737554045 0.1761033872 0.1757920672 0.1742773842 0.1703057625 0.0078617972 0.0078617972 0.0062795174 0.0031397277 0.0015625013 0.0015625013 0.0015625013 0.0000000000 [0.0193138669][0.0192624396][0.0189971992][0.0181461927][0.0193437138][0.0189529137]

[26] 0.1811443398 0.1830983642 0.1830983642 0.1830983642 0.1810106785 0.1970624698 0.1963987291 0.1993348192 0.1930840283 0.1571649812 0.1587847912 0.1586036706 0.1568898057 0.1566155964 0.1625130923 0.1624278429 0.1841793867 0.1799510317 0.1841793867 0.1799510317 0.1841793867 0.1820607395 0.1841793867 0.1820607395 0.1820607395 [0.0032700255][0.0187442918][0.0112497462][0.0203508620][0.0203120752]

[27] 0.1832363931 0.1851948033 0.1851948033 0.1851948033 0.1830983642 0.1991946692 0.2031102393 0.2058004266 0.1994807040 0.1591609919 0.1607888019 0.1605996812 0.1588818402 0.1586036706 0.1645211271 0.1624278429 0.1820607395 0.1778501883 0.1820607395 0.1778501883 0.1820607395 0.1799510317 0.1820607395 0.1799510317 0.1799510317 0.0062992959 [0.0192920869][0.0112824294][0.0201076136][0.0200796057]

[28] 0.1514179949 0.1533350821 0.1533350821 0.1533350821 0.1513310714 0.1913834748 0.1939194566 0.1943235990 0.1915982140 0.1788101577 0.1694309108 0.1754321725 0.1775198583 0.1775198583 0.1697317196 0.1698291312 0.1784738060 0.1806014687 0.1784738060 0.1727681533 0.1742454510 0.1763551587 0.1784738060 0.1763551587 0.1763551587 0.1617377892 0.1680669876 [0.0185028930] [0.0202375222][0.0200911423]

[29] 0.1548007064 0.1566995534 0.1566995534 0.1566995534 0.1547154239 0.1927042520 0.1852943740 0.1844567601 0.1824911212 0.1572495808 0.1568832618 0.1586915880 0.1569740831 0.1566995534 0.1646157670 0.1625130923 0.1673404115 0.1612303558 0.1673404115 0.1612303558 0.1673404115 0.1652954189 0.1673404115 0.1652954189 0.1652954189 0.0731271784 0.0731271784 0.1615694039 [0.0202809524] [0.0203104232]

[30] 0.1642434099 0.1661845656 0.1661845656 0.1661845656 0.1641561653 0.1639981665 0.1750834737 0.1689184426 0.1663727911 0.1491672134 0.1482185610 0.1500807670 0.1483832908 0.1481238174 0.1505648833 0.1486436780 0.1901570607 0.1880650075 0.1880650075 0.1866531274 0.1859816711 0.1839069793 0.1859816711 0.1839069793 0.1839069793 0.2003876052 0.1982136887 0.2017444704 0.1961974277 [0.0035837854]

[31] 0.1662759330 0.1682212283 0.1682212283 0.1682212283 0.1661845656 0.1619860914 0.1750834737 0.1709760587 0.1643361284 0.1511396026 0.1462616114 0.1481238174 0.1503440776 0.1500807670 0.1486040965 0.1466867283 0.1859816711 0.1839069793 0.1839069793 0.1824950993 0.1818408607 0.1797832446 0.1818408607 0.1797832446 0.1797832446 0.1982136887 0.1960491831 0.1995985443 0.1983666285 0.0079619517

Estimates of Evolutionary Divergence between Sequences

The number of base substitutions per site from between sequences are shown. Standard error estimate(s) are shown above the diagonal. Analyses were conducted using the Kimura 2-parameter model [1]. This analysis involved 31 nucleotide sequences. Codon positions included were 1st+2nd+3rd+Noncoding. All ambiguous positions were removed for each sequence pair (pairwise deletion option). There was a total of 641 positions in the final dataset. Evolutionary analyses were conducted in MEGA X [2]

1. Kimura M. (1980). A simple method for estimating evolutionary rate of base substitutions through comparative studies of nucleotide sequences. Journal of Molecular Evolution 16:111-120.
2. Kumar S., Stecher G., Li M., Knyaz C., and Tamura K. (2018). MEGA X: Molecular Evolutionary Genetics Analysis across computing platforms. Molecular Biology and Evolution 35:1547-1549.

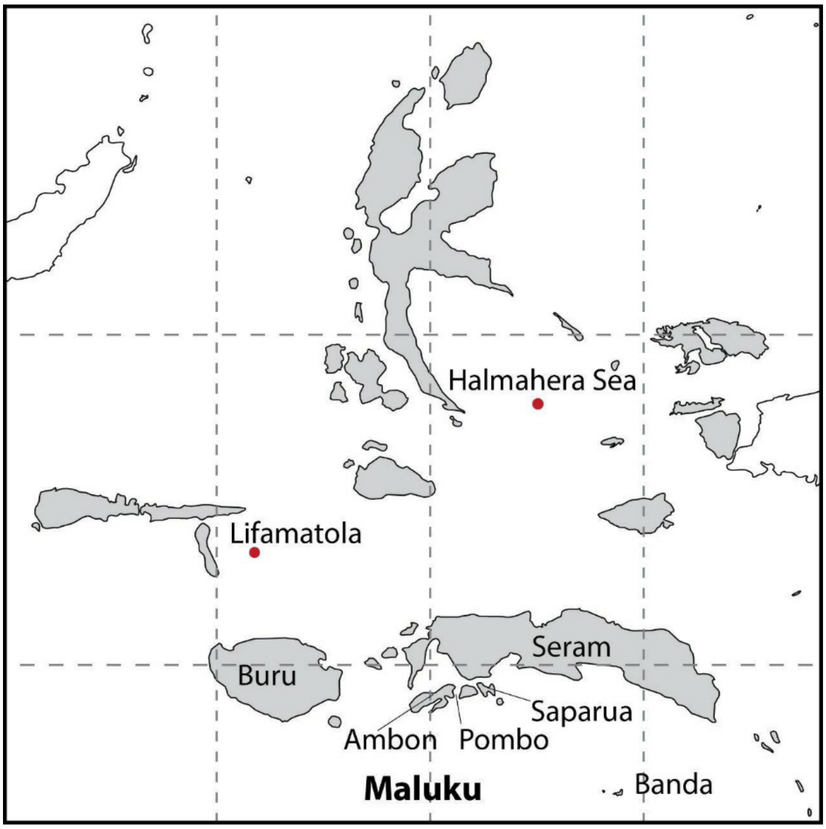

Figure 7.1. The occurrence of *Heteralepas japonica* in the Moluccas (red dots).

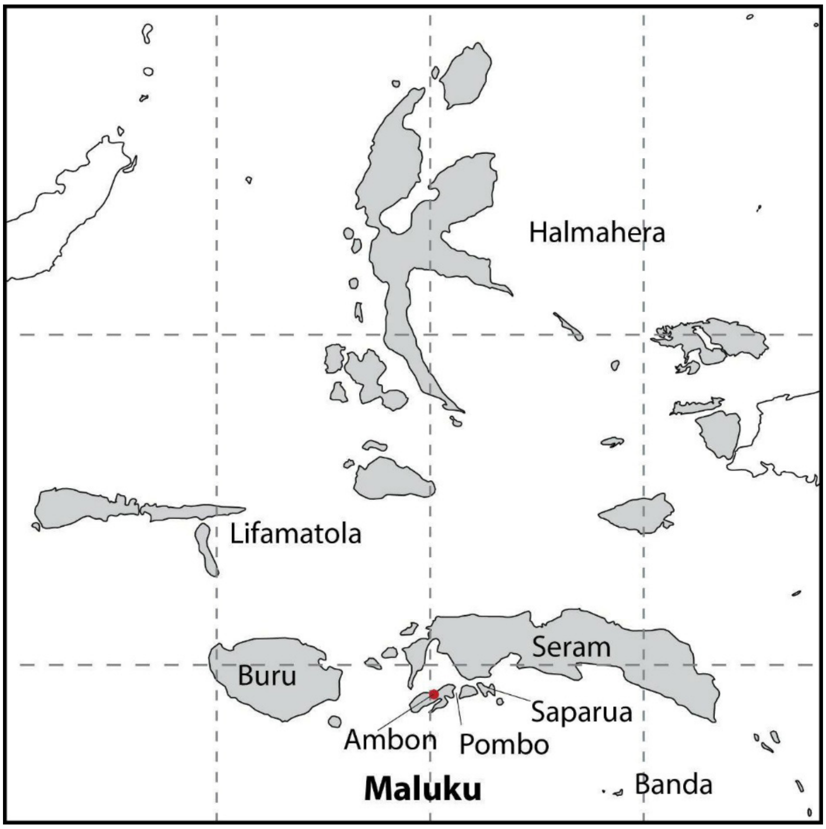

Figure 7.2. The occurrence of *Amphibalanus reticulatus*, *Dosima fascicularis*, *Euraphia hembeli, Hexechamaesipho pilsbryi, Megabalanus zebra, Nesochthamalus intertextus, Newmanella spinosus, Pseudoctomeris sulcata, Tetraclitella divisa* and *Tetraclitella karandei* in the Moluccas (the red dot indicates that the species occurs on the coastline of the island).

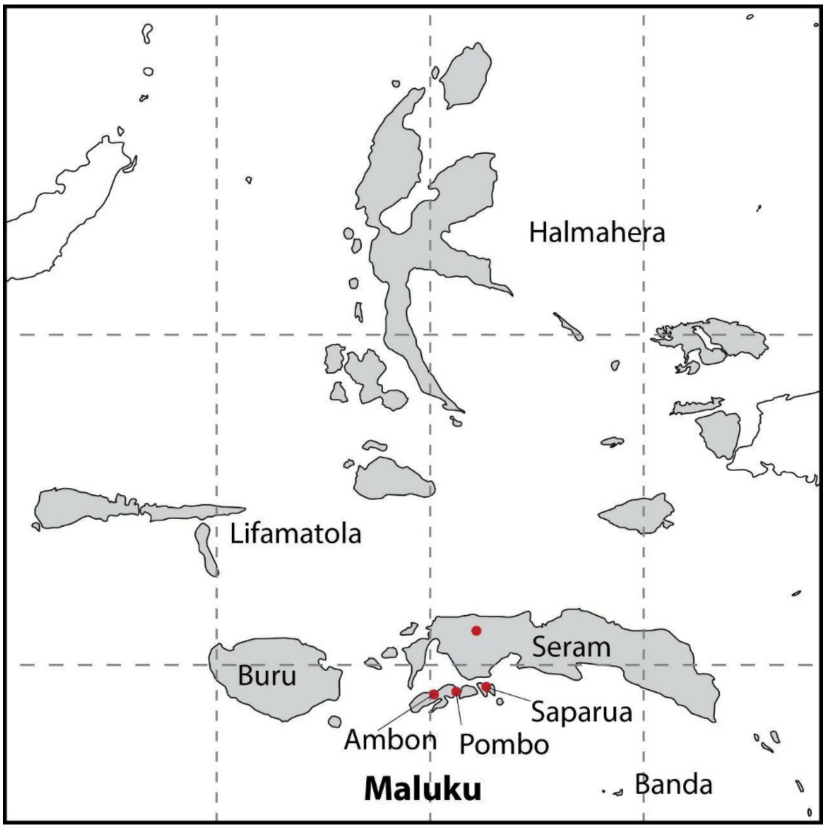

Figure 7.3. The occurrence of *Chthamalus moro* and *Lepas anserifera* in the Moluccas (the red dots indicate that the species occurs on the coastline of the islands).

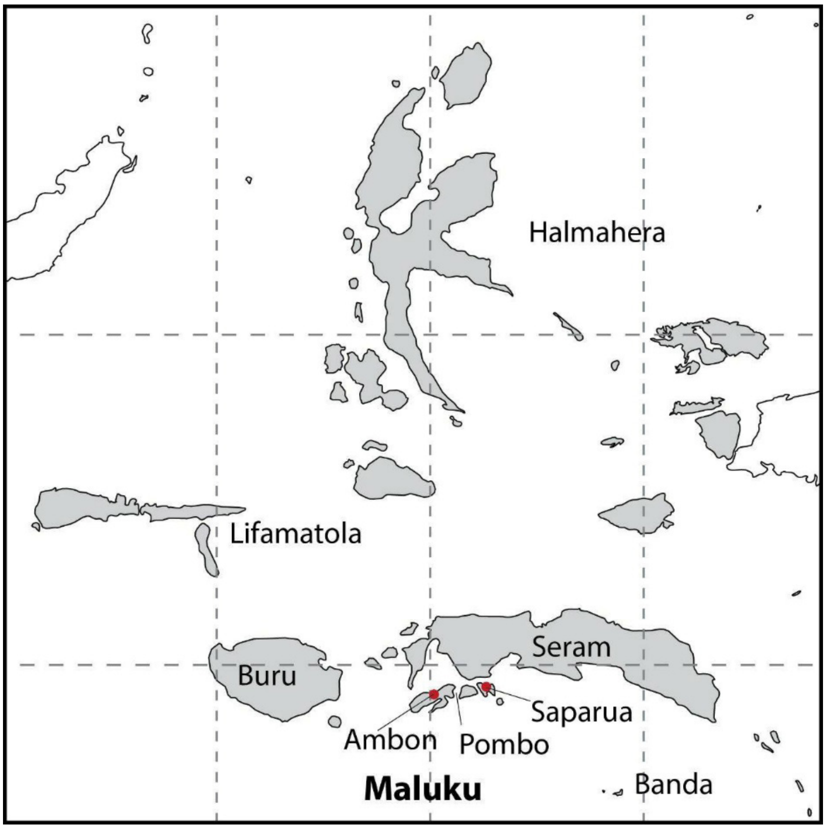

Figure 7.4. The occurrence of *Amphibalanus amphitrite*, *Amphibalanus variegatus*, *Capitulum mitella, Megabalanus tintinnabulum, Tesseropora rosea, Tetraclita kuroshioensis* and *Tetraclita squamosa* in the Moluccas (the red dots indicate that the species occurs on the coastline of the islands).

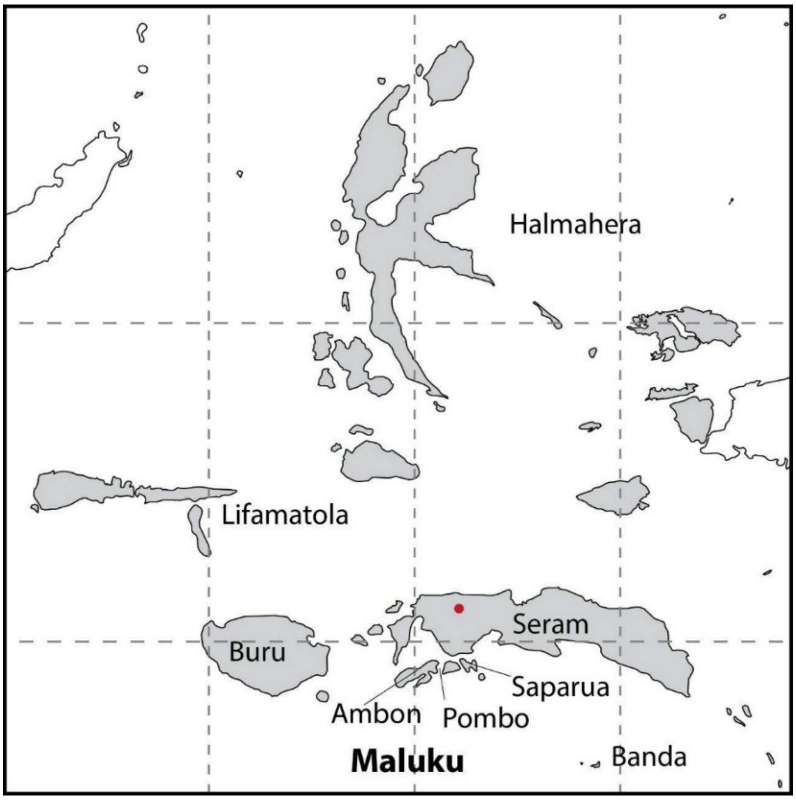

Figure 7.5. The occurrence of *Microeuraphia* sp. in the Moluccas (the red dot indicates that the species occurs on the coastline of the island).

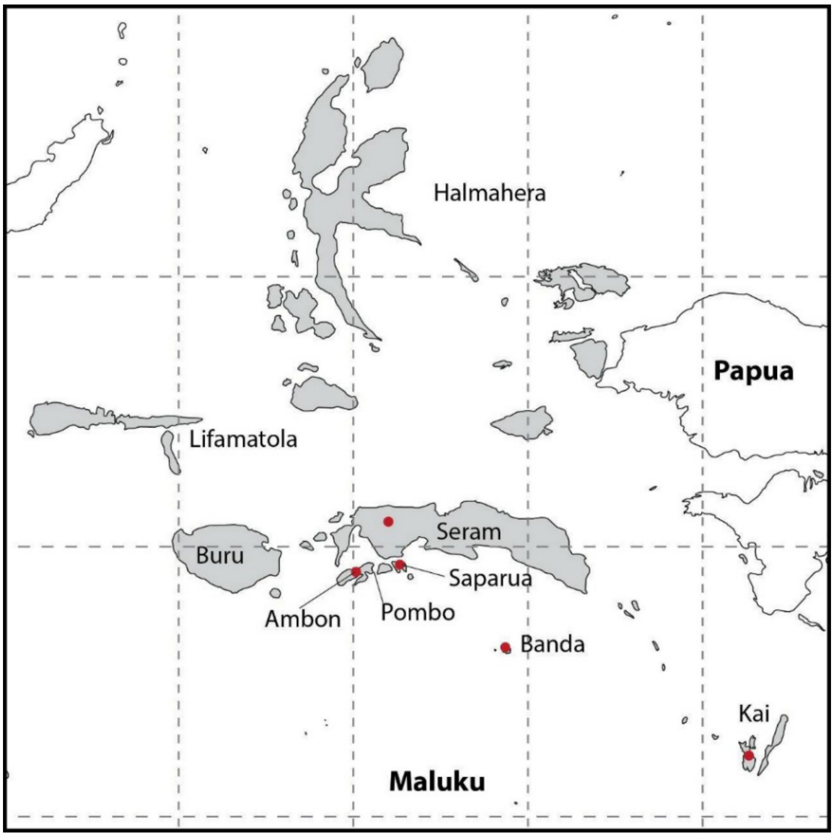

Figure 7.6. The occurrence of *Yamaguchiella coerulescens* in the Moluccas (the red dots indicate that the species occurs on the coastline of the islands).

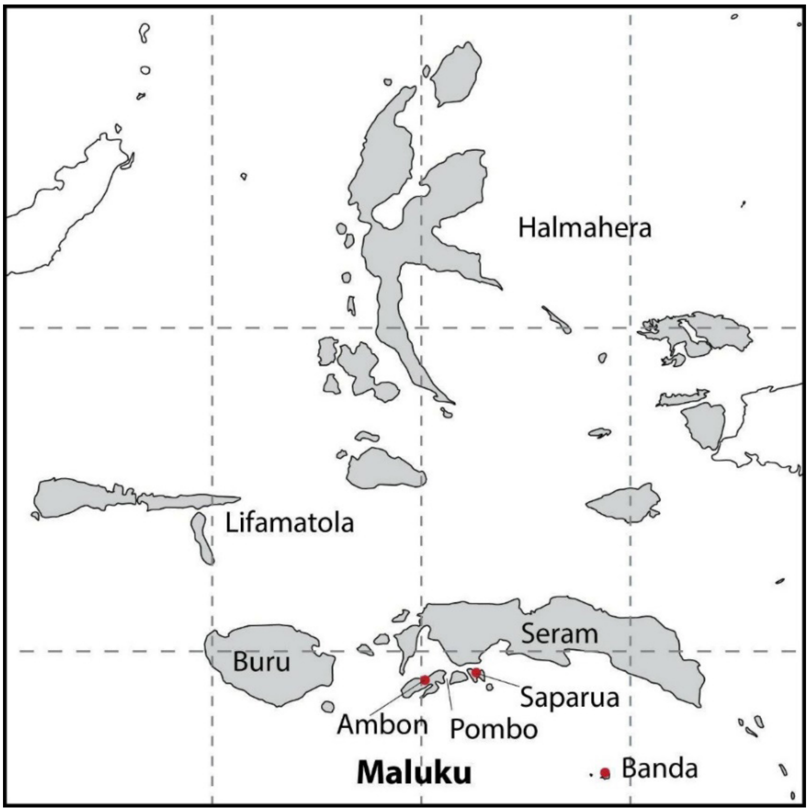

Figure 7.7. The occurrence of *Neonrosella vitiata* in the Moluccas (the red dots indicate that the species occurs on the coastline of the islands).

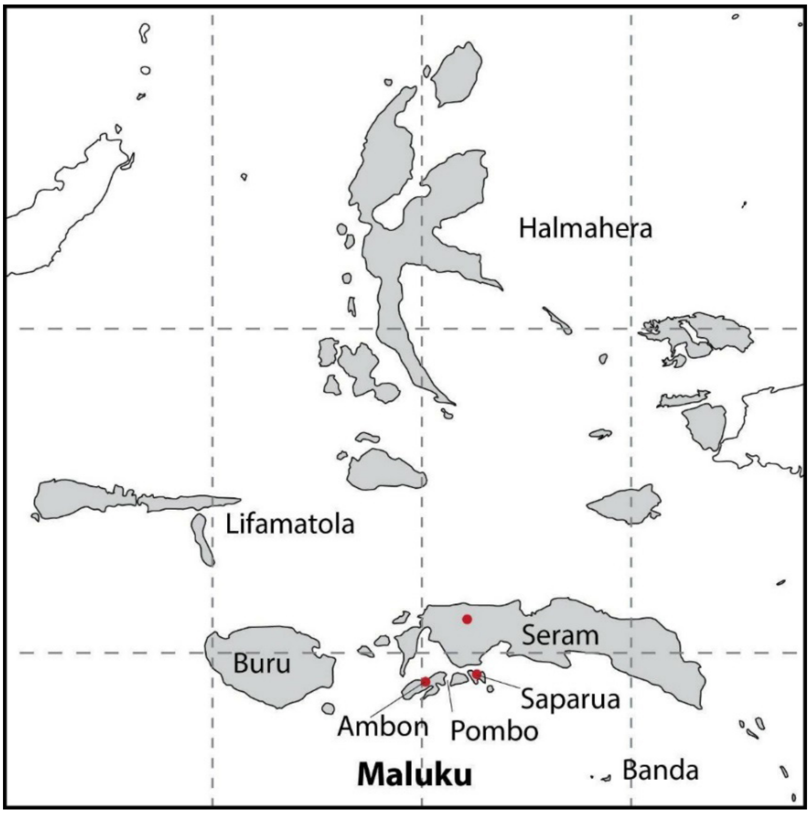

Figure 7.8. The occurrence of *Amphibalanus zhujiangensis* in the Moluccas (the red dots indicate that the species occurs on the coastline of the islands).

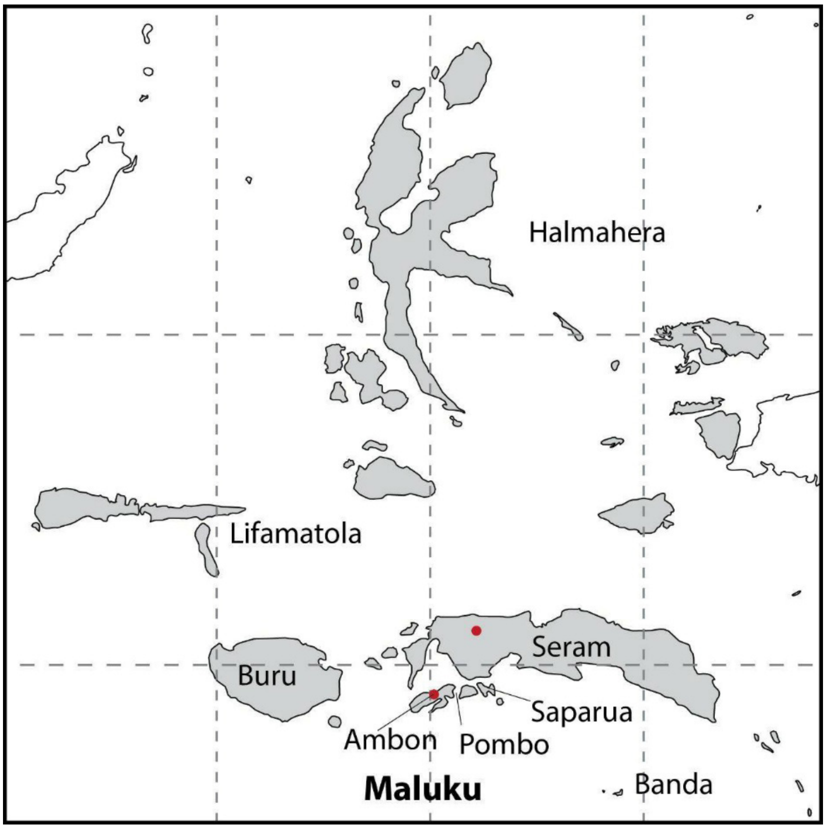

Figure 7.9. The occurrence of *Amphibalanus* sp. in the Moluccas (the red dots indicate that the species occurs on the coastline of the islands).

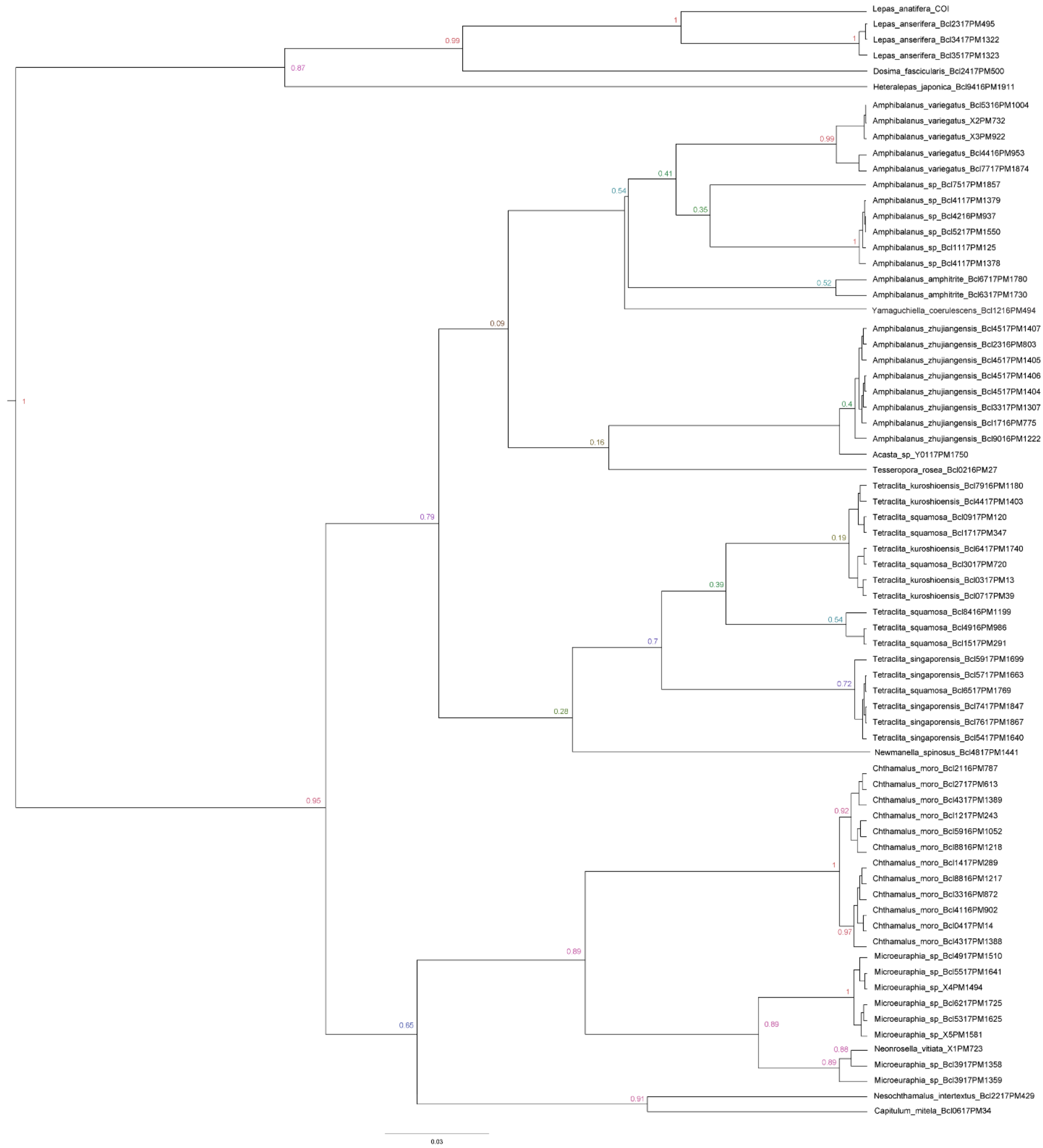

Figure 7.10. Bayesian phylogeny of concatenated COI and 18S gene sequences. Values next to nodes are support values.

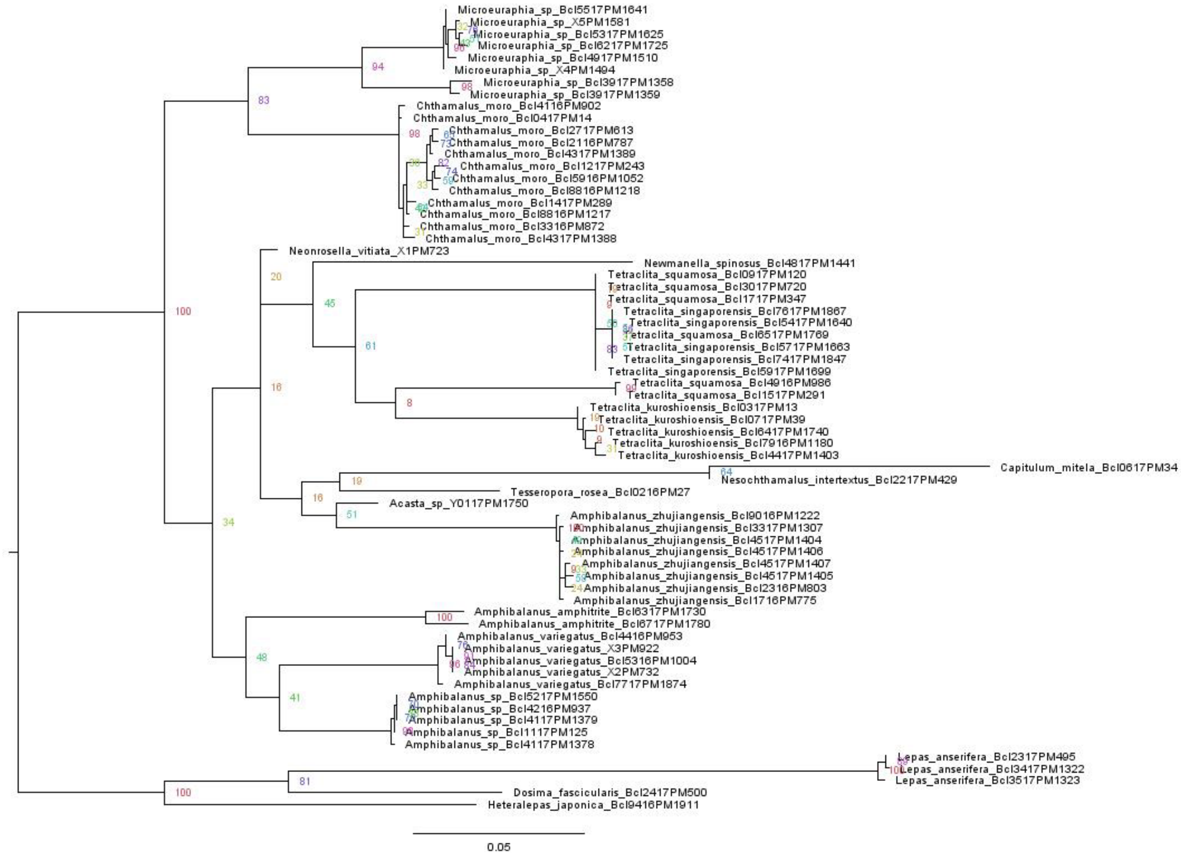

Figure 7.11. ML phylogeny of concatenated COI and 18S gene sequences. Values next to nodes are support values.

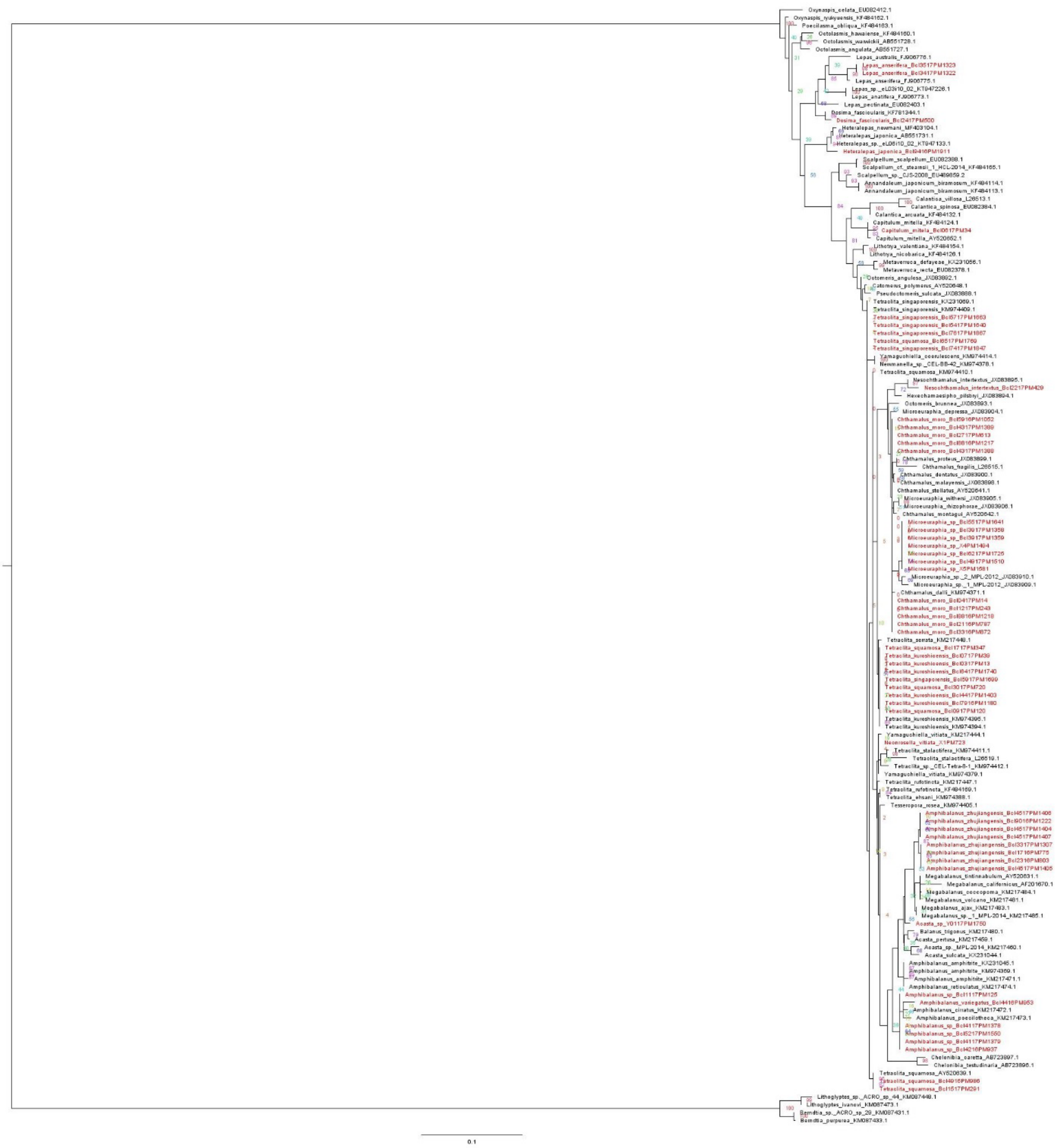

Figure 7.12. ML phylogeny of 18S gene sequences. Tips coloured in red are the new samples sequenced for this paper. Values next to nodes are support values.

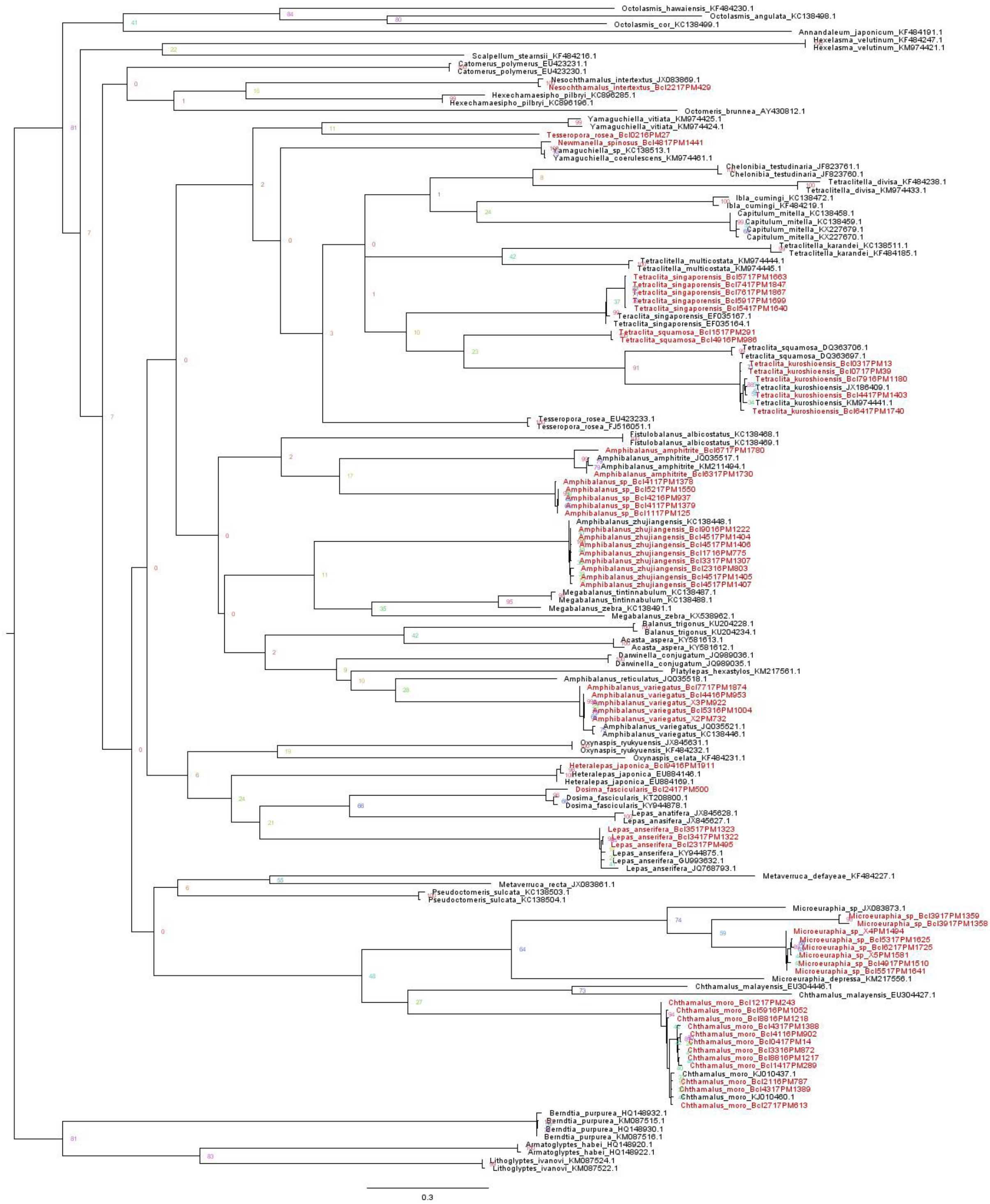

Figure 7.13. ML phylogeny of COI gene sequences. Tips coloured in red are the new samples sequenced for this paper. Values next to nodes are support values.

7.2 Supplementary material for New insights gained from museum collections: Deep-sea barnacles (Crustacea, Cirripedia, Thoracica) in the Muséum National d'Histoire Naturelle, Paris, collected during the *Karubar* expedition in 1991

Table 7.29. Checklist of barnacle species collected during the Karubar expedition (1991) and deposited in MNHN, Paris.

ORDER Suborder	Family Subfamily	Species	Depth in meter	Substrate
LEPADIFORMES Heteralepadomorpha	Heteralepadidae	*Heteralepas japonica* (Aurivillius, 1892)	271–273	
		Paralepas minuta (Philippi, 1836)	240–346	Attached to dead stem of gorgonian and spine of sea urchin
		Paralepas morula (Hoek, 1907)	836–869	Attached to spine of sea urchin
Lepadomorpha	Poecilasmatidae	*Dianajonesia amygdalum* (Aurivillius, 1894)	250–239	Attached to crab leg
		Dianajonesia excavatum (Hoek, 1907)	295–284	
		Dichelaspis orthogonia Darwin, 1852	230–314	
		Glyptelasma gracile (Hoek, 1883)	603–869	Attached to spines of sea urchins
		Megalasma striatum Hoek, 1883	206–459	Attached to spines of sea urchin
SCALPELLIFORMES	Scalpellidae Scalpellinae	*Diotascalpellum rubrum* (Hoek, 1883)	330–389	Attached to gorgonian
		Regioscalpellum moluccanum (Hoek, 1883)	206–1266	
		Scalpellum sp.	210–206	
		Scalpellum stearnsi Pilsbry, 1890	287–480	Attached to glass rope sponge
	Scalpellidae Meroscalpellinae	*Alcockianum persona* (Annandale, 1916)	477–620	Attached to glass rope sponge

		Annandaleum japonicum (Hoek, 1883)	1026–1053	
		Annandaleum laccadivicum (Annandale, 1906)	836–869	Attached to gastropod shell
		Annandaleum lambda (Annandale, 1910)	1058–1266	Attached to pumice
		Litoscalpellum juddi (Calman, 1918)	477–699	
		Litoscalpellum recurvirostrum (Hoek, 1883)	285–299	
		Litoscalpellum walleni Newman & Ross, 1971	884–891	
	Scalpellidae Arcoscalpellinae	*Amigdoscalpellum costellatum* (Withers, 1935)	688–694	Attached to glass rope glass
		Amigdoscalpellum tenue (Hoek, 1883)	769–809	
		Catherinum rossi (Rao & Newman, 1972)	209–240	
		Planoscalpellum distinctum (Hoek, 1883)	210–206	
		Teloscalpellum ecaudatum (Calman, 1918)	390–502	
		Trianguloscalpellum balanoides (Hoek, 1883)	223–349	Attached to crinoid
		Trianguloscalpellum hirsutum (Hoek, 1883)	884–891	
		Verum australicum (Hoek, 1883)	1084–1058	
		Verum carinatum (Hoek, 1883)	205–212	
		Verum novaezelandiae (Hoek, 1883)	1017–1024	
SESSILIA Verrucomorpha	Verrucidae	*Altiverruca navicula* (Hoek, 1913)	884–891	Attached to peduncle of Alcockianum persona (Annandale, 1916)

		Newmaniverruca albatrossiana (Pilsbry, 1912)	688–694	Attached to glass rope sponge
Balanomorpha	Pachylasmatidae Hexelasmatinae	*Hexelasma arafurae* Hoek, 1913	205–212	
	Archaeobalanidae Archaeobalaninae	*Conopea cymbiformis* (Darwin, 1854)	111–850	
		Conopea navicula (Darwin, 1854)	206–220	Attached to gorgonian
		Solidobalanus auricoma (Hoek, 1913)	206–502	Attached to lateral plate of *Chirona tenuis,* spines of sea urchin, antipatharian, arm of crinoid, and dead gorgonian
		Solidobalanus pseudauricoma (Broch, 1931)	82–349	Attached to gorgonian, coral, crinoid, and spines of sea urchins
		Striatobalanus amaryllis (Darwin, 1854)	174–176	Attached to broken sea urchin shell
		Striatobalanus tenuis (Hoek, 1883)	174–389	Attached to shell of gastropod shell
	Pyrgomatidae Megatrematinae	*Pyrgomina* sp.	225–223	Attached to coral
	Balanidae Amphibalaninae	*Amphibalanus amphitrite* (Darwin, 1854)	1244–1266	

Table 7.30. Measurements for *Heteralepas japonica* (Aurivillius, 1892) (N = 1).

No	Sample number	Parameter					
		a	b	c	d	e	f
1	MNHN-IU-2019-4877	18.50	12.82	15.26	8.46	5.97	5.55

Key to parameters: a = capitulum height; b = capitulum width; c = peduncle length; d = orifice height; e = capitulum thickness; f = peduncle width.

Table 7.31. Measurements for *Paralepas minuta* (Philippi, 1836) (N = 1).

No	Sample number	Parameter					
		a	b	c	d	e	f
1	MNHN-IU-2019-4882	8.34	6.67	3.84	3.31	4.53	2.60

Key to parameters: a = capitulum height; b = capitulum width; c = peduncle length; d = orifice height; e = capitulum thickness; f = peduncle width.

Table 7.32. Measurements for *Paralepas morula* (Hoek, 1907) (N = 1).

No	Sample number	Parameter					
		a	b	c	d	e	f
1	MNHN-IU-2019-4878	5.14	3.69	5.08	2.02	1.81	1.31

Key to parameters: a = capitulum height; b = capitulum width; c = peduncle length; d = orifice height; e = capitulum thickness; f = peduncle width.

Table 7.33. Measurements for *Dianajonesia amygdalum* (Aurivillius, 1894) (N = 1).

No	Sample number	Parameter							
		TH	CH	DBC	CS	LS	WS	LT	WT
1	MNHN-IU-2019-4861	10.40	7.03	0.94	4.49	5.85	4.11	3.13	1.00

Key to parameters: TH = total height; CH = capitulum height; DBC = diameter of the base of capitulum; LS = scutum length; WS = scutum width; LT = tergum length; WT = tergum width.

Table 7.34. Measurements for *Dianajonesia excavatum* (Hoek, 1907) (N = 1).

No	Sample number	Parameter							
		TH	CH	DBC	CS	LS	WS	LT	WT
1	MNHN-IU-2019-4859	12.69	7.12	1.06	3.95	6.09	3.08	3.47	1.30

Key to parameters: TH = total height; CH = capitulum height; DBC = diameter of the base of capitulum; LS = scutum length; WS = scutum width; LT = tergum length; WT = tergum width.

Table 7.35. Measurements for *Dichelaspis orthogonia* Darwin, 1852 (N = 1).

No	Sample number	Parameter							
		TH	CH	DBC	CS	LS	WS	LT	WT
1	MNHN-IU-2019-4864	10.47	8.69	1.89	4.75	7.16	3.5	6.53	0.80

Key to parameters: TH = total height; CH = capitulum height; DBC = diameter of the base of capitulum; LS = scutum length; WS = scutum width; LT = tergum length; WT = tergum width.

Table 7.36. Measurements for *Glyptelasma gracile* (Hoek, 1883) (N = 1).

No	Sample number	Parameter							
		TH	CH	DBC	CS	LS	WS	LT	WT
1	MNHN-IU-2019-4876	13.99	10.44	1.45	5.16	9.01	4.79	5.07	1.87

Key to parameters: TH = total height; CH = capitulum height; DBC = diameter of the base of capitulum; LS = scutum length; WS = scutum width; LT = tergum length; WT = tergum width.

Table 7.37. Measurements for *Megalasma striatum* Hoek, 1883 (N = 1).

No	Sample number	Parameter							
		TH	CH	DBC	CS	LS	WS	LT	WT
1	MNHN-IU-209-4870	9.36	9.36	2.14	4.82	7.28	3.81	4.29	1.58

Key to parameters: TH = total height; CH = capitulum height; DBC = diameter of the base of capitulum; LS = scutum length; WS = scutum width; LT = tergum length; WT = tergum width.

Table 7.38. Measurements for *Diotascalpellum rubrum* (Hoek, 1883) (N = 2).

No	Sample number	Parameter				
		a	b	c	d	e
1	MNHN-IU-2019-4925	20.57	10.55	6.51	5.10	6.62
2	MNHN-IU-2019-4926	12.51	7.39	4.09	7.76	4.36

Key to parameters: a = capitulum height; b = capitulum width; c = capitulum thickness; d = peduncle length; e = diameter of peduncle.

Table 7.39. Measurements for *Regioscalpellum moluccanum* (Hoek, 1883) (N = 5).

No	Sample number	Parameter				
		a	b	c	d	e
1	MNHN-IU-2019-4909-1	12.92	10.20	4.91	9.11	6.04
2	MNHN-IU-2019-4909-2	8.75	5.52	3.11	5.89	3.45
3	MNHN-IU-2019-4909-3	7.88	4.81	2.91	8.43	3.30
4	MNHN-IU-2019-4910	8.27	5.40	2.15	3.38	2.09
5	MNHN-IU-2019-4912	14.89	10.65	5.24	9.13	5.39

Key to parameters: a = capitulum height; b = capitulum width; c = capitulum thickness; d = peduncle length; e = diameter of peduncle.

Table 7.40. Measurements for *Scalpellum* sp. (N = 1).

No	Sample number	Parameter				
		a	b	c	d	e
1	MNHN-IU-2019-4929	15.90	10.29	4.58	6.97	5.67

Key to parameters: a = capitulum height; b = capitulum width; c = capitulum thickness; d = peduncle length; e = diameter of peduncle.

Table 7.41. Measurements for *Scalpellum stearnsi Pilsbry*, 1890 (N = 5).

No	Sample number	Parameter				
		a	b	c	d	e
1	MNHN-IU-2019-4888	31.69	28.20	11.19	28.29	11.39
2	MNHN-IU-2019-4889	44.75	35.46	11.93	37.19	14.94
3	MNHN-IU-2019-4892	40.43	31.57	17.54	53.18	15.47
4	MNHN-IU-2019-4893	39.34	31.15	14.21	33.23	14.42
5	MNHN-IU-2019-4894	52.00	40.11	18.56	86.59	17.94

Key to parameters: a = capitulum height; b = capitulum width; c = capitulum thickness; d = peduncle length; e = diameter of peduncle.

Table 7.42. Measurements for *Alcockianum persona* (Annandale, 1916) (N = 5).

No	Sample number	Parameter				
		a	b	c	d	e
1	MNHN-IU-2019-4903	21.06	17.72	11.35	14.41	9.54
2	MNHN-IU-2019-4904-1	35.06	28.06	18.20	28.67	10.79
3	MNHN-IU-2019-4904-2	27.01	20.04	11.22	23.61	9.72
4	MNHN-IU-2019-4906-1	25.44	19.76	10.19	21.49	8.06
5	MNHN-IU-2019-4906-2	17.71	12.91	4.96	13.42	6.66

Key to parameters: a = capitulum height; b = capitulum width; c = capitulum thickness; d = peduncle length; e = diameter of peduncle.

Table 7.43. Measurements for *Annandaleum japonicum* (Hoek, 1883) (N = 4).

No	Sample number	Parameter				
		a	b	c	d	e
1	MNHN-IU-2019-4932-1	9.56	4.67	1.85	3.71	1.83
2	MNHN-IU-2019-4932-2	11.66	5.82	2.53	3.84	2.01
3	MNHN-IU-2019-4932-3	12.04	6.00	2.82	3.37	3.27
4	MNHN-IU-2019-4932-4	12.73	7.13	3.21	4.77	2.75

Key to parameters: a = capitulum height; b = capitulum width; c = capitulum thickness; d = peduncle length; e = diameter of peduncle.

Table 7.44. Measurements for *Annandaleum laccadivicum* (Annandale, 1906) (N = 1).

No	Sample number	Parameter				
		a	b	c	d	e
1	MNHN-IU-2019-4931	18.88	11.41	6.30	11.45	4.89

Key to parameters: a = capitulum height; b = capitulum width; c = capitulum thickness; d = peduncle length; e = diameter of peduncle.

Table 7.45. Measurements for *Annandaleum lambda* (Annandale, 1910) (N = 5).

No	Sample number	Parameter				
		a	b	c	d	e
1	MNHN-IU-2019-4913	21.76	13.04	5.59	7.74	5.47
2	MNHN-IU-2019-4914	16.61	8.73	3.17	6.08	3.73
3	MNHN-IU-2019-4915-1	22.94	13.81	6.31	15.27	6.26
4	MNHN-IU-2019-4915-2	24.27	14.49	6.70	11.06	5.81
5	MNHN-IU-2019-4915-3	20.00	12.27	4.80	5.54	4.63

Key to parameters: a = capitulum height; b = capitulum width; c = capitulum thickness; d = peduncle length; e = diameter of peduncle.

Table 7.46. Measurements for *Litoscalpellum juddi* (Calman, 1918) (N = 5).

No	Sample number	Parameter				
		a	b	c	d	e
1	MNHN-IU-2019-4896-1	16.94	11.39	5.20	16.87	5.63
2	MNHN-IU-2019-4896-2	21.21	13.78	7.08	17.06	6.33
3	MNHN-IU-2019-4896-3	39.25	28.28	19.89	35.99	16.87
4	MNHN-IU-2019-4896-4	24.17	13.69	8.09	15.02	7.17
5	MNHN-IU-2019-4898	30.32	21.09	7.25	52.02	11.42

Key to parameters: a = capitulum height; b = capitulum width; c = capitulum thickness; d = peduncle length; e = diameter of peduncle.

Table 7.47. Measurements for *Litoscalpellum recurvirostrum* (Hoek, 1883) (N = 5).

No	Sample number	Parameter				
		a	b	c	d	e
1	MNHN-IU-2019-4934	16.15	10.39	5.07	8.37	4.96
2	MNHN-IU-2019-4935-1	16.78	10.49	5.25	10.02	5.10
3	MNHN-IU-2019-4935-2	16.39	9.24	4.45	7.25	4.13
4	MNHN-IU-2019-4937-1	26.05	16.29	8.18	20.90	8.95
5	MNHN-IU-2019-4937-2	24.26	16.59	7.59	19.14	8.70

Key to parameters: a = capitulum height; b = capitulum width; c = capitulum thickness; d = peduncle length; e = diameter of peduncle.

Table 7.48. Measurements for *Litoscalpellum walleni* Newman & Ross, 1971 (N = 1).

No	Sample number	Parameter				
		a	b	c	d	e
1	MNHN-IU-2019-4927	14.56	8.09	2.50	7.52	3.89

Key to parameters: a = capitulum height; b = capitulum width; c = capitulum thickness; d = peduncle length; e = diameter of peduncle.

Table 7.49. Measurements for *Amigdoscalpellum costellatum* (Withers, 1935) (N = 2).

No	Sample number	Parameter				
		a	b	c	d	e
1	MNHN-IU-2019-4922-1	12.44	7.52	3.47	3.15	2.94
2	MNHN-IU-2019-4922-2	13.88	6.97	2.77	2.99	3.24

Key to parameters: a = capitulum height; b = capitulum width; c = capitulum thickness; d = peduncle length; e = diameter of peduncle.

Table 7.50. Measurements for *Amigdoscalpellum tenue* (Hoek, 1883) (N = 1).

No	Sample number	Parameter				
		a	b	c	d	e
1	MNHN-IU-2019-4921	7.26	3.74	1.40	3.00	1.99

Key to parameters: a = capitulum height; b = capitulum width; c = capitulum thickness; d = peduncle length; e = diameter of peduncle.

Table 7.51. Measurements for *Catherinum rossi* (Rao & Newman, 1972) (N = 1).

No	Sample number	Parameter				
		a	b	c	d	e
1	MNHN-IU-2019-4933	9.67	5.52	2.58	2.79	2.29

Key to parameters: a = capitulum height; b = capitulum width; c = capitulum thickness; d = peduncle length; e = diameter of peduncle.

Table 7.52. Measurements for *Planoscalpellum distinctum* (Hoek, 1883) (N = 2).

No	Sample number	Parameter				
		a	b	c	d	e
1	MNHN-IU-2019-4928-1	6.80	3.68	1.26	1.39	1.80
2	MNHN-IU-2019-4928-2	7.90	4.36	1.24	2.49	2.04

Key to parameters: a = capitulum height; b = capitulum width; c = capitulum thickness; d = peduncle length; e = diameter of peduncle.

Table 7.53. Measurements for *Teloscalpellum ecaudatum* (Calman, 1918) (N = 2).

No	Sample number	Parameter				
		a	b	c	d	e
1	MNHN-IU-2019-4917	12.07	6.17	2.68	8.33	3.21
2	MNHN-IU-2019-4918	18.59	11.47	5.41	6.30	5.41

Key to parameters: a = capitulum height; b = capitulum width; c = capitulum thickness; d = peduncle length; e = diameter of peduncle.

Table 7.54. Measurements for *Trianguloscalpellum balanoides* (Hoek, 1883) (N = 1).

No	Sample number	Parameter				
		a	b	c	d	e
1	MNHN-IU-2019-4923	8.20	4.40	1.75	5.06	2.10

Key to parameters: a = capitulum height; b = capitulum width; c = capitulum thickness; d = peduncle length; e = diameter of peduncle.

Table 7.55. Measurements for *Trianguloscalpellum hirsutum* (Hoek, 1883) (N = 1).

No	Sample number	Parameter				
		a	b	c	d	e
1	MNHN-IU-2019-4908	12.18	6.50	3.74	4.10	3.43

Key to parameters: a = capitulum height; b = capitulum width; c = capitulum thickness; d = peduncle length; e = diameter of peduncle.

Table 7.56. Measurements for *Verum australicum* (Hoek, 1883) (N = 1).

No	Sample number	Parameter				
		a	b	c	d	e
1	MNHN-IU-2019-4930	10.33	6.09	2.08	4.62	2.24

Key to parameters: a = capitulum height; b = capitulum width; c = capitulum thickness; d = peduncle length; e = diameter of peduncle.

Table 7.57. Measurements for *Verum carinatum* (Hoek, 1883) (N = 1).

No	Sample number	Parameter				
		a	b	c	d	e
1	MNHN-IU-2019-4920	9.14	4.53	1.74	2.54	2.20

Key to parameters: a = capitulum height; b = capitulum width; c = capitulum thickness; d = peduncle length; e = diameter of peduncle.

Table 7.58. Measurements for *Verum novaezelandiae* (Hoek, 1883) (N = 1).

No	Sample number	Parameter				
		a	b	c	d	e
1	MNHN-IU-2019-4919	13.46	6.98	2.99	6.02	3.23

Key to parameters: a = capitulum height; b = capitulum width; c = capitulum thickness; d = peduncle length; e = diameter of peduncle.

Table 7.59. Measurements for *Hexelasma arafurae* Hoek, 1913 (N = 1).

No	Sample number	Parameter				
		LB	LO	H	WO	WB
1	MNHN-IU-2019-4951	14.32	8.00	12.39	6.49	13.76

Key to parameters: LB = basal lenght; LO = orifice lenght; H = carinal heigth; WO = orifice width; WB = basal width.

Table 7.60. Measurements for *Conopea cymbiformis* (Darwin, 1854) (N = 1).

No	Sample number	Parameter				
		LB	LO	H	WO	WB
1	MNHN-IU-2019-4824	7.73	4.60	8.70	3.88	4.94

Key to parameters: LB = basal lenght; LO = orifice lenght; H = carinal heigth; WO = orifice width; WB = basal width.

Table 7.61. Measurements for *Conopea navicula* (Darwin, 1854) (N = 4).

No	Sample number	Parameter				
		LB	LO	H	WO	WB
1	MNHN-IU-2019-4822-1	3.75	2.02	2.38	1.59	2.62
2	MNHN-IU-2019-4822-2	3.40	1.61	2.75	0.94	2.61
3	MNHN-IU-2019-4822-3	2.23	1.09	2.04	1.22	1.79
4	MNHN-IU-2019-4822-4	4.22	1.57	3.09	0.94	2.80

Key to parameters: LB = basal lenght; LO = orifice lenght; H = carinal heigth; WO = orifice width; WB = basal width.

Table 7.62. Measurements for *Solidobalanus auricoma* (Hoek, 1913) (N = 5).

No	Sample number	Parameter				
		LB	LO	H	WO	WB
1	MNHN-IU-2019-4850-1	8.18	5.83	5.61	3.14	5.24
2	MNHN-IU-2019-4850-2	6.75	4.18	4.39	2.58	4.92
3	MNHN-IU-2019-4850-3	6.11	4.51	5.24	2.59	4.93
4	MNHN-IU-2019-4850-4	6.36	4.74	4.11	2.72	4.51
5	MNHN-IU-2019-4850-5	7.29	4.62	6.30	3.19	5.96

Key to parameters: LB = basal lenght; LO = orifice lenght; H = carinal heigth; WO = orifice width; WB = basal width.

Table 7.63. Measurements for *Solidobalanus pseudauricoma* (Broch, 1931) (N = 5).

No	Sample number	Parameter				
		LB	LO	H	WO	WB
1	MNHN-IU-2019-4818-1	11.25	9.62	11.28	6.33	9.13
2	MNHN-IU-2019-4818-2	11.37	7.52	13.22	5.22	7.80
3	MNHN-IU-2019-4818-3	12.08	9.29	11.42	5.88	9.56
4	MNHN-IU-2019-4818-4	6.50	5.34	3.86	3.66	5.98
5	MNHN-IU-2019-4818-5	6.23	4.63	3.48	3.24	5.66

Key to parameters: LB = basal lenght; LO = orifice lenght; H = carinal heigth; WO = orifice width; WB = basal width.

Table 7.64. Measurements for *Striatobalanus amaryllis* (Darwin, 1854) (N = 1).

No	Sample number	Parameter				
		LB	LO	H	WO	WB
1	MNHN-IU-2019-4814	16.76	9.13	9.89	7.84	15.14

Key to parameters: LB = basal lenght; LO = orifice lenght; H = carinal heigth; WO = orifice width; WB = basal width.

Table 7.65. Measurements for *Striatobalanus tenuis* (Hoek, 1883) (N = 5).

No	Sample number	Parameter				
		LB	LO	H	WO	WB
1	MNHN-IU-2019-4820-1	25.78	14.37	18.02	11.80	28.03
2	MNHN-IU-2019-4820-2	18.92	13.78	18.31	10.15	20.51
3	MNHN-IU-2019-4820-3	28.30	15.11	18.68	11.85	27.39
4	MNHN-IU-2019-4820-4	24.84	16.29	19.06	12.10	24.32
5	MNHN-IU-2019-4833	27.72	15.93	20.24	13.70	25.10

Key to parameters: LB = basal lenght; LO = orifice lenght; H = carinal heigth; WO = orifice width; WB = basal width.

Table 7.66. Measurements for *Pyrgomina* sp. (N = 1).

No	Sample number	Parameter				
		LB	LO	H	WO	WB
1	MNHN-IU-2019-4817	7.46	2.42	10.45	1.41	6.15

Key to parameters: LB = basal lenght; LO = orifice lenght; H = carinal heigth; WO = orifice width; WB = basal width.

Table 7.67. Measurements for *Amphibalanus amphitrite* (Darwin, 1854) (N = 4).

No	Sample number	Parameter				
		LB	LO	H	WO	WB
1	MNHN-IU-2019-4815-1	12.10	7.89	5.65	5.22	12.03
2	MNHN-IU-2019-4815-2	6.25	4.36	3.82	2.72	6.32
3	MNHN-IU-2019-4815-3	5.27	3.81	3.64	3.01	4.62
4	MNHN-IU-2019-4815-4	6.02	4.15	5.13	3.04	4.92

Key to parameters: LB = basal lenght; LO = orifice lenght; H = carinal heigth; WO = orifice width; WB = basal width.

7.3 List of publications, presentations, seminars, symposiums, trainings, courses, and interviews

International peer-reviewed articles

Pitriana, P., Valente, L., von Rintelen, T., Jones, D.S., Prabowo, R.E. & von Rintelen, K. 2020. An annotated checklist and integrative biodiversity discovery of barnacles (Crustacea, Cirripedia) from the Moluccas, East Indonesia. ZooKeys, 945: 17–83. https://doi.org/10.3897/zookeys.945.39044.

Pitriana, P., Jones, D.S., Corbari, L. & von Rintelen, K. 2020. New insights gained from museum collections: Deep-sea barnacles (Crustacea, Cirripedia, Thoracica) in the Muséum National d'Histoire Naturelle, Paris, collected during the Karubar expedition in 1991. Zoosystematics and Evolution, 96(2): 649–698. https://doi.org/10.3897/zse.96.55733.

Pitriana, P., Wessel, A., Aschenbach, T. & von Rintelen, K. 2020. Exploring sponge-inhabiting barnacles of eastern Indonesia using micro-CT scanning. Journal of Treubia, submitted.

Pitriana, P., von Rintelen, K., Wessel, A. 2020. Non-invasive 3D visualization of the sponge-inhabiting barnacle *Acasta sulcata* (Crustacea, Cirripedia, Balanomorpha) from the Moluccas, Indonesia. [Dataset]. Data Publisher of Museum für Naturkunde Berlin (MfN) - Leibniz Institute for Evolution and Biodiversity Science. https://doi.org/10.7479/87tp-gr35.

Talks, abstracts, and posters presentations

Pitriana, P. 2017. Barnacles on the coast of Ambon Island: Pasca Siboga Expedition 1899. Poster presentation and Abstract Proceeding in SAGE 2017 – the 3rd Southeast Asian Gateway Evolution Meeting: p.169.

Pitriana, P. 2018. Barnacles on the coast of Ambon Island: Pasca Siboga Expedition 1899. Talk presentation in 19th Annual Meeting of the Gesellschaft für Biologische Systematik (GfBS), Vienna, Austria: 11th-14th February 2018.

Pitriana, P. 2018. Integrative taxonomy, phylogeny and biogeography of barnacles (Crustacea: Cirripedia) from the Spice Islands, Indonesia. Talk presentation in Evolutionary Biology Seminar Series at Museum für Naturkunde Berlin, 1st November 2018.

Pitriana, P. 2020. Past, present and future: Integrative taxonomy of barnacles (Crustacea: Cirripedia) from eastern Indonesia. Talk presentation in 21st Annual Meeting of the Gesellschaft für Biologische Systematik (GfBS), Hamburg, Germany: 12nd-15th February 2020.

Pitriana, P. 2020. Biodiversity discovery of barnacles *Acasta sulcata* (Crustacea: Cirripedia) from the Moluccas, eastern Indonesia. Talk presentation in the Webinar of East Indonesian seas as a global epicentre of marine biodiversity, 6th August 2020. The video availabe online at https://www.youtube.com/watch?v=6C_teRcVLmg.

Participation in courses, trainings, workshops, seminars, symposiums, and interviews

- Göttingen SPIRIT Summer School "Molecular Genetics for Zoologists", in Göttingen, Germany (13 – 18 August 2017).
- IOC-WESTPAC Training Course on "Molecular Taxonomy based on Single DNA Barcoding and Metabarcoding", in Jakarta and Pari Island, Indonesia (25 September – 5 October 2017).
- 59th Phylogenetisches Symposium "Phylogeny in The Post-Genomic Era", in Berlin, Germany (17 – 19 November 2017).

- Course of Molecular Phylogenies for Biodiversity, in Berlin, Germany (9 – 13 April 2018).
- Intensive course and training of “Molecular Diagnostics for Species Identification and Evolutionary Analysis”, in The Natural History Museum London, UK (13 – 19 May 2018).
- Workshop of “Good Scientific Practice”, in MfN Berlin, Germany (3 – 4 July 2018).
- Workshop of “Introduction and practice of Amira/3D”, in MfN Berlin, Germany (4 – 5 September 2018).
- “Data Management Training” in Botanic Garden & Botanical Museum (BGBM), Berlin, Germany (25 – 26 September 2018).
- Course of “The First Aid for Fieldworkers” in Wittenberg, Germany (2 – 4 November 2018).
- “Global Summit of Research Museums” in Berlin, Germany (4 – 6 November 2018).
- Distributed European School of Taxonomy (DEST): “Integrative taxonomy course in the big data era” at the Muséum National d’Histoire Naturelle, Paris, France (18 – 22 April 2019).
- Workshop “Imaging with Adobe Photoshop - Professional Image Editing and Retauching” in Berlin, Germany (27 – 28 May 2019).
- Symposium of “Imaging technology: Advances in CT Technology for Lifescience and Natural History Science Museum Collections”, in Berlin, Germany (12 – 14 June 2019).
- Workshop “Scientific writing” in Berlin, Germany (7 – 8 August 2019).
- Basic Collection Techniques Workshop at the Museum fur Naturkunde Berlin (25 – 26 November 2019).
- Workshop of Centre for Integartive Biodiversity Discovery at the Museum fur Naturkunde Berlin, Germany (27 – 28 November 2019).
- Interviewed by Science Newsletter of MfN Berlin in December 2019. “The barnacles of eastern Indonesia”, the article available online at
- https://www.museumfuernaturkunde.berlin/en/science/barnacles-eastern-indonesia.
- Interviewed by Deutsche Welle (DW) Indonesia. 2019. “Teritip: Terkenal Sebagai Hama Tapi Menyimpan Banyak Potensi”, the article is in Bahasa and available online at https://www.dw.com/id/teritip-terkenal-sebagai-hama-tapi-menyimpan-banyak-potensi/a-52038998.
- Interviewed by Deutsche Welle (DW) Indonesia. 2019. “Menguak Potensi Hewan Laut Teritip Melalui Taksonomi Integratif”, the article is in Bahasa and available online at https://www.dw.com/id/menguak-potensi-hewan-laut-teritip-melalui-taksonomi-integratif/g-52038787.
- Filmed by Deutsche Welle (DW) Indonesia. 2020. “Teritip Laut Harta Terpendam Kaya Manfaat”, the film is in Bahasa and available online at https://www.youtube.com/watch?v=QB8_3L7Ihu4.

7. 4 Curriculum vitae

For reasons of data protection, the curriculum vitae is not published in the electronic version.

For reasons of data protection, the curriculum vitae is not published in the electronic version.

7. 5 Declaration of originality

Berlin, September 2020

Hereby I declare that I wrote this doctoral thesis by myself without sources other than those indicated in the text and related reference list. The work has not been previously submitted to the Freie Universität Berlin or any other university.

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Pipit Pitriana

7. 6 Statement from proof reader

For reasons of data protection, the statement from proof reader is not published in the electronic version.