SESARMID CRABS (BRACHUYRA: GRAPSOIDEA: SESARMIDAE) IN WEST PENINSULAR MALAYSIA AND BRUNEI BAY MANGROVES: HISTORICAL REVIEW AND UPDATES ON ECOLOGY AND BIODIVERSITY AT COMMUNITY AND SPECIES LEVELS

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THESIS SUBMITTED IN FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE OF DOCTOR OF PHYLOSOPHY

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SESARMID CRABS (BRACHUYRA: GRAPSOIDEA: SESARMIDAE) IN WEST PENINSULAR MALAYSIA AND BRUNEI BAY MANGROVES: HISTORICAL REVIEW AND UPDATES ON ECOLOGY AND BIODIVERSITY AT COMMUNITY AND SPECIES LEVELS

ABSTRACT

Sesarmid crabs (Brachyura: Grapsoidea: Sesarmidae) are dominant components of the mangrove macrofauna worldwide. In particular, South East Asia hosts one of the highest diversity of sesarmid species, living in intertidal and supratidal wetlands. However, despite their well documented ecological role as primary consumers and ecosystem engineers, information on ecology and biology of many species is scarce, and their taxonomy is constantly being revised, with several new species described in the past few years. On the other hand, mangroves and other wetlands are being rapidly converted to other uses. The sesarmid communities of the Malay Peninsula (Peninsular Malaysia and Singapore) and northern Borneo have been investigated in several studies. However, a comprehensive review on the available information in this area is not available. The main objectives of this project are (i) to historically review the state of knowledge on sesarmid crabs in Peninsular Malaysia, Singapore and northern Borneo, (ii) to provide a synopsis of the Malaysian sesarmid species, containing any published information available for each species, (iii) to update the local checklists, through field surveys in several localities, and (iv) to provide new information on the ecology and distribution of the local species, through ecological analyses. First, a comprehensive literature research was conducted, considering any work ever published on each sesarmid species recorded from Malaysia. A historical review and a synopsis of the species were presented, providing a detailed source of information for researchers and conservationists in this region, and a biodiversity guide for educational purposes. Surveys were conducted in several mangrove forests along the West coast of Peninsular

Malaysia (Kuala Selangor, Tanjung Tuan, Langkawi, Pulau Besar, Pulau Kukup and Pulau Merambong). Sesarmid and other grapsoid crabs were collected to obtain species inventories for each site, most of which have not been investigated before. Several environmental variables at different scales were also recorded (type of substrate, forest type and size, and insularity). Ecological analyses investigated the spatial distribution of species relatively to the recorded variables. The results highlighted differences in communities living in different sites and environments, with few common species able to cope with different conditions, and numerous non-common species which were found only in a few study sites. Field surveys were conducted also in the Brunei Bay (Borneo), to update existing checklists from Bornean peritidal systems, and to investigate the community structure, diversity, and distribution. Several new records were reported for Borneo and Brunei Darussalam. The specimens were collected through a time- and area-based sampling method, in several sites, hosting different types of peritidal systems (mangroves, *Nypa* forests, peat swamps, disturbed grass meadows). A few variables were chosen to describe the ecological conditions (salinity, substrate, type of vegetation, distance from the mangrove seaward fringe). Assemblages of different ecosystems differed in terms of both species richness and taxonomic composition. High intertidal zones hosted peculiar communities, differentiated both among themselves, and between them and lower intertidal communities. These results highlighted the importance of preserving different types of coastal wetlands, maintaining the intertidal transition to avoid loss of diversity in these communities.

Keywords: Sesarmidae, Grapsoidea, mangrove ecosystems, biodiversity, Malaysia

KETAM SESARMID (BRACHYURA: GRAPSOIDEA: SESARMIDAE) DI HUTAN BAKAU DARI SEMENANJUNG MALAYSIA BARAT DAN BRUNEI BAY: KAJIAN SEJARAH DAN KEMAS KINI MENGENAI EKOLOGI DAN KEPELBAGAIAN BIOLOGI DI PERINGKAT KOMUNITI DAN SPESIES.

ABSTRAK

Ketam Sesarmid (Brachyura: Grapsoidea: Sesarmidae) adalah komponen utama makrofauna bakau, dan Asia Tenggara mempunyai antara kepelbagaian spesies tertinggi. Walaupun peranan mereka didokumentasikan sebagai pengguna utama dan jurutera ekosistem, maklumat mengenai ekologi dan biologi beberapa spesies ini adalah terhad. Manakala, kepantasan kawasan bakau dan *wetlands* yang lain diubah untuk kegunaan lain telah mendorong strategi pemuliharaan yang mencukupi. Objektif utama projek ini adalah untuk mengkaji semula pengetahuan tentang ketam sesarmid di Malaysia, untuk mengemaskini senarai semak tempatan dengan menjalankan tinjauan lapangan di tapak kajian yang berlainan, dan menjalankan siasatan ekologi mengenai struktur dan kepelbagaian komuniti tersebut, dan perkaitan mereka dengan parameter persekitaran yang terpilih. Dalam seksyen pertama, penyelidikan literatur komprehensif telah dijalankan, merangkumi setiap penerbitan mengenai spesies sesarmid yang dilaporkan dari Semenanjung dan Malaysia Timur. Kajian semula sejarah telah dibentangkan, dengan sinopsis untuk setiap spesies. Khususnya, pemeriksaan literatur mengesahkan bahawa autoekologi bagi beberapa spesies hampir tidak diketahui. Sesetengah spesies ini juga endemik di kawasan geografi ini, oleh itu perhatian khusus perlu diberikan untuk pemuliharaan mereka. Siri pertama tinjauan lapangan dijalankan di enam sistem bakau yang berlainan di sepanjang pantai Barat Semenanjung Malaysia. Sesarmid dan ketam grapsoid yang lain diperoleh untuk mendapatkan inventori spesies untuk setiap tapak kajian, yang kebanyakannya tidak pernah disiasat sebelum ini. Pembolehubah persekitaran telah direkodkan, seperti jenis substrat, jenis dan lanjutan hutan, dan

insulariti. Komposisi spesies berbeza di antara tapak kajian yang mempunyai jenis substrat dan lanjutan hutan yang berlainan, dan khususnya pulau berbatu / berpasir yang kecil didapati mempunyai komuniti yang berbeza dari sistem di tanah besar. Satu lagi siri tinjauan dijalankan di Teluk Brunei (Borneo). Kaedah penyampelan berasaskan masa telah digunakan untuk mendapatkan spesimen ketam di beberapa tapak bakau dan sistem berhampiran, dan beberapa pembolehubah persekitaran telah direkodkan, seperti saliniti, jenis substrat, ketumpatan liputan vegetasi, dan min jarak dari pinggir laut bakau. Hasil kajian menunjukkan beberapa spesies yang dilaporkan sebagai rekod baru untuk kawasan ini (*Episesarma singaporense*, *Haberma kamora*, *Neosarmatium inerme*, *Pseudosesarma moeschii*, *Varuna yui* untuk Borneo; *Episesarma chenotngense*, *E. mederi*, *Fasciarma fasciatum*, *Nanosesarma batavicum*, *N. edamense*, *N. pontianacense*, *Pseudosesarma bocourti*, *Metopograpsus latifrons* untuk Brunei Darussalam). Struktur dan kepelbagaian himpunan di antara dan di dalam tapak kajian berbeza dari segi kekayaan dan komposisi taksonomi. Secara amnya, kepelbagaian menurun menuju ke arah kawasan daratan, manakala sistem berhampiran laut menyokong kepelbagaian himpunan yang lebih tinggi. Dalam kedua-dua kajian lapangan, komuniti yang diselidik terdiri daripada banyak spesies khusus, yang hanya dijumpai dalam beberapa kajian, dan segelintir spesies umum, yang terdapat dalam beberapa tinjauan, yang mana menunjukkan ciri-ciri ekologi stenotipik untuk kebanyakan ketam ini. Di Brunei, beberapa spesies khusus telah direkodkan dengan kepadatan tinggi, mencadangkan penyesuaian kepada keadaan persekitaran tempatan yang tertentu, di mana spesies ini dapat berkembang. Umumnya, siasatan lapangan ini memberikan maklumat baru tentang ciri-ciri ekologi bagi spesies yang berlainan, yang mana sebahagiannya hanya direkodkan dalam artikel taksonomi atau laporan anekdotal. Akhir sekali, strategi pemuliharaan juga telah dibincangkan bagi menggunakan data ekologi yang ada untuk merekabentuk pelan pemuliharaan dan pengurusan untuk kawasan *wetlands* pesisiran di kawasan ini.

Kata kunci: Sesarmidae, Grapsoidea, hutan bakau, biodiversiti, Malaysia

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LIST OF SYMBOLS AND ABBREVIATIONS

AEP: Atlantic East Pacific, i.e. the biogeographic region including West Africa, East and West America.

AF: areal extension of the forest

C: carbon

CCA: Canonical Correspondence Analysis

C/N: carbon/nitrogen ratio

CW: carapace width

DM: mean distance from the mangrove seaward fringe

DsAT: number of collected individuals per unit area (100 m^2) and time (60 min)

DV: type and density of vegetation coverage

IG: linear extension of the forest along the intertidal gradient

IN: insularity

IWP: Indo-West Pacific, i.e. the biogeographic region including East Africa, Indian subcontinent, South East Asia, East Asia, and Australasia.

J: Jaccard index

KS: Kuala Selangor

LK: Langkawi

N: nitrogen

PB: Pulau Besar

PK: Pulau Kukup

PM: Pulau Merambong

SA: salinity

SD: type of sediment

S_{eff}: effective number of species

ST: substrate type

TT: Tanjung Tuan

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CHAPTER 1: GENERAL INTRODUCTION

Mangrove forests and other coastal wetlands (e.g. nipah forests) are at the interface between the marine and terrestrial domains. These ecosystems can be particularly affected by shifts in biological diversity, while at the same time providing ecosystem services critical to the land and marine adjacent ecosystems, thus being defined as "critical transition zones" (CTZs, Levin et al., 2001), whose conservational importance has been widely recognised (MAP, 2005; Duke et al., 2007).

Mangroves provide important ecological services, acting as soil stabilisers, nurseries for several fish and prawn species, link between terrestrial and marine systems through foodweb (export of carbon from mangrove to offshore systems), carbon storage, and shoreline protection (Yahaya & Ramu, 2003; Andreetta et al., 2014; Hutchison et al., 2014).

In the past decades, however, the worldwide areal of mangrove forests has been declining considerably, due to conversion of these forests into agricultural lands, aquaculture ponds, and urban areas (Valiela et al., 2001; Giesen et al., 2006; Feller et al., 2017). For instance, in South East Asia ~ 15% of the mangrove forests have been lost in just 20 years (1980-2000; see Giesen et al., 2006), while several countries, such as the Philippines, Thailand, and Vietnam, have lost ~ 40-60% of their mangrove systems (see Yahaya & Ramu, 2003).

Grapsoid crabs (Crustacea: Brachyura: Grapsoidea), and especially the Sesarmidae family, are one of the dominant macrofaunal components of the Indo-West Pacific mangrove ecosystems (Lee, 1998; Hogarth, 2007). In particular, because of their important ecological role in the foodweb and in the soil dynamics, these crabs have been considered as "key-stone species" (Smith et al., 1991) and "ecosystem engineers" (Kristensen, 2008).

The Malay Peninsula (including Peninsular Malaysia and Singapore) and Borneo are part of a biodiversity hotspot for several marine and terrestrial taxa, being included in both the Sundaland ecoregion (Myers et al., 2000) and the East Indies Triangle (Briggs, 1999) or Indo Australian Archipelago (Renema et al., 2008). However, knowledge on the distribution of sesarmid species in this area is still fragmentary. In particular, the brachyuran assemblages of several mangrove areas have not been investigated before, while others have only been surveyed in the early literature, while no data are available on the current status of these ecosystems.

A number of studies conducted in this area have investigated ecological aspects of selected mangrove sites (e.g. Sasekumar, 1974; Ashton et al., 2003a,b), or species (e.g. Sivasothi, 2000). However, data on the autecological niche of most species are still scarce or missing, while the dynamics of interactions among species and the role of the environmental conditions on the assemblages are almost unknown (Lee et al., 2017).

Several authors have advocated for the need of investigating the assemblages and building inventories and checklist of species (e.g. Wafar et al., 2011; Latiff, 2012), which are an important tool in management plans and conservation programs. Moreover, providing information on biodiversity can raise awareness in the general public on the importance of preserving these systems and the rich biodiversity heritage of this country. A review on the studies conducted in this area would also provide a base of information for other biologists, conservation ecologists and managers operating in these ecosystems.

This project intends to provide an overview of the state of knowledge on sesarmid crabs in Malaysian mangrove systems, and also to obtain new information on distribution, community structure and composition, and autecological traits of the species.

Research Questions

1) What is the current state of knowledge on the sesarmid crabs in the Malay Peninsula (i.e. Peninsular Malaysia and Singapore) and northern Borneo? Which species are present in this area? Which biological aspects have been investigated?

2) How is the sesarmid biodiversity of previously uninvestigated mangrove forests and other coastal wetlands? What is the current status of assemblages previously investigated?

3) How is the diversity and structure of assemblages of different sites? Is the diversity related to environmental conditions such as substrate type, forest extension, salinity, type of vegetation? Are the species co-occurring? Are they associated to specific habitat types?

Objectives of this project

The present thesis is articulated in three distinct articles, reflecting three main objectives:

1) A revision of the state of knowledge of sesarmid crabs in the Malay Peninsula (Peninsular Malaysia and Singapore) and northern Borneo. This article reviews the available studies conducted in this area on this brachyuran family. Moreover, for each of the sesarmid species recorded here, all the information available worldwide have been obtained and presented in a synopsis.

2) An update on the distribution of sesarmid crabs in this geographic area. In particular, sampling field trips have been conducted in several sites both in Peninsular Malaysia (West coast) and northern Borneo (Brunei Darussalam). This article provides new inventories for most of the sites, which have not been investigated before, and updates existing checklists, available only for a few sites. Moreover, several new distribution records have been found, highlighting the necessity of further investigations in this area.

3) An investigation of ecological aspects of the investigated assemblages. The datasets obtained from the field collections (see objective 2) have been analysed with univariate and multivariate techniques, in order to investigate the structure and diversity of the sesarmid assemblages in each of the studied sites. Moreover, selected environmental variables have been measured or recorded in the field, and the association of the species with such variables has been explored.

CHAPTER 2: LITERATURE REVIEW

2.1 Taxonomy and systematics of the Sesarmidae family

Sesarmid crabs (Sesarmidae Dana, 1851) are currently considered as a family within the superfamily Grapsoidea MacLeay, 1838 (see Ng et al., 2008). The taxa was first established by Dana (1851) as Sesarminae, a subfamily of the family Grapsidae MacLeay, 1838, which included also the subfamilies Grapsinae, Plagusiinae and Varuninae.

A few years later, H. Milne Edwards (1853) proposed an alternative classification, which considered grapsoid crabs as a tribe, subdivided into six "agèles" (subtribes): Grapsacaea, Varunacaea, Cyclograpsacaea, Sesarmacaea, Plagusiacaea, and Gecarcinacaea. However, several authors chose to adopt the previous classification into subfamilies (e.g. Alcock, 1900; Rathbun, 1918a; Tweedie, 1936). Later, Guinot (1978) proposed to elevate the Grapsidae family to the superfamily level, with the name Grapsidoidea (today Grapsoidea), and the subfamilies were elevated to family level (Guinot, 1978).

More recently, several molecular, morphological and larval studies (e.g. Von Sternberg & Cumberlidge, 1998; Cuesta & Schubart, 1999; Cuesta et al., 2000; Schubart et al., 2000; Spivak & Cuesta, 2000) have further supported the family status. Therefore, the latest checklists of the extant brachyuran species of the world have considered Sesarmidae Dana, 1851 as the currently valid classification (Martin and Davis, 2001; Ng et al., 2008). However, throughout years the use of Sesarmidae or Sesarminae has been alternatively chosen by researchers (e.g. Diesel et al., 2000; Rahayu & Davie, 2002; Kristensen et al., 2010).

To date, the Sesarmidae family includes 34 genera (see Ng et al., 2008; Schubart et al., 2009; Naruse & Ng, 2012; Brösing et al., 2014; Shahdadi & Schubart, 2017), which are distributed throughout the whole tropical and subtropical belts (Abele, 1992; Hogarth, 2007). In particular, in their annotated checklist of extant brachyuran crabs of the world, Ng et al. (2008) provided a comprehensive species list for this family, which included 245 species. Since then, ~50 new species were described, increasing the number of species to ~300 (Naruse & Ng, 2008; Naderloo & Turkay, 2009; Rahayu & Ng, 2009; Schubart et al., 2009; Wowor & Ng, 2009; Davie, 2010, 2012; Davie & Pabriks, 2010; Husana et al., 2010; Koller et al., 2010; Naderloo & Schubart, 2010; Promdam & Ng, 2010; Ng, 2012, 2013, 2017, 2018; Ng & Davie, 2011; Ragionieri et al., 2012; Komai & Ng, 2013; Lee et al., 2013; Rahayu & Li, 2013; Brösing et al., 2014; Schubart & Ng, 2014; Thiercelin & Schubart, 2014; Ng et al., 2015a, 2016, 2017; Manuel-Santos et al., 2016; Cannicci & Ng, 2017; Cannicci et al., 2017; Ng & Schubart, 2017; Shahdadi et al., 2017, 2018a, 2019; Poupin et al., 2018; Wowor & Ng, 2018).

Several authors have pointed out that while the taxonomy and phylogenetic relationships within this family have undergone numerous modifications and re-adjustments, they still remain confusing and require further revision (e.g. Tan & Ng, 1994; Schubart et al., 2006; Ng et al., 2008). This taxonomic confusion has been attributed to the morphological similarity of the species within this family (Hogarth, 2007), and to the difficulty of finding reliable diagnostic characters. For instance, Shahdadi and Schubart (2015) examined the validity of the dactylar tubercles, one of the main characters traditionally utilised to discriminate the species of the genus *Perisesarma*. These authors highlighted how, although this feature remains a good diagnostic character, intraspecific variability in number and shape of the tubercles, and overlaps between species, can make the identification difficult (Shahdadi & Schubart, 2015).

2.2 Historical review of the sesarmid genera

The earliest studies on sesarmid crabs were conducted in the nineteen century, when only a few genera were described, namely *Aratus* H. Milne Edwards, 1853, *Chiromantes* Gistel, 1848, *Clistocoeloma* A. Milne Edwards, 1873, *Holometopus* H. Milne Edwards, 1853, *Geosesarma* De Man, 1892, *Metagrapsus* H. Milne Edwards, 1837, *Metasesarma* H. Milne Edwards, 1853, *Metopaulias* Rathbun, 1896, *Pachysoma* De Haan, 1833, *Sarmatium* Dana, 1851, and *Sesarma* Say, 1817.

In particular, *Chiromantes* Gistel, 1848 was defined to replace *Pachysoma* De Haan, 1833, which was a pre-occupied name (by *Pachysoma* MacLeay, 1821, Coleoptera). *Geosesarma* De Man, 1892 was considered invalid by De Man (1902) himself, and its species transferred again to *Sesarma* Say, 1817.

Most of the described species were initially included in the genus *Sesarma* Say, 1817, which De Man (1895) subdivided in 4 subgenera, i.e. *S.* (*Sesarma*), *S.* (*Episesarma*), *S.* (*Parasesarma*), and *S.* (*Perisesarma*). However, due to nomenclature reasons, Rathbun (1897) modified the first two subgenera in *S.* (*Holometopus*) and *S.* (*Sesarma*), while Rathbun (1909) changed *S.* (*Perisesarma*) in *S.* (*Chiromantes*). This nomenclature was adopted by Tesch (1917), which provided a general synopsis of the species described until then.

Some of the species included in *S.* (*Sesarma*) (*sensu* Rathbun 1897) were included by Tesch (1917) and Tweedie (1936) in a species group which Serène and Soh (1967) called "*mederi*" group. Such group was later defined as a new subgenus, *Neoepisesarma* (*Neoepisesarma*), by Serène and Soh (1970) (see below). Later, Holthuis (1978) considered this subgenus as a junior synonym of *Episesarma* De Man, 1895, and Tan and Ng (1994) officially reconsidered *Episesarma* De Man, 1895 as the correct generic name for this group of species.

Tweedie (1950c) described the new genus *Nanosesarma*, to host a group of species previously included in *S.* (*Sesarma*) (*sensu* Rathbun 1897) and *S.* (*Parasesarma*). Later, this genus was subdivided by Serène and Soh (1970) into two sub-genera, *Nanosesarma* (*Nanosesarma*) and *Nanosesarma* (*Beanium*). However, Holthuis (1977) and Abele (1979) stated that *Nanosesarma* (*Beanium*) was a junior synonym of *Nanosesarma* (*Nanosesarma*) and reunified the genus.

Serène and Soh (1970) proposed a new classification for the Indo-West Pacific (IWP) species. In particular, these authors considered *Chiromantes* Gistel, 1848, *Holometopus* H. Milne Edwards, 1853, and *Parasesarma* De Man, 1895 as distinct and valid genera. They also resurrected and redefined *Geosesarma* De Man, 1892, adding to this genus several species previously included in *S.* (*Sesarma*) (*sensu* Rathbun 1897). Moreover, they established 10 new genera, to host species previously included in *S.* (*Sesarma*) (*sensu* Rathbun, 1897): *Neosesarma*, *Neoepisesarma*, *Neosarmatium*, *Tiomanium*, *Bresedium*, *Pseudosesarma*, *Sesarmops*, *Labuanium*, *Sesarmoides*, *Namlacium*. In particular, *Neoepisesarma* was further subdivided in three subgenera, i.e. *Neoepisesarma* (*Muradium*), *Neoepisesarma* (*Neoepisesarma*), and *Neoepisesarma* (*Selatium*).

A few years later, Holthuis (1977) considered the modifications by Rathbun (1897, 1909) as invalid. He therefore re-transferred again the species previously included in *S.* (*Chiromantes*) to *S.* (*Perisesarma*), and considered *S.* (*Chiromantes*) as the correct name for the IWP species previously included in *S.* (*Holometopus*). Apparently, however, this author did not followed the previous upgrade of these sub-genera to generic level proposed by Serène and Soh (1970).

Von Hagen (1978) discussed the taxonomic position of the American sesarmid species, and recognized the presence of two groups, which were previously placed in *S.* (*Sesarma*) and *S.* (*Holometopus*) [= *S.* (*Chiromantes*) after Holthuis (1977)]. Abele (1992) reviewed the American species, and officially placed the two groups in the genus *Sesarma*, and in a newly established genus, *Armases*, respectively.

More recently, several new genera have been described, to host newly discovered species (e.g. Schubart et al., 2003), or to include species previously placed in other genera (e.g Davie & Ng, 2007).

In particular, Ng and Liu (1999) established a new genus, *Stelgistra*, to include a single species, *Sesarma stormi* De Man, 1895, which was previously included in *Chiromantes*, but differed markedly from the other species of this genus. Ng and Schubart (2002) described a new genus, *Haberma*, on the basis of samples previously collected and deposited by Raoul Serène in the Raffles Museum of Biodiversity of Singapore, and newly collected specimens. R. Serène considered his specimens as a new species, tentatively belonging to *Chiromantes*, although he did not describe it (Ng & Schubart, 2002).

Schubart et al. (2003) described a new genus, *Scandarma*, to host a sesarmid species newly discovered from Taiwan. Davie and Ng (2007) established a new genus, *Karstarma*, to include a group of species previously placed in *Sesarmoides*, and typically found in anchialine cave systems. Schubart et al. (2009) officially elevated *Neoepisesarma* (*Selatium*) to generic level (i.e. *Selatium*), and established a new genus, *Lithoselatium*, to host two newly described species.

Naruse and Ng (2012) transferred *Cyclograpsus lophopus* Nobili, 1905 from the Varunidae to the Sesarmidae family, and established a new genus, *Cyclorma*, to host this species. Brösing et al. (2014) described a new genus, *Eneosesarma*, to include a new species described from the Red Sea. These authors based their description both on new samples, and on specimens collected by Beat Schätti in 1989 and deposited in the Muséum d'Histoire Naturelle of Genève (Brösing et al., 2014).

Shahdadi and Schubart (2017) re-examined the genera *Parasesarma* and *Perisesarma*, which several authors had suggested to be phylogenetically closely related (e.g. Guerao et al., 2004; Fratini et al., 2005; Schubart et al., 2006). These authors conducted morphological and molecular analyses, which led to transferring most of the species of *Perisesarma* to *Parasesarma*. Moreover, they established two new genera, *Fasciarma* and *Guinearma*, to host the aberrant *Perisesarma fasciatum*, and the West African species (*P. alberti*, *P. huzardi* and *P. kamermani*), respectively (Shahdadi & Schubart, 2017).

Several genera (i.e. *Chasmagnathus*, *Cyclograpsus*, *Helice*-group, *Helograpsus*, *Paragrapsus* and *Metaplax*), previously placed in Sesarmidae, have been recently moved to the family Varunidae, on the basis of new molecular and ontogenetic data (Schubart & Cuesta, 1998; Schubart et al., 2000, 2002; Kitaura et al., 2002).

2.3 Biogeographic distribution

Most of the sesarmid species are distributed throughout the Indo-West Pacific region (IWP, see Hogarth, 2007), while only a few genera are present in the Atlantic East Pacific region (AEP), i.e. *Aratus*, *Armases*, *Guinearma*, *Metopaulias*, and *Sesarma* (Abele, 1992; Shahdadi & Schubart, 2017; Thiercelin & Schubart, 2014). This trend has been observed in several taxa, including also mangrove species and other macrofaunal taxa, which have many more species and genera present in the IWP, than in the AEP region (Jones, 1984; Hogarth, 2007).

Along the latitudinal gradient, sesarmid crabs have been reported from tropical and subtropical areas (Lee, 1998; Hogarth, 2007). In particular, in the IWP region, their distribution range goes from South Korea and Japan (e.g. Lee et al., 2010; Yuhara et al., 2014), in the northern hemisphere, to northern Australia in the south (e.g. Robertson & Daniel, 1989; Salgado Kent & McGuinness, 2010).

The areal distribution of each species can vary from species largely distributed across several regions (e.g. *Clistocoeloma merguiense*, see Subchapter 3.3.2.2 for references), to others reported from a very restricted area only (e.g. *Nanosesarma tweediei*, see Subchapter 3.3.7.7 for references). However, since the knowledge of the distribution ranges relies on the available literature, detailed information is available only for species which have been investigated more regularly (e.g. *Neosarmatium meinerti* species complex, see Ragionieri et al., 2012; *Episesarma* spp., see Subchapter 3.3.3), or species whose distribution has been officially reviewed (e.g. *Parasesarma semperi* and *Parasesarma longicristatum*, Shahdadi et al., 2018b; *Sesarma* spp. and *Armases* spp., Abele, 1992).

In fact, data on distribution inferred from the available publication may underestimate the actual areal of certain species, such as those reported in a few studies only (e.g. *Bresedium sedilense*, *Nanosesarma nunongi*, see Chapter 3). For these species, it is not clear whether their distribution range is actually restricted (endemisms), or it covers instead a larger area, including localities not yet investigated. For instance, several works have published new records which have extended the areal distribution of species which were scarcely investigated (e.g. *Clistocoeloma sinense*, Hsueh & Huang, 1996). Moreover, macrofaunal assemblages of several mangrove sites (and also other coastal wetlands) remain uninvestigated (e.g. Wafar et al., 2011; see also Chapter 3).

2.4 Ecological diversity

The sesarmid family include semi-terrestrial and terrestrial species, which occupy a wide range of ecological niches in different coastal and inland ecosystems (Lee, 1998). Most species, however, live in intertidal mangrove forests (Lee, 1998), where they are considered as one of the dominant macrofaunal component, both in term of specific richness and biomass (Jones, 1984).

Some species, such as *Bresedium* spp. (Tweedie, 1940, 1950a; Frusher et al., 1994) and *Pseudosesarma* spp. (Tweedie, 1940; McLauglin et al., 1996), can be found in nipah palm (*Nypa fruticans*) forests, where they are able to cope with brackish and freshwater conditions (Frusher et al., 1994). A few species have been collected also from other wetlands, such as peat swamps (e.g. *Pseudosesarma bocourti*; Ng, 1995), *Zoysia tenuifolia* marshes (*Clistocoeloma sinense*; Hsueh, 1995), and *Spartina* marshes (*Sesarma reticulatum*, *Armases cinereum*; Abele, 1992).

Some species of the genera *Armases* and *Sesarma* have been found in inland river systems and mountain streams (Abele, 1992; Diesel et al., 2000), while species of the genera *Geosesarma*, *Labuanium*, *Metopaulias* and *Scandarma* have been reported from tropical rainforests, up to several kilometers from the coast (e.g. Tweedie, 1940; Ng & Lim, 1987).

A few species can be found instead in rocky intertidal ecosystems, such as the species of the genera *Eneosesarma* and *Lithoselatium* (Schubart et al., 2009; Brösing et al., 2014), and the species *Nanosesarma sarii* (Naderloo & Turkay, 2009), *Parasesarma cognatum* and *P. liho* (Rahayu & Li, 2013; Koller et al., 2010). *Stelgistra stormi* has been reported from dead coral rocks in the supralittoral zone (Ng & Liu, 1999); *Clistocoeloma suvaense* and *Nanosesarma batavicum* were instead recorded on coral reefs (Edmondson, 1951; Dong et al., 2015), although these species can be found also in mangrove forests.

All the species of the genus *Karstarma* have been found exclusively in karst and limestone caves (Davie & Ng, 2007), while *Sesarma verleyi* and *Armases miersii* have been reported from anchialine caves (Hartnoll, 1964; Abele, 1992). Another species, *Labuanium trapezoideum*, has been found living on vertical to nearly vertical rock faces along flowing streams (Jeng et al., 2003), while *Fasciarma fasciatum* and *Haberma* spp. are able to colonise artificially altered areas within mangrove forests, such as portions of the forest partially cleared (Berry, 1972), sites artificially altered by dumping of sand (Sasekumar, 1974), or disturbed areas covered by man-made debris (Ng & Schubart, 2002).

2.4.1 Adaptations to terrestrial ecosystems

Sesarmid species exhibit different degrees of adaptation to semi-terrestrial ecological conditions, and they have adopted physiological, ecological and ontogenetic strategies to cope with the extreme conditions of this kind of environment (e.g. Macintosh, 1988; Anger, 1995; Diesel et al., 2000; Anger et al., 2007). In particular, since these crabs are active mainly at low tide, they have adapted to breathe in an aerial environment, which is also subjected to wide fluctuations in temperature and salinity conditions (Macintosh, 1988).

In order to optimise the respiratory process, the gills are reduced in size, minimising the amount of water required to moisten the respiratory surface, and the walls of the branchial chambers are vascularised, to enhance gas exchange (Gray, 1957; Veerannan, 1974; Takeda et al., 1996). Moreover, sesarmid species have been found to recycle water, by actively creating a flow on their body surface which allows gas exchange with the atmosphere, and consequent re-oxygenation (Macnae, 1968). Water is pumped from exhalant openings at the side of the buccal cavity, from where it spreads by capillary action on the carapace surface, and it is directed back to the branchial chamber through an inhalant opening at the base of the legs (Hogarth, 2007). This process is helped by a regular grid-like array of short bristles that cover the frontal carapace plates, and by lines of short bristles on the dorsal surface of the carapace, which help to direct the water flow (Felgenhauer & Abele, 1983).

Sesarmid crabs can generally tolerate salinity fluctuations, which in the landward mangrove zones can be extreme (e.g. 3-48 ppt; Sasekumar, 1974) and rapid, due to the alternation of strong evaporation processes and sudden rainfall events (Macintosh, 1988). For instance, *Parasesarma onychophorum* was found to be able to survive for several days at 5 ppt (Macintosh, 1988), while certain species have been found able to tolerate fluctuations even wider than the ones tolerated by mangrove trees (Macintosh, 1988; Jones, 1984).

While most of the species are found on the forest soil, where many of them dig burrows in the soft sediment (see also Subchapter 2.5.2), some species have diversified their ecological niche by occupying peculiar microhabitats (Lee, 1998). For instance, species of the genus *Nanosesarma* can be found living inside crevices of decaying wood material, cobbles, or oyster clusters (e.g. Hsueh, 1996; Chertoprud et al., 2012; pers. obs.), which provide them with shelter and protection from desiccation and heat.

Some of the species living in rainforests have been found in phytotelmic habitats (see Cumberlidge et al., 2005), i.e. small pools of rainwater trapped in plants' cavities and hollow parts, which provide the crabs with a water supply and occasional food source (insect material). For instance, *Metopaulias depressus* is considered an obligate inhabitant of bromeliad plants (Diesel, 1989; Diesel & Schubart, 2007), since this species spends its entire life-cycle inside these plants. In particular, the larvae are released in a nursery axil water reservoir, where they go through an abbreviated development. The juveniles remain on the plant, where the mother performs parental care, by actively defending them from predators and providing them with food (Diesel, 1989). After a few months, the juveniles can either start dispersing and finding other plants, or they remain with the mother, forming family groups of different generations (Diesel & Schubart, 2007).

Several species have been observed instead on tree trunks and canopies, or in other arboreal habitats (e.g. *Parasesarma leptosoma*, Vannini & Ruwa, 1994; *Episesarma* spp., *Selatium brockii*, Sivasothi, 2000; *Scandarma* spp., Schubart et al., 2003). Fratini et al. (2005) highlighted how this tree climbing behaviour evolved several times within the Sesarmidae and Grapsidae families, resulting in several species from different genera performing tree climbing, with different degree of dependence on arboreal life. Vannini et al. (1997) proposed a classification based on the species tree-climbing abilities: non-arboreal species or only occasionally seen on roots; species that mostly or exclusively live on tree trunks (e.g. *Episesarma* spp., *Selatium elongatum*, *S. brockii*); and the most specialized species, which thrive in the tree canopy and often feed on fresh leaves (e.g. *Aratus pisonii*, *Armases elegans*, *Parasesarma leptosoma*).

For instance, the East African species *Parasesarma leptosoma* has been found to perform regular migrations (twice a day) to the tree canopies, where the crabs feed on mangrove leaves (Vannini & Ruwa, 1994), while the American species *Aratus pisonii* spends its entire adult life on trees, probably to avoid predation by another crab, *Goniopsis cruentata* (Warner, 1967, 1969). Species of the genus *Episesarma* have been observed climbing on tree trunks during high tide, when they remain motionless on the tree trunks, probably to avoid predators, and at night, when they regularly ascend to the tree canopy (Sivasothi et al., 1993; Sivasothi, 2000).

Specimens of *Scandarma lintou* have been found commonly associated with the pandan screw pine (*Pandanus odoratissimus*), where they hide in leaf axils at daytime, and climb on the thorny leaves at night (Schubart et al., 2003). However, this species has been reported also from areas where *P. odoratissimus* is not present, where it was found under man-made concrete blocks on the forest floor, or in crevices of vertical concrete walls (Schubart et al., 2003). Some species of the genus *Geosesarma* are instead associated with pitcher plants (*Nepenthes* spp., Ng & Lim, 1987; Tan & Ng, 2008), epiphytes (Ng, 1986) and trees (Ng, 1992), although the association is not necessarily obligate (Tan & Ng, 2008). Ng and Liu (2003) and Cumberlidge et al. (2005) reported species of *Labuanium* being associated with phytothelmic habitats such as tree holes and leaf axiles of *Pandanus* palms, where these crabs find shelter and water supply.

In order to cope with the challenging conditions of terrestrial and semi-terrestrial ecosystems, sesarmid crabs exhibit different ontogenetic strategies (e.g. Tan & Ng, 1995; Diesel et al., 2000). For instance, some of the sesarmid species inhabiting mangrove forests perform nocturnal migrations to the sea to release eggs, while others show a lunar or semi-lunar rhythm of larval release, which is synchronised with the spring tides (see Jones, 1984).

Studies on the sesarmid crabs from Jamaica have highlighted how the different species have been able to colonise different habitats along a sea-to-land gradient (e.g. Schubart et al., 1998; Diesel et al., 2000). In particular, this island hosts several species of the genera *Sesarma* and *Armases*, which have adopted different ecological strategies to cope with freshwater and terrestrial habitats. Diesel et al. (2000) distinguished three groups of species, namely a "marine group", with a classic larval off-shore development, a "brackish group" where the larval development occurs in brackish water nurseries (such as land-locked pools or supratidal ponds), and a "freshwater group", with larval development in freshwater (rivers, cave systems, or small water bodies within the rainforest). Brackish and freshwater species show an abbreviated larval development, larger egg sizes, and tolerance to diverse salinity conditions, which allow them to cope with the challenging conditions of these kind of environments (Diesel et al., 2000).

In the IWP region, *Geosesarma* species do not need to go back to the sea to release the eggs, which hatch into particularly adapted zoeae with internal yolk or directly into miniature of the adult (Ng & Tan, 1995). In *G. notophorum*, the females have also been observed carrying the newly hatched juveniles on their back for a few days (Ng & Tan, 1995).

2.4.2 Species distribution in the mangrove systems

Within the mangrove ecosystems, sesarmid crabs have been found along the whole intertidal gradient, from the seaward pioneer shore to the most landward portions of the forest (e.g. Sasekumar, 1974; Frusher et al., 1994). Several studies have attempted to describe the distribution patterns of the different species, and their association with environmental variables (e.g. Frusher et al., 1994; Dahdouh-Guebas et al., 2002; Ashton et al., 2003b).

Earlier ecological works provided an account of the distribution and abundance of mangrove macrofauna along transects parallel to the intertidal gradient, which were arbitrarily subdivided into zones (e.g. Sasekumar, 1974; Frith et al., 1976). These authors provided also a qualitative description of the tree species composition of each zone, and investigated the associations between macrofaunal species and selected environmental variables, such as temperature, salinity, pH, sediment grain size and organic content of the soil (Sasekumar, 1974; Frith et al., 1976).

More recently, researchers have further investigated the role of selected environmental variables on the distribution patterns of sesarmid crabs (e.g. Frusher et al., 1994; Ashton et al., 2003a,b). For instance, Frusher et al. (1994) conducted a study on the sesarmid community of the Murray River estuary (Australia), investigating the influence of the intertidal position and environmental factors (salinity, soil texture and chemical properties) on the crab distribution patterns. These authors reported distinct zonation patterns along the salinity gradient and between high and low intertidal forests, while the sediment characteristics explained a significant amount of the variation for a few of the investigated species (Frusher et al., 1994).

Dahdouh-Guebas et al. (2002) investigated the link between the spatial distribution of selected crab species, and the distribution of mangrove tree species, in East African mangrove forests. Their results suggested an association of the different crab species with different zones along the intertidal gradient, each characterised by a specific tree association, suggesting that the tree composition may play a role in the crab zonation patterns (Dahdouh-Guebas et al., 2002).

Ashton et al. (2003a) conducted a study on the brachyuran communities of four mangrove systems along the West coast of the Malay Peninsula (Malaysia and Thailand), each undergoing a different management system. Their results showed that the management history strongly affected the crab community structure, which was also found to be related to the age of the mangrove forest stand (Ashton et al., 2003a).

Ashton et al. (2003b) investigated the sesarmid community in a Bornean mangrove forest (Sarawak, East Malaysia), and the relationship with vegetation, topographic height, and selected environmental parameters (water salinity, pH, temperature, and redox potential, measured at the soil surface and at a 50 cm depth). This study found that the crab community structure was correlated with topographical height, and surface water pH and salinity. The community structure and species richness were positively correlated also with tree and seedling community structure and diversity (Ashton et al., 2003b).

2.5 Ecological role in the mangrove ecosystem

For the relatively large biomass, intermediate trophic level, and significant ecological impact, sesarmid crabs were described as dominant components of mangrove macrofaunal communities (Lee, 1998) and "key-stone species" in mangrove ecosystems (e.g. Smith et al., 1991; Ellison, 2008).

In particular, these crabs have been acknowledged as a crucial element in IWP mangrove forests, since their feeding habits and burrowing activities deeply affect the ecosystem dynamics (Lee, 1998; Cannicci et al., 2008; Kristensen, 2008). Because of the effects of burrowing and foraging activities, sesarmid crabs have been defined as "ecosystem engineers", defined as organisms that "directly or indirectly modulate the availability of resources (other than themselves) to other species, by causing physical state changes in biotic or abiotic materials. In so doing they modify, maintain and/or create habitats" (Kristensen, 2008, p. 31).

2.5.1 Feeding ecology

Although studies on diet and feeding habits of sesarmid crabs have been conducted on a few species only (e.g. *Aratus pisonii*, Beever et al., 1979; *Episesarma versicolor*, Thongtham et al., 2008; *Parasesarma onychophorum*, Malley, 1978), the available literature has shown that these crabs feed mainly on leaf litter (e.g. Thongtham & Kristensen, 2005), mangrove leaves (e.g. Sivasothi et al., 1993), and propagules (e.g. Bosire et al., 2004).

The earliest studies on the feeding ecology analysed the stomach contents of selected species, which were found to be composed mainly of mangrove leaf litter and, in smaller percentages, sediment and animal particles (e.g. Malley, 1978; Leh &

Sasekumar, 1985; Dahdouh-Guebas et al., 1997). Malley (1978) reported also that the mean size of the particles decreases along the crab digestive tract, thus suggesting a role of these crabs in consuming and partially digesting mangrove material, and returning them to the ecosystem “in a more finely-divided state” (Malley, 1978).

Further studies investigated the diet of these crabs through feeding experiments, conducted in the laboratory and in the field, on the food preference of selected species (e.g. Micheli et al., 1991; Steinke et al., 1993). For instance, Micheli et al. (1991), Steinke et al. (1993) and Dahdouh-Guebas et al. (1997) conducted studies on the food preference of *Neosarmatium meinerti*, by providing the experimental crabs with a choice of leaves or propagules of various mangrove species, in various stages of decomposition.

In general, several of these studies reported a preference for decaying leaves (yellow or brown), compared to fresh (green) leaves (e.g. Micheli, 1993a; Steinke et al., 1993; Thongtham et al., 2008). In fact, mangrove leaves have high tannin contents and C/N ratios, higher than the values suggested as a general maximum for sustainable animal nutrition (Russell-Hunter, 1970; Skov & Hartnoll, 2002). Giddens et al. (1986) suggested that these crabs can store leaves inside their burrows, to allow tannins to leach and increase the digestibility of leaves, and to increase the leaf nitrogen content during breakdown (“leaf-ageing hypothesis”). This theory was indirectly supported by subsequent studies, which either demonstrated that crabs preferred decayed leaves (e.g. Camilleri, 1989; Lee, 1989), and leaves with lowered tannin content (Neilson et al., 1986), or showed that aged leaves improved the general crab growth (Micheli, 1993b; Kwok & Lee, 1995).

However, a study by Skov and Hartnoll (2002) tested this theory by investigating whether leaves stored in the burrows had C, N or C/N values significantly different from those of senescent leaves on the forest floor. Their results showed no significant differences between the two kind of leaves, therefore rejecting the leaf-ageing hypothesis. Moreover, these authors observed their investigated species in the field feeding largely on sediment, and proposed sediment detritus as a richer source of nitrogen, as shown by lower C/N ratios and regular ingestion by crabs (Skov & Hartnoll, 2002). Recent works by Thongtham and Kristensen (2005), Boon et al. (2008), Thongtham et al. (2008), Kristensen et al. (2010) and Nordhaus et al. (2011) also argued that the nutritive value of leaf and mangrove litter would be insufficient to sustain the crab growth, and suggested these species may rely on occasional consuming of animal carcasses to sustain their nitrogen needs.

On the other hand, a couple of species, namely *Aratus pisonii* and *Parasesarma leptosoma*, have been found to feed on fresh leaves mainly (e.g. Beever et al., 1979; Vannini & Ruwa, 1994). In particular, *A. pisonii* is able to climb on the mangrove trees and access leaves all the way up to the top of the canopy (Hartnoll, 1965; Wilson, 1989), where it mainly scrapes away tissue from the surface of the leaves (Erickson et al., 2003). This species, however, can also consume bark (Hartnoll, 1965; Beever et al., 1979) and fresh wood pulp (Lacerda, 1981), and it has been occasionally observed scavenging or actively preying on other arboreal arthropods (Beever et al., 1979). *P. leptosoma* has been observed living among the mangrove roots, and performing a vertical migration to the canopy twice a day, to feed on fresh leaves and leaf buds (Vannini & Ruwa, 1994). These migrations follow a relatively constant time frame, with the crabs moving upwards around 6 am, descending around 9 am, climbing upwards again around 4 pm, and finally coming back downwards before 7 pm (Vannini et al., 1995, see also Subchapter 2.4.1).

Sesarmid crabs are known to be massive consumers within the mangrove foodweb, processing a relatively large amount of leaf litter, and representing therefore an important link in the energy flow dynamics of mangrove ecosystems (Lee, 1998). In particular, several studies throughout the IWP region have documented substantial consumption rates (> 25% of the forest leaf litter removed by crabs), thus suggesting a role of these crabs in the litter turnover (e.g. Camilleri, 1989; Lee, 1989; Emmerson & McGwynne, 1992). Smith et al. (1989) found that grapsoid crabs (including mainly sesarmid species) were capable of consuming more than 90% of the mangrove propagules in their study sites from IWP (Australia and Malaysia).

Moreover, the digestive process can affect remarkably the physical and chemical conditions of the ingested leaf litter, enhancing the nutritional values of the resulting faecal material, which is then available as food source for other benthic invertebrate consumers (e.g. Lee, 1997; Werry & Lee, 2005). In particular, since the assimilation rate of the leaf litter during digestion is generally low (<50%; Lee, 1997), a relatively high percentage of ingested litter is egested as faecal matter, resulting in high faecal rate production by crabs.

For instance, Lee (1997) provided evidence that the faecal material of *Parasesarma messa* can support a coprophagous food chain of small invertebrates, such as the hyalid amphipod *Parhyalella* sp. This author conducted experiments by feeding this species with either crab faecal material, a mixture of faecal material and mangrove detritus, or mangrove detritus only. The results showed that the amphipods fed with faecal material attained significantly higher moulting frequency and lower mortality rates than those feeding on mangrove detritus (Lee, 1997).

A study on *Parasesarma erythrodactyla* by Werry and Lee (2005) showed that the ingested leaf litter is shredded to microscopic fragments in the faeces, and the bacteria colonising the faecal material are 70 times more abundant than those on the leaf litter undergoing normal decomposition. The increase in bacterial density corresponds also to higher values of nitrogen content, showing therefore that the digestive process operated by the crabs can enrich the mangrove organic matter (Werry & Lee, 2005).

Predation of mangrove propagules and seedlings by sesarmids affects also mangroves' distribution patterns, ecological zonation and even forestry management (e.g. Smith, 1987; Cannicci et al., 2008; Van Nedervelde et al., 2015). For instance, in a study in a reforested mangrove plantation from Kenya, Bosire et al. (2005) reported that predation on propagules by sesarmid crabs acts as a regulator of competition in high-density mangrove stands, actually affecting the trees' density and distribution patterns.

In general, the role of sesarmid crabs in the mangrove litter turnover effects the whole foodweb, which is linked to the offshore systems. For instance, Lee (1997) and Werry and Lee (2005) found that an experimental diet of crab-processed leaf litter can sustain copepod species common in the estuarine and off-shore waters, which are often the main food source for larval and juvenile fishes (Werry & Lee, 2005).

2.5.2 Burrowing ecology

Sesarmid crabs are known to actively dig and maintain burrows in the mangrove soil, creating an underground network of interconnected tunnels (Lee, 1998; Kristensen, 2008). Although several studies reported burrowing activities by sesarmid crabs, for many species there is not an official documentation (Gillikin & Kamanu, 2005). In particular, data are available only for a few species, such as *Chiromantes ortmanni* (Gillikin & Kamanu, 2005), *Neosarmatium* spp. (Gillikin et al., 2001; Berti et al., 2008;

Andreetta et al., 2014), *Parasesarma messa* (Stieglitz et al., 2000), and *Episesarma versicolor* (Thongtham & Kristensen, 2003).

Some species have been found to dig and occupy their own burrows (e.g. *Episesarma versicolor*; Thongtham & Kristensen, 2003), while others use tunnels dug by other species (e.g. *Armases ricordi*, *Parasesarma catenatum*; Macnae, 1963; Hartnoll, 1965; see also Warner, 1969). Other species have been observed to be opportunistic, building burrows only if other natural shelters (e.g. roots and crevices) are not available (e.g. *Parasesarma guttatum*; Gillikin & Kamanu, 2005).

The structure and size of the burrows can vary notably, even within a species (e.g. Thongtham & Kristensen, 2003; Berti et al., 2008). For instance, Berti et al. (2008) investigated the burrow morphology of *Neosarmatium meinerti* from Kenya, and reported that, while most of the burrows have a simple linear shape, others include also bends, rooms and accessory branches. These authors suggested that the complexity of the tunnels may be influenced by obstacles encountered during the digging process (e.g. roots), while rooms and accessory branches are utilised by the crab to store food (Berti, et al. 2008).

A study on the burrowing activity of *Episesarma versicolor* from Thailand (Thongtham & Kristensen, 2003) found that this large sesarmid crab can dig burrows up to >1m deep, whose shape and morphology vary from simple vertical tunnels with few branches, to complex structures with several tunnels, openings, dead-ends and small chambers. These authors reported also that the structure of the burrows is affected by their age, soil characteristics, and type and abundance of associated fauna (Thongtham & Kristensen, 2003).

Burrows have been found to act as a shelter from desiccation, high temperature, and predators (Sivasothi, 2000; Thongtham & Kristensen, 2003), especially for juvenile specimens (Sivasothi, 2000). In some species, such as *Neosarmatium meinerti*, juveniles have been found in small lateral branches of large adult burrows where they can obtain shelter and food, since this species store leaves underground (Emmerson, 2001). In fact, burrows serve also as a storage for leaves, which are actively transported and stocked before consumption (e.g. Giddins et al., 1986).

The intense burrowing activity by sesarmid crabs affects mangrove topography, hydrology, sediment dynamics, and soil biogeochemistry (Smith et al., 1991; Stieglitz et al., 2000; Kristensen, 2008). Moreover, burrows significantly affect nutrient cycling and the neutralisation of toxic metabolites (Kristensen & Holmer, 2001; Kristensen, 2008), and they have been found to positively increase forest productivity (Smith et al., 1991).

In particular, burrows increase the soil aeration, allowing intrusion of oxygen, which enhances aerobic decomposition (Kristensen & Holmer, 2001), and neutralizes toxic metabolites from anaerobic processes (e.g. sulfide) (Kristensen, 2008). For instance, Smith et al. (1991) found that the concentration of soil sulfide and ammonium significantly increased in experimental plots in which crabs were excluded, compared to unaltered control plots. Moreover, burrows by sesarmid crabs have been found to contribute to the soil carbon sequestration, by increasing carbon storage in the sediment (Andreetta et al., 2014).

Burrows affect the soil microbial activity, because they enhance the soil heterogeneity, they contribute in relocating organic material (mangrove litter and leaves buried by the crab), and they introduce oxygen into the sediment through passive irrigation with water and air (see Kristensen, 2008).

Burrowing activities create also habitat and trophic niches for associated macrofauna and meiofauna (ecosystem engineers; Jones et al., 1994; Gillikin et al., 2001; Kristensen, 2008). For instance, Gillikin et al. (2001) reported the alpheid shrimp *Merguia oligodon* from inside burrows of *Neosarmatium smithi*, where the shrimps were observed feeding on the crab faeces, while Berti et al. (2008) recorded the presence of the gobiid fish *Acentrogobius simplex* in crabs burrows, which are probably utilised as a temporary refuge.

Figure 2.1: Burrow systems on the mangrove forest floor (above: Pulau Kukup, below: Kuala Selangor). In these sites, burrows are dug mainly by sesarmid crabs, ocypodid crabs, and mudskippers (personal observation).

2.6 Status of mangrove systems in Peninsular Malaysia and northern Borneo

Peninsular Malaysia and northern Borneo host extensive mangrove forests, which are one of the main wetland types in this area, and are considered one of the most diverse in the world (Giesen et al., 2006; Mazlan et al., 2005). In particular, Giesen et al. (2006) reported Malaysia as the 2nd most diverse country in South East Asia (after Indonesia), hosting 42 "true mangrove species"(i.e. species found in the mangrove habitat only). These authors listed 221 species of plants found in Malaysian mangrove forests (including also non arboreal species, such as ferns, grasses, herbs, epiphytes, palms, climbers, and shrubs) (Giesen et al., 2006). Malaysia is the second country in South East Asia (after Indonesia) also in term of areal extent of the mangrove forests, accounting for ~12% of mangrove forests of this region (Giesen et al., 2006).

Latiff (2012) recently provided data on the areal extent of Malaysian mangrove forests in 2005, estimated to be ~100,000 ha for Peninsular Malaysia, and ~460,000 ha for East Malaysia. In particular, Sabah hosts more than half of the Malaysian mangrove forests (~60%), while ~22% and ~18% of mangroves are found in Sarawak and Peninsular Malaysia, respectively (Latiff, 2012). In general, larger mangrove systems are found in sheltered estuaries, in brackish salinity conditions, and on fine substrates, while on more exposed coastlines, mangroves are confined to protected landward sides on the sheltered side of sandbars (Yahaya & Ramu, 2003).

In Peninsular Malaysia, the sheltered West coast bordering the Straits of Malacca hosts the majority of mangrove forests, which are found mainly in the states of Kedah, Perak, Selangor and Johor (Yahaya & Ramu, 2003). Mangroves can be found also in near-shore islands, such as the Klang Islands (Selangor) and Pulau Kukup (Johor), and in small patches along rocky shores (e.g. Tanjung Tuan, Negeri Sembilan) (Yahaya & Ramu, 2003).

On the East coast, mangroves can be found mainly in sheltered estuaries (e.g. Kemaman river, Terengganu; Bebar river, Pahang) (Yahaya & Ramu, 2003). In particular, the forests of the East coast have been found to be less diverse, probably because the rougher hydrodynamic conditions of the South China Sea hamper mangrove development (Latiff, 2012).

Mangrove forests have been traditionally exploited for timber extraction, in particular for production of poles or charcoal making. For instance, poles obtained from *bakau* (the local term for *Rhizophora* spp.) are regularly utilised to protect river banks, ponds, and lake margins from erosion (Latiff, 2012). Mangroves are also an important food resource for coastal local communities, providing fish, molluscs and crustaceans, while in some areas nipah forests are harvested to collect flower and fruits, and nipah leaves are traditionally utilised as an alternative "paper" in rolling tobacco (Latiff, 2012).

These traditional uses of mangroves have been existing harmoniously for centuries (Yahaya & Ramu, 2003; Latiff, 2012). However, from the 1960's, population growth increased the demand for coastal land, especially on the West coast of Peninsular Malaysia, leading to a conversion of many wetlands into agricultural, industrial or residential land (Yahaya & Ramu, 2003). A large portion of inland mangrove forests has been converted into oil palm plantations, while in certain states (e.g. Johor, Selangor, Perak, Kedah) mangroves have been removed to host aquaculture ponds (mainly for prawn aquaculture) (Latiff, 2012). In some areas, mangroves have been cleared to build housing estates, or because of coastal road development (Giesen et al., 2006).

Mangrove loss has been particularly heavy in Peninsular Malaysia (Giesen et al.. 2006), especially in the states of Terengganu, Johor, Selangor and Negeri Sembilan (Yahaya & Ramu, 2003). Overall, Giesen et al. (2006) reported a decline of ~20% in the previous two decades (1980-2000; 96,900 ha lost, i.e. ~4,850 ha per year). However, these authors also stated that in this time frame, according to the Malaysian Nature Society, the country has lost more than 30% (i.e. one third) of its mangrove forests. Chan et al. (1993) stated that 12% of mangroves have been lost in the country in just 10 years (i.e. 1980-1990). More recently, Richards and Friess (2016) reported a mangrove loss of 3% in Malaysia between 2000 and 2012, which is considerably lower than the percentage loss estimated for previous decades. These authors attributed this difference to either an actual decreased rate of mangrove conversion (possibly linked to improved conservation policies), or to differences in the methodologies utilised to estimate the mangrove coverage (Richards & Friess, 2016).

Locally, Kanniah et al. (2015) analysed the mangrove decline in Iskandar Malaysia (Johor), the fastest growing special economic region in this country, and reported a loss of 33% of mangrove coverage in the area in the past 25 years. In Selangor, Razani (1982, see Latiff, 2012) reported a decline of 30% between 1955 and 1980. On the other hand, in Sabah, the introduction of legal control measures for wood chipping in 1985 has contribute to preserving mangrove forests, which in this state have undergone minor losses (Yahaya & Ramu, 2003).

A few authors highlighted how the conversion of mangroves has been particularly heavy also because of a lack of understanding and appreciation of the ecological roles of these systems, and of the direct or indirect services to the local economy (Yahaya & Ramu, 2003; Latiff, 2012). For instance, Mukrimah et al. (2016) estimated the economic value of the Delta Kelantan Mangrove Forest (DKMF) system for the local communities, finding that the net economic benefits (Total Economic Valuation) of this area were between RM 3.6 million and RM 6.1 million per year. Bennett and Reynolds (1993) estimated that in the Sarawak Mangrove Forest Reserve mangroves largely support the local economy, in term of marine fisheries (US$21.1 millions per year), timber products (US$123,217 per year), and tourist industry (US$3.7 millions per year).

Destruction of mangrove systems has resulted in accelerated coastal erosion, since these forests naturally protect the coastline by reducing the erosion rate (Thampanya et al., 2006), stabilising and trapping the sediment, and dissipating waves and currents (Davies & Claridge, 1993; Othman, 1994).

In many cases, the landward part of the forests has been isolated from tidal action by artificial embankments, which are meant to protect the inland reclaimed agricultural lands (e.g. Hashim et al., 2010). This has resulted in a loss of connectivity between adjacent ecosystems, and alteration of the hydrological systems, with negative effects on the ecosystem health (Hashim et al., 2010).

Moreover, several areas previously converted into agricultural land or aquaculture ponds are currently not utilised, because unproductive, due to the formation of acid sulfate soils when the previously flooded mangrove soil is exposed to air (MCRST, 1992; Clough, 1993; Yahaya & Ramu, 2003). For instance, more than 1000 ha of mangrove forest in the Sungai Merbok estuary (Kedah) which have been converted into rice fields, remained idle because of the acid sulfate soils (Latiff, 2012).

Mangrove extension has been also affected by urban development, especially around coastal cities like Penang, Malacca, and Port Dickson, where large-scale reclamation projects were conducted to make space to new residential and commercial areas (Bahrin & Teh, 1991; Chong & Sasekumar, 2002; Mohamed & Razman, 2018). In the long run, mangrove degradation is likely to affect offshore stocks of fish and other species of commercial interest, which utilise mangroves as nurseries (e.g penaeid prawns, Chong et al., 1996), therefore affecting the local economy. For instance, the coastal reclamation occurred in Malacca has already affected the livelihood of the local fishermen community, that in some cases faced a 70% decrease in their daily income, due to pollution, change in sedimentation patterns, and destruction of spawning and nursery grounds affecting fish stocks in the area (Mohamed & Razman, 2018).

Malaysia does not have a specific law for mangrove management and conservation, and these forests are therefore managed following the National Forestry Policy of 1978 (revised in 1992) for Peninsular Malaysia, and the Forest Policy of Sabah and Sarawak for East Malaysia (Yahaya & Ramu, 2003). Moreover, management of these ecosystems involves also other national legislation, such as the Land Conservation Act (1960), Protection of Wildlife Act (1972), National Park Act (1980), Environmental Quality Act (1974) and Water Enactment (1935), and international conventions, namely the United Nations Forum on Forests (UNFF), Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES), Convention on Biological Diversity (CBD), United Nation Framework Convention on Climate Change (UNFCCC), and Convention on Wetlands of International Importance especially as Waterfowl Habitat (Ramsar Convention) (Jusoff & Taha, 2008). The management of wetland areas is also regulated by the National Wetlands Policy of 2004, which enforces the goals of the Ramsar Convention and Convention on Biological Diversity (Barau & Stringer, 2015).

The Forestry Department has established forest reserves and parks to manage and protect several mangrove sites (Latiff, 2012). In particular, Yahaya and Ramu (2003) stated that at the time of their study, 86% of mangrove forests of Peninsular Malaysia were considered forest reserves, while the remaining 14% were administrated as stateland. In particular, 54 forest reserves were established on the West coast, while 13 occurred on the East coast (Yahaya & Ramu, 2003). Forest reserves, however, are not protected areas, and they can be exploited as production forests, being logged on a 20-30 year cycle, while in some cases they have been converted to other uses (e.g. Sungai Pulai, see below; Giesen et al., 2006).

The first mangrove forest reserve in this country was established in 1904, in Matang (Perak), which is also the largest reserve in Peninsular Malaysia. This reserve includes productive areas exploited for timber and charcoal production (74%), and other areas fully unproductive or protected as Virgin Jungle Reserves (26%, Malaysian Timber Council, 2009; Latiff, 2012). Matang has been acknowledged as an example of good sustainable management, in which productive areas are clear-felled once they reach 30 years old, with intermediate felling being conducted during the 15th and the 20th years (Othman et al., 2004; Malaysian Timber Council, 2009). This area is also an important source of fishes, crustaceans and molluscs, which are exploited by local fishing communities (Giesen et al., 2006). Overall, this forest reserve is of considerable economic relevance for Perak state, generating revenues of several million US$ per year (Sasekumar et al., 1994; Giesen et al., 2006).

In the past decades, several parks have been established to preserve mangrove areas, such as the Kuala Selangor Nature Park (Selangor), Pulau Kukup State Park, Tanjung Piai State Park, Sungai Pulai Forest Reserve (Ramsar Sites, Johor), Klias Wetland, Tawau Mangrove Forest Reserve, Sepilok (Sabah), Pulau Bruit, Rajang Delta (Sarawak) (Giesen et al., 2006). In Langkawi, mangroves on the eastern side of the island are protected under three UNESCO Geoparks, namely the Machinchang Cambrian, Kilim Karst and Dayang Bunting Marble Geoforest Parks, which protect their unique geological landscape (Leman et al., 2008). Beside their conservation value, these parks have become increasingly important also for ecotourism, education, and research (Giesen et al., 2006). However, these efforts in preserving the mangrove heritage of the country have been sometimes hampered by economic interests. For instance, in Sungai Pulai Forest Reserve, the largest riverine mangrove system in Johor state, portions of the gazetted area have been converted into land for aquaculture, charcoal making industries, industrial and residential purposes (Giesen et al., 2006).

CHAPTER 3: ARTICLE 1 - SESARMID CRABS IN PENINSULAR MALAYSIA AND NORTHERN BORNEO: REVIEW OF THE STATE OF KNOWLEDGE

3.1 Introduction and brief Literature Review

Knowledge on regional biodiversity is a prerequisite, in order to monitoring and managing natural resources in a sustainable way (Macintosh & Ashton, 2002). Data on biological diversity are currently taken into account in decision-making processes regarding managing of natural resources (Wafar et al., 2011). However, in several areas, checklists and accounts of biodiversity are unavailable, or outdated (Wafar et al., 2011). For instance, a recent review on the state of knowledge of marine and coastal biodiversity for the Indian Ocean highlighted how in several countries data are scarce, especially for taxa of little or no economic interest (Wafar et al., 2011).

Sesarmid crabs have been acknowledged as an important component of mangrove macrofauna, and the Indo-Malayan Archipelago hosts a particularly high diversity for this group (Jones, 1984; Lee, 1998). However, in Malaysia no comprehensive overview is available for the species recorded in the country, and the available information on species distribution and biology is scattered in several papers, which cover a wide range of scopes and time frame (e.g. De Man, 1892; Sasekumar, 1974; Ashton et al., 2003a,b). Additionally, taxonomy and systematics of this family have been continuously revised, creating confusion in the understanding of the species assemblages and distribution (e.g. synonymy, changes in nomenclature, splitting of species in different taxonomic units; e.g. see Serène & Soh, 1970; Rahayu & Ng, 2010; Ragionieri et al., 2012; see also Subchapter 2.1).

Considering the current rate of decline in mangrove areas in the country (and worldwide, see Subchapter 2.6), knowledge of the biodiversity of key mangrove macrofaunal groups is particularly needed. In fact, disappearance of mangrove sites may lead to local extinction, or total extinction in case of species with restricted areal distribution. Therefore, individuating distribution and ecological niche of local species is crucial, in order to preserve their habitats.

In order to review the available information on sesarmid crabs recorded from this area (Peninsular Malaysia and northern Borneo), a thorough research of the literature was conducted to investigate:

i) which species have been reported from this geographic area until now;

ii) what information is available for each of these species.

3.2 Methodology

A thorough research on the available literature has been conducted, in order to document all the species of sesarmid crabs reported until now from mangrove systems in Peninsular Malaysia, northern Borneo and Singapore. Singapore was included because this island is geographically included in the Malay Peninsula. Genera which occur exclusively in "non-mangrove" ecosystems, such as rainforests, limestone caves, and rocky shores (i.e. *Geosesarma*, *Karstarma*, *Lithoselatium*, *Metasesarma*, *Scandarma*; see Subchapter 2.4), have not been included in this account.

The research was conducted by utilising the Google (https://www.google.com) and Google Scholar (https://scholar.google.com) search engines, and the following databases: Assembling the Tree of Life - Decapoda (https://decapoda.nhm.org/references/search.html), and Biodiversity Heritage Library (https://www.biodiversitylibrary.org). The following keywords were utilised: Sesarmidae, Malaysia, Malay Peninsula, Borneo, Singapore, South East Asia, Southeast Asia, Sesarmidae, Sesarminae, sesarmid, Grapsoidea, grapsoid, mangrove crabs, mangrove macrofauna. Moreover, in order to confirm and corroborate the obtained list of species, Tan and Ng (1994) was consulted, since this work provided the most recent checklist of grapsoid crabs from Malaysia (Peninsular and East Malaysia) and Singapore.

Subsequently, a literature research has been conducted on each of these species, utilising the same search engines (Google, Google Scholar, Assembling the Tree of Life - Decapoda, Biodiversity Heritage Library). The scientific names of each genus and species (including synonyms and invalid names, see Ng et al., 2008) were utilised as keywords. Any information available worldwide (i.e. not only from Malaysia) was therefore obtained for each species, and a synopsis of the genera and species has been presented.

The research was conducted during a period of one year (2015), on an average base of 3 days per week, and 3 hours per day. In the following years (2016-2019), the same research was repeated, in order to update the literature dataset with newly published studies. In this phase, the years themselves (e.g. “2016”, “2017”, “2018”, “2019”) were added to the previous keywords, in order to narrow down the search to the studies published in this specific time frame.

In a further subchapter (3.3.17), research trends and gaps in knowledge have been highlighted, and the ecological data available for each species have been summarised in a table, which provides a synthethic and comprehensive source of information. Finally, an historical review of the studies conducted in this area has been presented (Subchapter 3.3.18).

3.3 Results

57 species from 16 genera have been reported until now from mangrove systems of Peninsular Malaysia, northern Borneo and Singapore (see Subchapters 3.3.1 - 3.3.16 for references). A list of these genera and species is reported below.

***Bresedium* Serène & Soh, 1970**

B. sedilense (Tweedie, 1940)

***Clistocoeloma* A. Milne-Edwards, 1873**

C. lanatum (Alcock, 1900)

C. merguiense De Man, 1888

C. suvaense Edmondson, 1951

***Episesarma* De Man, 1895**

E. chentongense (Serène & Soh, 1967)

E. mederi (A. Milne Edwards, 1853)

E. palawanense (Rathbun, 1914)

E. singaporense (Tweedie, 1936)

E. versicolor (Tweedie, 1940)

***Fasciarma* Shahdadi & Schubart, 2017**

F. fasciatum (Lanchester, 1900)

***Haberma* Ng & Schubart, 2002**

H. kamora Rahayu & Ng, 2005

H. nanum Ng & Schubart, 2002

***Labuanium* Serène & Soh, 1970**

L. politum (De Man, 1887)

***Nanosesarma* Tweedie, 1950**

N. andersonii (De Man, 1888)

N. batavicum (Moreira, 1903)

N. edamense (De Man, 1887)

N. minutum (De Man, 1888)

N. nunongi Tweedie, 1950

N. pontianacense (De Man, 1895)

N. tweediei (Serène, 1967)

***Neosarmatium* Serène & Soh, 1970**

N. asiaticum Ragionieri, Fratini & Schubart, 2012 (considered *N. meinerti* until 2012)

N. indicum (A. Milne-Edwards, 1868)

N. smithi (H. Milne-Edwards, 1853)

N. spinicarpus Davie, 1994

***Neosesarma* Serène & Soh, 1970**

N. gemmiferum (Tweedie, 1936)

N. rectipectinatum (Tweedie, 1950)

***Parasesarma* De Man, 1895**

P. batavianum (De Man, 1890)

P. calypso (De Man, 1895)

P. eumolpe (De Man, 1895)

P. indiarum (Tweedie, 1940)

P. kuekenthali (De Man, 1902)

P. lanchesteri (Tweedie, 1936)

P. lenzii (De Man, 1894)

P. lepidum (Tweedie, 1950)

P. melissa (De Man, 1887)

P. onychophorum (De Man, 1895)

P. peninsulare Shahdadi, Ng & Schubart, 2018

P. plicatum (Latreille, 1803)

P. raouli Rahayu & Ng, 2009

P. rutilimanum (Tweedie, 1936)

P. semperi (Bürger, 1893)

P. ungulatum (H. Milne Edwards, 1853)

***Perisesarma* De Man, 1895**

P. dussumieri (H. Milne Edwards, 1853)

***Pseudosesarma* Serène & Soh, 1970**

P. bocourti (A. Milne Edwards, 1869)

P. crassimanum (De Man, 1887)

P. edwardsii (De Man, 1888)

P. granosimanum (Miers, 1880)

P. johorense (Tweedie, 1940)

P. laevimanum (Zehntner, 1894)

P. moeschi (De Man, 1888)

***Sarmatium* Dana, 1851**

S. germaini (H. Milne-Edwards, 1869)

S. striaticarpus Davie, 1992 (considered *S. crassum* until 1992)

***Selatium* Serène & Soh, 1970**

S. brockii (De Man, 1887)

S. elongatum (A. Milne-Edwards, 1869)*

***Sesarmoides* Serène & Soh, 1970**

S. borneensis (Tweedie, 1950)

S. kraussi (De Man, 1887)

***Tiomanum* Serène & Soh, 1970**

T. indicum (H. Milne Edwards, 1837)

*this species has not been recorded from Peninsular Malaysia, Singapore, or northern Borneo, but it has been reported from the Andaman Sea (i.e. geographically part of the Malay Peninsula), and therefore has been included in this account

A synopsis of the published information available for each species is presented below, followed by an analysis of the general state of knowledge on sesarmid crabs and research trends in this area.

3.3.1 Genus *Bresedium* Serène & Soh, 1970

The genus *Bresedium* Serène & Soh, 1970 includes 3 species, distributed throughout Indonesia (De Man, 1892, 1895, 1902), Philippines (Rathbun, 1914), Malaysia (Tweedie, 1940, 1950a), Australia (Frusher et al., 1994), and Japan (Maenosono & Naruse, 2016).

The genus has been described by Serène and Soh (1970), and it is characterised by the peculiar shape of the male abdomen, whose last segment (telson) is deeply inserted into the distal border of the 6th segment (Serène & Soh, 1970).

Little is known about the biology and ecology of this genus. All the species have been found in mangrove and nipah (*Nypa fruticans*) forests, in freshwater or brackish water conditions (Tweedie, 1940, 1950a; Frusher et al., 1994). In fact, in a study conducted in the Murray River estuary (Australia), Frusher et al. (1994) found that *Bresedium brevipes* has a high tolerance to low salinity level, suggesting that these species are adapted to freshwater and brackish conditions.

Only one species, *Bresedium sedilense* (Tweedie, 1940), has been reported from Peninsular Malaysia, Singapore, and/or northern Borneo.

Table 3.1: List of the main studies conducted on the genus *Bresedium* (including taxonomic studies and reviews of the genus).

Author and Year	**Subject of the study**
Serène & Soh 1970	genus description

3.3.1.1 *Bresedium sedilense* (Tweedie, 1940)

This species has been described as *Sesarma sediliensis* by Tweedie (1940), from nipah forests on the bank of the Sedili River (Johor, Peninsular Malaysia), where it was found "among stems of nipah palms", on a muddy substrate. It has been recorded later in Sarawak (East Malaysia), from a freshwater ditch (as *Sesarma sedilensis*; Tweedie, 1950a). Both these works reported mixed freshwater and brackish water (Tweedie, 1940), or freshwater conditions (Tweedie, 1950a).

Serène and Soh (1970) included this species in the newly established genus *Bresedium*, and changed its name to *B. sedilense* (see also Subchapter 3.3.1).

To date, the ecology and biology of this species remain almost unknown.

Table 3.2: List of the studies conducted on *Bresedium sedilense.*

Author and Year	Subject of the study	Field	Country
Tweedie 1940	species description as *Sesarma sediliensis* (Johor, Peninsular Malaysia)	taxonomy	Malaysia (Peninsular Malaysia)
Tweedie 1950a	new distribution record (Sarawak, East Malaysia), as *Sesarma sedilensis*	distribution record (only)	Malaysia (East Malaysia)

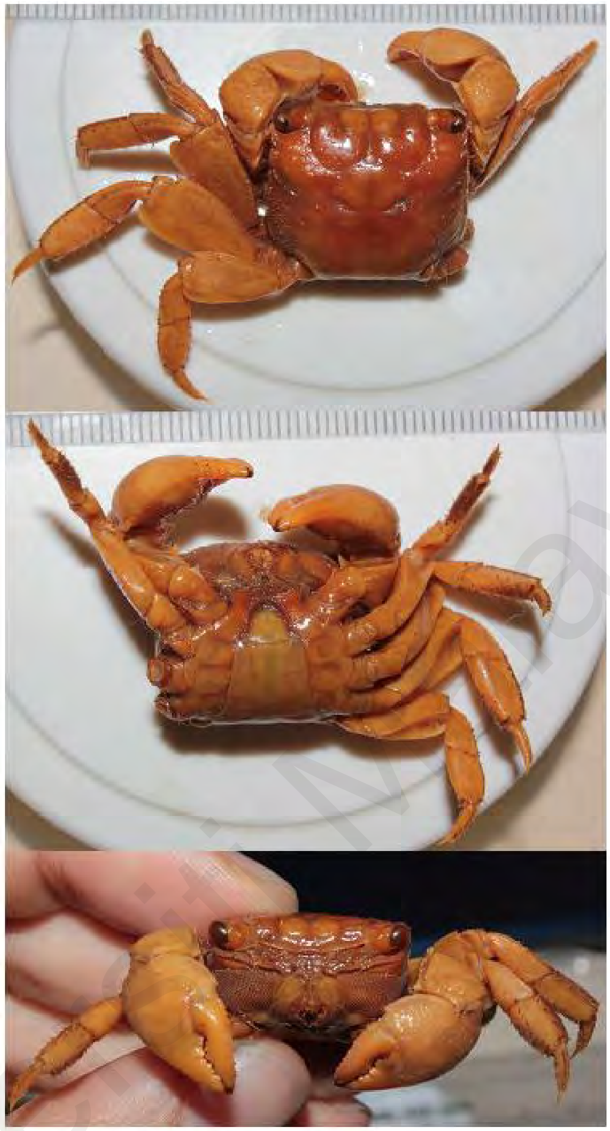

Figure 3.1: ***Bresedium sedilense.*** Male specimen, from the reference collection of the Raffles Museum of Biodiversity Research in Singapore (Lee Kong Chian Natural History Museum, National University of Singapore), visited by the author in 2011-2012. Specimen number: ZRC 1965-7-29-101-113. Dorsal (above), ventral (middle) and frontal view (below). Scales are in mm.

3.3.2 Genus *Clistocoeloma* A. Milne-Edwards, 1873

The genus *Clistocoeloma* has been described by A. Milne-Edwards (1873), to include species having the antennal peduncle entirely excluded from the orbit, i.e. the tooth at the inner angle of the lower border of the orbit meets the front (A. Milne-Edwards, 1873; Alcock, 1900; Tesch, 1917; Serène & Soh, 1970). Moreover, the whole body and the appendages are covered with a dense adherent fur of setae, and the dorsal surface of the carapace present numerous irregular clumps, giving therefore a rough aspect to the whole crab (Alcock, 1900; Lee et al., 2014).

The genus currently includes 9 species (Ng et al., 2008; Lee et al., 2013), distributed throughout the whole Indo-West Pacific region, from the western Indian Ocean to the western Pacific Ocean (Edmonson, 1951; Hsueh & Huang, 1996; Ghory & Siddiqui, 2007; Lee et al., 2013).

Information on the biology and ecology of this genus is scarce (Lee et al., 2014). Most of the species have been reported from mangrove and nipah forests (e.g. Rahayu & Takeda, 2000; Lee et al., 2013), although a few species have been collected also from other systems, such as marshes of the grass *Zoysia tenuifolia* (Hsueh, 1995), and reefs (Edmondson, 1951). *Clistocoeloma* species have been found burrowing in wet mud (Kemp, 1918), or finding shelter in dead and rotten wood (Hutchings & Recher, 1982; Rahayu & Takeda, 2000), or under piles of rocks (Hsueh, 1995). The recorded habitat salinity ranges from seawater to freshwater values (Kemp, 1918; Rahayu & Takeda, 2000; Lee et al., 2013).

The carapace and walking legs of these crabs are heavily covered by setae, which hold a dense layer of sediment and fine organic debris (Tesch 1917, Lee et al. 2014). Recently, Lee et al. (2014) investigated the role of this layer in *C. merguiense*, as “masking camouflage”, which generally refers to the use of exogenous materials attached to the body for the purpose of concealment, in order to avoid predation or to provide an advantage when hunting (Cott, 1940).

Figure 3.2: Example of *Clistocoeloma* specimen, showing the peculiar setae covering the body (masking camouflage). Preserved specimen of *C. merguiense* from the reference collection from Kuala Selangor (see also Chapter 4). The setae, holding sediment and organic debris, have been removed from the right part of the carapace, to show its surface. The scale is in mm.

For one of the species of this genus (*Clistocoeloma sinense*), a few studies have investigated the population dynamics and life history (Taiwan; Hsueh, 1995), the seasonal changes in population characters (abundance, time to sexual maturity, reproductive season, and recruitment of juveniles; Japan; Yuhara & Furota, 2014), and the genetic population structure (Japan; Yuhara et al., 2014) of selected communities.

Three species have been recorded from Peninsular Malaysia, Singapore, and/or northern Borneo:

- *C. lanatum* (Alcock, 1900)
- *C. merguiense* De Man, 1888
- *C. suvaense* Edmondson, 1951

Table 3.3: List of the main studies conducted on the genus *Clistocoeloma* (including taxonomic studies and reviews of the genus).

Author and Year	Subject of the study
A. Milne-Edwards 1873	genus description
Alcock 1900	taxonomic and morphological notes, distribution notes, drawings
Tesch 1917	taxonomic and morphological notes, distribution notes, drawings
Hsueh & Huang 1996	notes on the history of the genus, taxonomic and morphological notes
Rahayu & Takeda 2000	taxonomic and morphological notes, distribution notes, drawings
Kwok & Tang 2005	checklist of the sesarmid crabs of Hong Kong, ecological and taxonomic notes, key to the species
Lee et al. 2013	notes on the history of the genus, taxonomic and morphological notes, distribution notes, drawings

3.3.2.1 *Clistocoeloma lanatum* (Alcock, 1900)

This species has been described from India and Pakistan as *Sesarma lanatum*, by Alcock (1900). Subsequently, Tesch (1917) suggested a close similarity to other species of the genus *Clistocoeloma*, and Serène (1968) transferred the species to this genus.

C. lanatum was included in this synopsis because it was cited in the checklist of Tan and Ng (1994), although apparently no other work cited this species from Peninsular Malaysia, Singapore, or northern Borneo. In particular, Tan and Ng (1994) reported the species from Singapore, following a record by Serène (1968), which provided a checklist of the non-planktonic marine fauna of South East Asia. This author, however, did not state the country where this species was recorded, nor the authors of the record.

Kakati and Sankolli (1975) described the zoeal and megalopal stages of this species from laboratory larval cultures. Ghory and Siddiqui (2002, 2006, 2007) recently investigated the occurrence, abundance and distribution of the larvae of this species from the Manora Channel (Pakistan), which is bordered by mangroves.

Table 3.4: List of the studies conducted on *Clistocoeloma lanatum*.

Author and Year	**Subject of the study**	**Field**	**Country**
Alcock 1900	species description as *Sesarma lanatum* (India, Pakistan)	taxonomy	India, Pakistan
Tesch 1917	morphological notes; species included in checklist and in diagnostic key of sesarmid species	taxonomy	IWP
Serène 1968	species transferred to the genus *Clistocoeloma*; distribution record (South East Asia: Singapore?)	taxonomy	South East Asia
Kakati & Sankolli 1975	description of 4 zoeal stages and megalopa (India)	ontogenesis	India

Table 3.4, continued.

Ghory & Siddiqui 2002	occurrence and abundance of brachyuran larvae in the Manora Channel (Pakistan)	ontogenesis / larval ecology	Pakistan
Ghory & Siddiqui 2006	percentage composition of brachyuran larvae in the Manora Channel (Pakistan)	ontogenesis / larval ecology	Pakistan
Ghory & Siddiqui 2007	distributional patterns of brachyuran larvae in the Manora Channel (Pakistan)	ontogenesis/ larval ecology	Pakistan

3.3.2.2 *Clistocoeloma merguiense* De Man, 1888

This species has been described from Kanmaw Island, in the Mergui Archipelago (Myanmar), by De Man (1887-1888).

Subsequently, it has been reported from a wide range of localities, including Indonesia (Maluku Islands, De Man, 1890; Java, Nordhaus et al., 2009; Suli Islands, Ambon, Pratiwi & Rahmat, 2015), the Malay Peninsula (De Man, 1896; Alcock, 1900; Tweedie, 1936; Sasekumar, 1974; Ashton et al., 2003a; Sasekumar & Ooi, 2005; Taufek, 2013), Thailand (Kemp, 1918; Lundoer, 1974; Frith et al., 1976; Macintosh et al., 2002), Myanmar (Chopra & Das, 1937), Borneo (Labuan, Tweedie, 1950a; Brunei Darussalam, Choy, 1991; Choy & Booth, 1994; Sarawak, Ashton et al., 2003b), Australia (Frusher et al., 1994; Salgado Kent & McGuinness, 2006, 2010), Vietnam (Diele et al., 2013), Japan (Saba, 1972), and New Hebrids (Marshall & Medway, 1976).

A few studies recorded this species also from Taiwan (Sakai, 1939, 1976; Lin, 1949; Fukui et al., 1989); however, a re-examination of these samples by Hsueh and Huang (1996) diagnosed them as the congeneric species *Clistocoeloma sinense*.

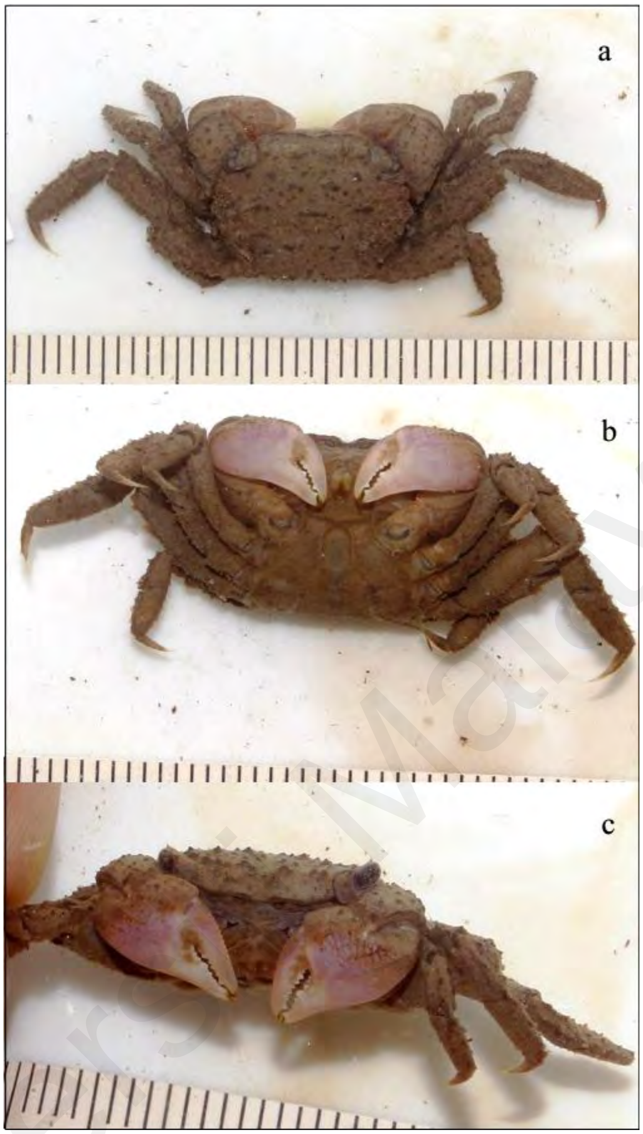

Figure 3.3: ***Clistocoeloma merguiense.*** Male specimen (KS_boleo-transect_091113_6, from the Peninsular Malaysia collection, loc. Kuala Selangor, see Chapter 4); a: dorsal view, b: ventral view, c: frontal view. Scales are in mm.

Specimens of this species have been collected from mangrove forests (Lundoer, 1974; Sasekumar, 1974; Choy and Booth, 1994; Ashton et al., 2003a,b), on muddy or sandy-muddy substrates (Sasekumar, 1974; Diele et al., 2013), and in brackish or brackish/saltwater conditions (e.g. Ashton et al., 2003a; Diele et al., 2013). Some of the specimens have been found sheltering inside dead wood (Sasekumar, 1974).

Among the sesarmid community, *Clistocoeloma merguiense* is considered a relatively ubiquitous species within the forest, since it has been found in a wide variety of environmental conditions within each study site (Ashton et al., 2003a,b; Sasekumar & Ooi, 2005; Diele et al., 2013; Taufek, 2013). Macintosh et al. (2002), Salgado Kent and McGuinness (2010) and Diele et al. (2013) reported this species among the most abundant within their investigated mangrove forests.

Berry (1972) reported this species in his account of the mangrove macrofauna of the West coast of Peninsular Malaysia, where it was collected from the seaward muddy eroding step of the investigated mangrove swamps. Frith et al. (1976) found this species in a mangrove forest (Phuket Island, Thailand) dominated by *Rhizophora apiculata*, with muddy substrate and saltwater salinity conditions. Choy and Booth (1994) recorded this species from a coastal wetland dominated by *Avicennia marina*. Leh et al. (2010) reported this species from samples collected in the 1980s from the upper intertidal mangroves of Selangor (Peninsular Malaysia), including an undisturbed area and a cleared one, with a tree coverage occupying less than 20% of the area.

Leh and Sasekumar (1985) investigated the gut content of *C. merguiense*, which was found to be composed mainly of mangrove plant materials (97% of the gut volumetric composition), while the remaining 3% of the gut composition was made of mineral and brachyuran debris. Lee et al. (2014) investigated the role of the setae covering the body of this species. Their structure retains fine debris, giving the crab a cryptic aspect against the muddy background (see also Subchapter 3.3.2). Saba (1972) provided a first description of the first zoeal stage. Later on, Cuesta et al. (2006) re-described the morphology of the first zoea, adding new characters.

Table 3.5: List of the studies conducted on *Clistocoeloma merguiense.*

Author and Year	Subject of the study	Field	Country
De Man 1887-1888	species description as *Clistocoeloma merguiensis* (Mergui Archipelago, Myanmar)	taxonomy	Myanmar
De Man 1890	new distribution records (Maluku Islands, Indonesia)	distribution record (only)	Indonesia
De Man 1896	new distribution records (Penang, Peninsular Malaysia); taxonomic and morphological notes; morphometric measurements	taxonomy	Malaysia (Peninsular Malaysia)
Alcock 1900	new distribution records (Nicobars); taxonomic and morphological notes and figures/drawings	taxonomy	East Indian Ocean (Nicobar Islands)
Tesch 1917	species included in checklist and in diagnostic key of sesarmid species	taxonomy	IWP
Kemp 1918	new distribution records (Patani River, Thailand)	distribution record (only)	Thailand
Tweedie 1936	new distribution records (Singapore; Johor Strait; Port Swettenham = Port Klang, Peninsular Malaysia; Nicobar Islands); taxonomic and morphological notes	taxonomy	Malaysia (Peninsular Malaysia), Singapore, Nicobar Islands
Chopra & Das 1937	new distribution record (Mergui Archipelago, Myanmar); taxonomic and morphological notes; morphometric measurements	taxonomy	Myanmar
Tweedie 1950a	new distribution record (Labuan, East Malaysia)	distribution record (only)	Malaysia (East Malaysia)
Berry 1972	mangrove macrofauna of the West coast of Peninsular Malaysia	spatial ecology	Malaysia (Peninsular Malaysia)
Saba 1972	description of the first zoeal stage	ontogenesis	Japan
Lundoer 1974	checklist of brachyuran crabs in the reference collection at Phuket Marine Biology Center (Thailand)	distribution record (only)	Thailand

Table 3.5, continued.

Sasekumar 1974	distribution, abundance and zonation of mangrove macrofauna (polychaetes, gastropods, crustaceans, sipunculids, fishes) in Port Klang (Malaysia)	spatial ecology	Malaysia (Peninsular Malaysia)
Frith et al. 1976	zonation and abundance of mangrove macrofauna on Phuket Island (Thailand)	spatial ecology	Thailand
Marshall & Medway 1976	new distribution record (New Hebrids, West Pacific); mangrove community zonation and composition	distribution record (only)	New Hebrids
Leh & Sasekumar 1985	food composition in the gut contents of Malaysian sesarmid crabs (Selangor, Peninsular Malaysia)	feeding ecology	Malaysia (Peninsular Malaysia)
Choy 1991	checklist of Crustacea of Brunei Darussalam	distribution record (only)	Brunei Darussalam
Choy & Booth 1994	macrofaunal community in a *Avicennia* dominated coastal wetland (Brunei Darussalam) before and after an inundation event	spatial ecology	Brunei Darussalam
Frusher et al. 1994	distribution and abundance of sesarmid crabs in the Murray River estuary (Australia), role of sediment characteristics and salinity, test on salinity tolerance and osmoregulatory ability	spatial ecology	Australia
Hsueh & Huang 1996	taxonomic and morphological notes, drawings	taxonomy	IWP
Rahayu & Takeda 2000	taxonomic and morphological notes, distribution notes, drawings	taxonomy	IWP
Macintosh et al. 2002	ecology-conservation, intertidal diversity and mangrove rehabilitation in the Ranong mangrove system (Thailand)	spatial ecology	Thailand
Ashton et al. 2003a	new distribution record (Klong Ngao, Thailand; Merbok, Matang, Kuala Selangor, Peninsular Malaysia); ecological comparison of the brachyuran crab community structure in differently managed mangrove forests	spatial ecology	Malaysia (Peninsular Malaysia), Thailand
Ashton et al. 2003b	ecology and diversity of crab and mollusc macrofaunal community in the Sematan mangrove forest (Sarawak)	spatial ecology	Malaysia (East Malaysia)
Sasekumar & Ooi 2005	faunal diversity in Langkawi mangrove forests (Peninsular Malaysia)	spatial ecology	Malaysia (Peninsular Malaysia)
Cuesta et al. 2006	larval morphology of 11 species of Sesarmidae from Indo-West Pacific	ontogenesis	IWP

Table 3.5, continued.

Salgado Kent & McGuinness 2006	comparison of methods for estimating relative abundance of grapsoid crabs (Australia)	sampling methods	Australia
Nordhaus et al. 2009	spatio-temporal variation of macrobenthic communities in an impacted mangrove-fringed lagoon (Segara Anakan lagoon, Indonesia)	spatial ecology	Indonesia
Leh et al. 2010	biomass and abundance of sesarmid crabs in a natural and disturbed mangrove area in Selangor (Peninsular Malaysia)	spatial ecology	Malaysia (Peninsular Malaysia)
Salgado Kent & McGuinness 2010	spatial and temporal variation in relative abundance of grapsoid crabs (Australia)	spatial ecology	Australia
Diele et al. 2013	impact of typhoon on diversity of key ecosystem engineers (Vietnam)	spatial ecology	Vietnam
Taufek 2013	crab community structure in Setiu lagoon (Terengganu, Peninsular Malaysia)	spatial ecology	Malaysia (Peninsular Malaysia)
Lee et al. 2014	masking camouflage strategy (Singapore)	behaviour	Singapore
Pratiwi & Rahmat 2015	checklist of brachyuran crabs in the reference collection at the Research Centre for Oceanografi, Indonesian Institute of Sciences (LIPI) collected from 1960 to 1970 (Indonesia)	distribution record (only)	Indonesia

3.3.2.3 *Clistocoeloma suvaense* Edmondson, 1951

Clistocoeloma suvaense has been described from a reef, from the Fiji Archipelago (Edmondson, 1951). Tan and Ng (1994) reported it in the checklist of the mangrove crabs from Malaysia and Singapore. These authors stated that this species has been recorded Singapore, although they did not provide further details about the record source. Apparently, no other information has been reported for this species.

Table 3.6: List of the studies conducted on *Clistocoeloma suvaense.*

Author and Year	Subject of the study	Field	Country
Edmondson 1951	species description (Suva Island, Fiji)	taxonomy	Fiji
Tan & Ng 1994	new distribution record (Singapore); checklist of the mangrove crabs of Malaysia and Singapore	distribution record (only)	Singapore

3.3.3 Genus *Episesarma* De Man, 1895

The genus *Episesarma* De Man, 1895 includes 7 species (Ng et al., 2008), widely distributed throughout Asia, from India (e.g. Ravichandran et al., 2007; Manikantan et al., 2016) to South East Asia (e.g. Supmee et al., 2012; Diele et al., 2013), Philippines (e.g. Rathbun, 1914; Tweedie, 1940), Hong Kong (e.g. Kwok & Tang, 2005), Taiwan (e.g. Ng et al., 2001), Japan (e.g. Islam et al., 2003), and Australia (e.g. Salgado Kent & McGuinness, 2010).

This genus has been first described by De Man (1895) as *Sesarma* (*Episesarma*), considered as a subgenus of *Sesarma* Say, 1817. Subsequently, Rathbun (1897) pointed out that the description of De Man (1895) was insufficient, and transferred again the species of this subgenus to the genus *Sesarma*.

Tesch (1917) referred to a group of species within the genus *Sesarma*, comprising *S. tetragona* Fabricius, 1798 (today *Muradium tetragonum*), *S. taeniolata* White, 1847 (today *Episesarma mederi*), *S. lafondi* Hombron & Jacquinot, 1846 (today *Episesarma lafondii*) and *S. palawanensis* Rathbun, 1914 (today *Episesarma palawanense*).

Later, Tweedie (1936) excluded *S. tetragona* from this group, and added the newly described *Sesarma singaporensis* Tweedie, 1936 (today *Episesarma singaporense*). He described this group of species as: "*Large, mangrove-dwelling Sesarmae in which the carapace is more or less quadrate and beset with tufts of hair. In the chelae the palm, at least in the male, carries a single longitudinal pectinated ridge and the dactylus, at least in the male, is beset with a row of closely and evenly placed tubercles. The number of these tubercles is large, in the male at least 35 and at most about 90*" (Tweedie, 1936, p. 57). Furthermore, he also provided a diagnostic key to the species (Tweedie, 1936).

Serène and Soh (1967b) described *Sesarma* (*Sesarma*) *chentongensis* (today *Episesarma chentongense*), and considered this species as part of a so-called "*mederi* group", which included the species group of Tweedie (1936), plus the later described species *Sesarma versicolor* Tweedie, 1940 (today *Episesarma versicolor*). In another work, Serène and Soh (1967a) provided a detailed diagnostic key and taxonomic notes for the 5 species of the *mederi* group recorded, until then, from Malaysia and Singapore (*E. chentongensis*, *E. mederi*, *E. palawensis*, *E. singaporensis*, *E. versicolor*).

A few years later, Serène and Soh (1970) defined the new genus *Neoepisesarma*, considered as an extension of the *mederi* group. The genus included part of the species previously included by De Man (1887) in his group A, and (or) in *Sesarma* (*Episesarma*) by De Man (1895), and it was subdivided in three sub-genera:

1) *Neoepisesarma* (*Neoepisesarma*), corresponding to the *mederi* group, and including *N.* (*N.*) *mederi* (H. Milne Edwards, 1853), *N.* (*N.*) *chentongensis* (Serène & Soh, 1967), *N.* (*N.*) *lafondi* (Hombron & Jacquinot, 1846), *N.* (*N.*) *singaporensis* (Tweedie, 1936), *N.* (*N.*) *versicolor* (Tweedie, 1940), and *N.* (*N.*) *palawanensis* (Rathbun, 1914).
2) *Neoepisesarma* (*Muradium*), including one species only, *N.* (*M.*) *tetragonum* (Fabricius, 1798).
3) *Neoepisesarma* (*Selatium*), including one species only, *N.* (*S.*) *brocki* (De Man, 1887).

A few years later, Holthuis (1978) pointed out that the new genus *Neoepisesarma* Serène & Soh, 1970 had to be considered as a junior synonym of *Episesarma* De Man, 1895, which has therefore priority, and should be used for the genus. As a consequence, Tan and Ng (1994) transferred all the species of *Neoepisesarma* (*Neoepisesarma*) to the genus *Episesarma* De Man, 1895.

Lee et al. (2015) revised the taxonomy of the five species of *Episesarma* present in Singapore, providing an updated diagnostic key, based on morphological and colour characters.

Figure 3.4: Chelipeds of *Episesarma chentongense.* Specimen Sg. Bunga_111013_1, from the Brunei Bay collection, loc. Sungai Bunga, see Chapter 4. The arrow shows the row of small tubercles on the dactylus, one of the main diagnostic character of this genus.

Episesarma species have been reported from several ecological studies, investigating the diversity and distribution of brachyuran communities in mangrove systems (e.g. Sasekumar, 1974; Ashton et al., 2003a,b; Chertoprud et al., 2012), the feeding ecology of selected species (e.g. Thimdee et al., 2004; Kristensen et al., 2010; Nordhaus et al., 2011), the interspecific interactions within the mangrove systems (e.g. Offenberg et al., 2004, 2006), and the role of crabs in the mangrove foodwebs and biogeochemical processes (e.g. Rodelli et al., 1984; Poovachiranon & Tantichodok, 1991; Herbon & Nordhaus, 2013).

Moreover, a few studies have been conducted on the burrowing ecology (e.g. Thongtham & Kristensen, 2003; Masagca, 2009) and the tree-climbing behaviour of these species (e.g. Sivasothi, 2000; Masagca, 2009). According to Sivasothi (2000), the species of this genus have been observed to be nocturnal low tide foragers, herbivorous, burrow-dwelling, and facultative tree-climbers, i.e. climbing on tree trunks at high tide and/or during night time.

Figure 3.5: *Episesarma versicolor* specimens observed on *Bruguiera* trees in Kuala Selangor mangrove forest, at night. This species has been regularly observed by the author, building mud burrows among mangrove roots, and climbing on the tree trunks at night and at high tide.

Fratini et al. (2005) conducted a study on the phylogenetic aspects of the tree-climbing grapsoid species, including *Episesarma* spp. and several other genera of arboreal crabs (see also Subchapter 2.4.1). *Episesarma* species have been included also in studies about larval morphology and physiology (Sudtongkong et al., 2012; Islam et al., 2003), and population genetic (Supmee et al., 2012).

Five species have been recorded from Peninsular Malaysia, Singapore, and/or northern Borneo:

- *E. chentongense* (Serène & Soh, 1967)
- *E. mederi* (A. Milne Edwards, 1853)
- *E. palawanense* (Rathbun, 1914)
- *E. singaporense* (Tweedie, 1936)
- *E. versicolor* (Tweedie, 1940)

Table 3.7: List of the main studies conducted on the genus *Episesarma* (including taxonomic studies and reviews of the genus).

Author and Year	Subject of the study
De Man 1895	genus description as subgenus of *Sesarma* Say, 1817
Rathbun 1909	*Sesarma* (*Episesarma*) trasferred again to *Sesarma*
Rathbun 1918	*Sesarma tetragonum* Fabricius, 1798 designed as type species
Tweedie 1936	key of the allies species of "large, mangrove-dwelling Sesarmae in which the carapace is more or less quadrate and beset with tufts of hair", i.e. *Sesarma* (*Sesarma*) *taeniolata* (today *Episesarma mederi*), *S.* (*Sesarma*) *lafondi = S. taeniolata crebristriata* (today *E. lafondii*), *S.* (*Sesarma*) *singaporensis* (today *E. singaporense*), *S.* (*Sesarma*) *palawanensis* (today *E. palawanense*)
Serène & Soh 1967a	morphological and taxonomic notes
Serène & Soh 1970	genus re-description as *Neoepisesarma*, subgenus *Neoepisesarma* (*Neoepisesarma*); *Neoepisesarma* (*Neoepisesarma*) *mederi* (H. Milne Edwards, 1853) designated as type species; taxonomic and historical notes
Holthuis 1978	subgenus *Neoepisesarma* (*Neoepisesarma*) considered as junior synonim of the genus *Episesarma* De Man, 1895; *Episesarma mederi* (H. Milne Edwards, 1853) designated as type species; taxonomic and historical notes
Tan & Ng 1994	taxonomic and historical notes
Lee et al. 2015	taxonomic and systematic notes; key to the species present in Singapore (*E. chentongense, E. palawanense, E. singaporense, E. versicolor, E. mederi*)

3.3.3.1 *Episesarma chentongense* (Serène & Soh, 1967)

This species has been described by Serène and Soh (1967b) from the Johor Straits and Singapore, as *Sesarma* (*Sesarma*) *chentongensis*. In the same year, Serène and Soh (1967a) provided a diagnostic key of the Malayan *Episesarma* species, with morphological details and pictures of *E. chentongense* too. In fact, Lee et al. (2015) pointed out that Serène and Soh (1967a) already provided a first description of the species, published a few months before the official description (Serène & Soh, 1967b).

The species has also been reported from Borneo and Indonesia (Nordhaus et al., 2009, 2011; Lee et al., 2015). Nordhaus et al. (2009, 2011) found this species in an estuarine lagoon mangrove system, on muddy substrate. Nordhaus et al. (2011) reported it burrowing on a steep bank slope in a station heavily colonised by shrubs of *Derris trifoliata*.

Sivasothi et al. (1993), Sivasothi (2000) and Nordhaus et al. (2011) recorded this species as an active burrower. In particular, Sivasothi et al. (1993) reported *E. chentongense* as a burrowing species in mangrove forests, facultative climber at nocturnal low tide or diurnal high tide, when it can be found on the tree trunks and canopy. These authors observed this species feeding mainly on vascular plant material, usually not fresh (i.e. leaf litter), foraging at night, and occasionally scavenging (Sivasothi et al., 1993).

Figure 3.6: *Episesarma chentongense.* Male specimen (Sg.Bunga_111013_1, from the Brunei Bay collection, loc. Sungai Bunga, see Chapter 4); dorsal (above) and frontal (below) view. CW = 4.01 cm.

Table 3.8: List of the studies conducted on *Episesarma chentongense.*

Author and Year	Subject of the study	Field	Country
Serène & Soh 1967a	diagnostic key and morphological notes on the Malayan *Episesarma* species	taxonomy	Malaysia (Peninsular Malaysia)
Serène & Soh 1967b	species description (Johor Strait; Singapore)	taxonomy	Singapore
Sivasothi et al. 1993	tree climbing and herbivory of mangrove crabs (Singapore)	feeding ecology/ tree climbing	Singapore
Sivasothi 2000	distribution and spatial strategy of *Episesarma* spp. in Singapore mangroves	spatial ecology	Singapore
Nordhaus et al. 2009	as *Neoepisesarma chentongensis*, spatio-temporal variation of macrobenthic communities in an impacted mangrove-fringed lagoon (Indonesia)	distribution record (only)	Indonesia
Nordhaus et al. 2011	distribution record (Indonesia); burrowing activity	burrowing ecology	Indonesia
Lee et al. 2015	taxonomy of 5 species of *Episesarma* in Singapore	taxonomy	Singapore

3.3.3.2 *Episesarma mederi* (H. Milne Edwards, 1853)

This species has been described by three different studies (White, 1847; H. Milne Edwards, 1853; Miers, 1877). In particular, White (1847) first cited it as *Sesarma taeniolata* in his list of the specimens of Crustacea in the collection of the British Museum. However, he only listed the number of specimens, the locality (Philippine Islands) and the collector (Mr. Cuming), without providing any description of the species (White, 1847). H. Milne Edwards (1853) reported this species as *Sesarma mederi* from Jakarta (Indonesia), and provided a very brief description. Miers (1877) described the species as *Sesarma taeniolata*, from Philippines. Targioni-Tozzetti (1877) provided a detailed description and morphometric measurements of a few specimens of *Sesarma mederi* from Singapore, Indonesia and China.

In the early literature, the species has been reported from several localities as *Sesarma taeniolata* (Java and Celebes, Indonesia, De Man, 1880; Borneo, Miers, 1880; Mergui Archipelago, Myanmar, De Man, 1888; Celebes, Indonesia, De Man, 1892; Philippines and Thailand, Bürger, 1893; Singapore, Ortmann, 1894a; Myanmar and Peninsular Malaysia, Alcock, 1900; Lanchester, 1900a; Tonle Sap Lake, Cambodia, Kemp, 1918). De Man (1895) recorded this species as *Sesarma* (*Episesarma*) *taeniolata* from Sumatra and Malaysia, while Nobili (1900) and Rathbun (1910a) reported it as *Sesarma* (*Sesarma*) *taeniolata* from Singapore and Borneo, and Thailand, respectively.

Tesch (1917), Tweedie (1936) and Chopra and Das (1937) provided taxonomic and systematic notes on the species, referred as *Sesarma* (*Sesarma*) *taeniolata*. Tweedie (1940) synonimised *Sesarma* (*Sesarma*) *taeniolata* with *Sesarma mederi* H. Milne Edwards, 1853; moreover, he proposed this species as "representative of a series of closely allied, large species of *Sesarma*" which include the species currently included in *Episesarma*. Serène and Soh (1967a) provided taxonomic notes and a morphological comparison between *E. mederi* and the other Malayan *Episesarma* species.

Figure 3.7: *Episesarma mederi.* Female specimen (Sg.Bunga_111013_9, from the Brunei Bay collection, loc. Sungai Bunga, see Chapter 4). Dorsal view (above), and detail of the right cheliped (below), showing the characteristic colouration pattern. CW: 3.05 cm.

Berry (1972) reported this species from the West coast of Peninsular Malaysia, from the middle and upper intertidal areas of the investigated mangrove forests. Lundoer (1974) recorded this species as *Neoepisesarma mederi* in the checklist of the brachyuran crabs collection at Phuket Marine Biology Center (Thailand).

In an ecological study on the zonation and abundance of macrofauna in a mangrove and mudflat system in Western Thailand, Frith et al. (1976) recorded the presence of this species from the landward part of the mangrove forest, in saltwater conditions, on muddy substrate. More recently, Ravichandran et al. (2007) recorded *E. mederi* in a freshwater area, and at the core of the investigated mangrove forest, in a study on the habitat preference of crabs in a mangrove system on the South-eastern coast of India. Nordhaus et al. (2009) reported this species as *Neoepisesarma mederi* from an estuarine lagoon mangrove system in Java (Indonesia), on muddy substrate.

A few studies on the mangrove foodwebs included *E. mederi* among the studied species (Rodelli et al., 1984; Poovachiranon & Tantichodok, 1991; Thimdee et al., 2004). In particular, Rodelli et al. (1984) and Thimdee et al. (2004) investigated the ratio of stable carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotopes in plants and animals from mangrove swamps, adjacent systems, and offshore waters in Peninsular Malaysia and Eastern Thailand, in order to understand primary food sources, and trophic relationships among organisms. Thimdee et al. (2004) found that the values of $\delta^{13}C$ and $\delta^{15}N$ of *E. mederi* were close to those of mangrove leaves and detritus. These data supported previous studies, indicating that this species feeds directly on fallen mangrove leaves and detritus (Leh & Sasekumar, 1985). Poovachiranon and Tantichodok (1991) investigated the gut contents, the leaf consumption rates, the food preference, and the leaf removal rates in 5 species of sesarmid crabs in Western Thailand. *E. mederi* was found to consume mainly vascular plant matter, and to prefer brown senescent mangrove leaves (Poovachiranon & Tantichodok, 1991).

Offenberg et al. (2004) studied the interspecific interactions among the ant *Oecophylla smaragdina*, the mangrove species *Rhizophora mucronata*, and the sesarmid crabs *Episesarma mederi* and *E. versicolor*. In particular, these authors found that the presence of ant nests on the mangrove trees provided an effective defense for the plant against the herbivorous crabs (Offenberg et al., 2004).

E. mederi was included in a phylogenetic study on the evolutionary origin of tree-climbing behaviour within the Grapsoidea (Fratini et al., 2005). These authors investigated whether the morphological and ecological similarities of the different tree-climbing grapsoid species were based on convergence or common ancestry, by comparing molecular markers. In particular, *E. mederi* was considered among the species found "mostly or exclusively on the tree trunks and roots" (Fratini et al., 2005).

Trivedi et al. (2015) recently reported *E. mederi* in a checklist of the Crustacean fauna of the Gujarat state, India.

Table 3.9: List of the studies conducted on *Episesarma mederi*.

Author and Year	Subject of the study	Field	Country
White 1847	species description as *S. taeniolata* nom. nud. (Philippines), later synonymised	taxonomy	Philippines
H. Milne-Edwards 1853	species description as *Sesarma mederi* (Batavia = Jakarta, Indonesia)	taxonomy	Indonesia
Miers 1877	species description as *S. taeniolata*, later synonymised (Philippines)	taxonomy	Philippines
Targioni-Tozzetti 1877	as *Sesarma mederi*, new distribution records (Singapore; Jakarta, Indonesia; Woosung = Wusong, China); morphological and taxonomic notes; morphometric measurements	taxonomy	Singapore, Indonesia, China
De Man 1880	as *Sesarma taeniolata*, new distribution records (Java and Celebes, Indonesia)	distribution record (only)	Indonesia
Miers 1880	as *Sesarma taeniolata*, new distribution records (Borneo)	distribution record (only)	Malaysia (East Malaysia)
De Man 1888	as *Sesarma taeniolata*, new distribution records (Myanmar)	distribution record (only)	Myanmar

Table 3.9, continued.

De Man 1892	as *Sesarma taeniolata*; new distribution records (Celebes, Indonesia); morphological and taxonomic notes; morphometric measurements	taxonomy	Indonesia
Bürger 1893	as *Sesarma taeniolata*; new distribution records (Philippines; Thailand)	distribution record (only)	Philippines, Thailand
Ortmann 1894a	as *Sesarma taeniolata*; new distribution records (Singapore)	distribution record (only)	Singapore
De Man 1895	as *Sesarma* (*Episesarma*) *taeniolata*; new distribution records (Penang, Peninsular Malaysia; Sarawak, East Malaysia); morphological and taxonomic notes; morphometric measurements	taxonomy	Malaysia (Peninsular Malaysia and East Malaysia)
Nobili 1900	as *Sesarma* (*Sesarma*) *taeniolata*; new distribution records (Singapore; Sarawak, East Malaysia); morphological and taxonomic notes	taxonomy	Singapore, Malaysia (East Malaysia)
Alcock 1900	as *Sesarma taeniolatum*; new distribution records (Myanmar; Andaman Islands; Penang, Peninsular Malaysia); morphological and taxonomic notes	taxonomy	Myanmar, Andaman Islands, Malaysia (Peninsular Malaysia)
Lanchester 1900a	as *Sesarma taeniolata*; new distribution records (Malacca, Peninsular Malaysia)	distribution record (only)	Malaysia (Peninsular Malaysia)
Tesch 1917	as *S. taeniolata*; morphological and taxonomic notes; species included in checklist and in diagnostic key of sesarmid species	taxonomy	IWP
Kemp 1918	as *S. taeniolatum*; new distribution records (Tonle Sap, Cambodia)	distribution record (only)	Cambodia
Tweedie 1936	as *Sesarma* (*Sesarma*) *taeniolata*, new distribution records (Singapore; Johor Strait); morphological and taxonomic notes	taxonomy	Singapore
Chopra & Das 1937	As *Sesarma (Sesarma) taeniolata*; new distribution records (Mergui Archipelago, Myanmar); taxonomic notes	taxonomy	Myanmar
Tweedie 1940	as *Sesarma mederi*; new distribution records (Johor, Penang, Peninsular Malaysia; Singapore; Sarawak, East Malaysia; Philippines); morphological and taxonomic notes	taxonomy	Malaysia, Singapore, Philippines

Table 3.9, continued.

Serène & Soh 1967a	diagnostic key and morphological notes on the Malayan *Episesarma* species	taxonomy	Malaysia (Peninsular Malaysia)
Berry 1972	mangrove macrofauna of the West coast of Peninsular Malaysia	spatial ecology	Malaysia (Peninsular Malaysia)
Lundoer 1974	record as *Neoepisesarma mederi* in the checklist of brachyuran crabs in the reference collection at Phuket Marine Biology Center (Thailand)	distribution record (only)	Thailand
Frith et al. 1976	zonation and abundance of mangrove macrofauna on Phuket Island (Thailand)	spatial ecology	Thailand
Rodelli et al. 1984	stable isotope ratio as a carbon tracer in mangrove ecosystems (West coast Peninsular Malaysia)	feeding ecology	Malaysia (Peninsular Malaysia)
Leh & Sasekumar 1985	food composition in the gut contents of Malaysian sesarmid crabs (Selangor, Peninsular Malaysia)	feeding ecology	Malaysia (Peninsular Malaysia)
Poovachiranon & Tantichodok 1991	role of sesarmid crabs in the mineralization of mangrove leaf litter (Thailand)	feeding ecology	Thailand
Offenberg et al. 2004	interspecific interactions, ecological role of ants (*Oecophylla smaragdina*) in protecting mangrove trees from beetles (Chrysomelidae) and crab (*Episesarma versicolor* and *E. mederi*) grazing (Thailand)	behaviour / interspecific interactions	Thailand
Thimdee et al. 2004	primary food sources and trophic relationships of aquatic animals (including *Episesarma mederi*, using stable isotopes (Thailand)	feeding ecology	Thailand
Fratini et al. 2005	phylogeny, evolutionary origin of tree-climbing behaviour in grapsoid crabs, convergence, 16S and 12S rRNA genes	phylogeny	world
Ravichandran et al. 2007	diversity and habitat preference of crabs in Pichavaram mangrove system (India)	spatial ecology	India
Nordhaus et al. 2009	as *Neoepisesarma mederi*, spatio-temporal variation of macrobenthic communities in an impacted mangrove-fringed lagoon (Segara Anakan lagoon, Indonesia)	distribution record (only)	Indonesia
Lee et al. 2015	taxonomy of 5 species of *Episesarma* in Singapore	taxonomy	Singapore

Table 3.9, continued.

Trivedi et al. 2015	checklist of crustacean fauna of Gujarat (India)	distribution record (only)	India

3.3.3.3 *Episesarma palawanense* (Rathbun, 1914)

This species has been described as *Sesarma* (*Sesarma*) *palawanense* from Palawan Island (Philippines), by Rathbun (1914). Tesch (1917) reported a specimen from New Guinea, and provides taxonomic and systematic notes. Both Rathbun (1914) and Tesch (1917) described female specimens only.

Tweedie (1936) recorded this species from the East coast of Peninsular Malaysia and Singapore, and provided a first description of the male specimen, taxonomic notes, and morphometric measurements. However, Tweedie (1940) rectified his previous description, stating that the male specimens described by Tweedie (1936) as *Sesarma* (*Sesarma*) *palawanense* belonged instead to *Sesarma versicolor*. The author provided therefore a new description and measurements for the male of *Sesarma palawanense*, based on a few specimens from Johor Straits and Singapore, previously attributed to *S. taeniolata* (=*mederi*) (Tweedie, 1940).

Serène and Soh (1967a) included this species in their diagnostic keys of the Malayan species of *Episesarma*, and added morphological and taxonomic notes.

Figure 3.8: ***Episesarma palawanense.*** Male specimen (PK_261212_20, from the Peninsular Malaysia collection, loc. Pulau Kukup, see Chapter 4). Dorsal view (above), and ventral view (below), showing the colour pattern of the chelipeds. CW: 4.02 cm.

This species has been recorded by Tweedie (1950a) as *Sesarma palawanensis* from Labuan (East Malaysia), and by Lundoer (1974) as *Neoepisesarma mederi*, as part of the brachyuran crabs collection at Phuket Marine Biology Center (Thailand). Nordhaus et al. (2009) reported this species as *Neoepisesarma palawanensis* from an estuarine lagoon mangrove system in Java (Indonesia), on muddy substrate. Chertoprud et al. (2012) recorded this species from Vietnam, from the upper part of a forest of *Rhizophora apiculata* on muddy substrate in the estuary of Dong Nai River, and on muddy-sandy shores of saltwater ponds near Nha Fu Lagoon.

A few studies investigated the ecology and feeding biology of this species (Sasekumar, 1974; Nordhaus et al., 2011; Diele et al., 2013). Sasekumar (1974) studied the distribution of the mangrove macrofauna in a mangrove forest reserve on the West coast of Peninsular Malaysia, where he recorded *E. palawanense* from the landward part of the mangrove forest. The studied forest was dominated by *Rhizophora* and *Bruguiera* species, and characterised by a silty-muddy soil, and salinity values ranging from brackish water to saltwater.

Nordhaus et al. (2011) investigated the diet, food preferences and consumption rates of a few species from Indonesia, including *E. palawanense* and other grapsoid crabs. In particular, the stomach content of *E. palawanense* was including mainly detritus, bark, and leaf material (Nordhaus et al. 2011). This species was found burrowing on steep muddy bank slopes in the inner part of the lagoon, in an area colonised by shrubs of *Derris trifoliata*.

Diele et al. (2013) investigated the impact of typhoon disturbance on the mangrove crab community in southern Vietnam, by comparing intact mangrove stands with typhoon gaps with 100% tree mortality. *E. palawanense* was relatively abundant, being present in more than half of the sampled plots.

E. palawanense has been included also in a study on the hepatopancreatic cellulase mechanisms involved in the digestive process of the cellulose (Adachi et al., 2012), which suggested that this species is able to endogenously digest cellulose.

Table 3.10: List of the studies conducted on *Episesarma palawanense.*

Author and Year	Subject of the study	Field	Country
Rathbun 1914	species description as *Sesarma* (*Sesarma*) *palawanense* (Palawan Island, Philippines)	taxonomy	Philippines
Tesch 1917	morphological and taxonomic notes; species included in checklist and in diagnostic key of sesarmid species	taxonomy	world
Tweedie 1936	as *Sesarma* (*Sesarma*) *palawanensis*; new distribution records (Singapore; Kuantan, Peninsular Malaysia); first description of a male specimen (species previously known from female specimens only), later rectified as *E. versicolor* by Tweedie 1940; morphological and taxonomic notes	taxonomy	Singapore, Malaysia (Peninsular Malaysia)
Tweedie 1940	as *Sesarma palawanensis*; new distribution records (Singapore; Kuantan, Peninsular Malaysia; Philippines); morphological and taxonomic notes; first description of a male specimen	taxonomy	Singapore, Malaysia (Peninsular Malaysia), Philippines
Tweedie 1950a	as *Sesarma palawanensis*; new distribution record (Labuan, East Malaysia)	distribution record (only)	Malaysia (East Malaysia)
Serène & Soh 1967a	diagnostic key and morphological notes on the Malayan *Episesarma* species	taxonomy	Malaysia (Peninsular Malaysia)
Lundoer 1974	checklist of brachyuran crabs in the reference collection at Phuket Marine Biology Center (Thailand)	distribution record (only)	Thailand
Sasekumar 1974	distribution, abundance and zonation of mangrove macrofauna (polychaetes, gastropods, crustaceans, sipunculids, fishes) in Port Klang (Peninsular Malaysia)	spatial ecology	Malaysia (Peninsular Malaysia)
Nordhaus et al. 2009	as *Neoepisesarma palawanensis*, spatio-temporal variation of macrobenthic communities in an impacted mangrove-fringed lagoon (Segara Anakan lagoon, Indonesia)	distribution record (only)	Indonesia
Nordhaus et al. 2011	feeding ecology, food preferences, stable isotopes, consumption rates, gut contents (Indonesia)	feeding ecology	Indonesia
Adachi et al. 2012	cellulase activity in hepatopancreas of mangrove crabs, feeding experiments (Thailand)	feeding ecology	Thailand
Chertoprud et al. 2012	diversity and functional structure of brachyuran crab assemblages of southern Vietnam, ecological notes	spatial ecology	Vietnam

Table 3.10, continued.

Diele et al. 2013	impact of typhoon on diversity of key ecosystem engineers (Vietnam)	spatial ecology	Vietnam
Lee et al. 2015	taxonomy of 5 species of *Episesarma* in Singapore	taxonomy	Singapore

3.3.3.4 *Episesarma singaporense* (Tweedie, 1936)

This species has been described by Tweedie (1936), as *Sesarma* (*Sesarma*) *singaporensis*, from riverine environments in Singapore. Tweedie (1940) added new distribution records (Penang, Peninsular Malaysia), and provided further morphological and taxonomic notes. Serène and Soh (1967a) included *E. singaporense* in their diagnostic keys of the Malayan species of *Episesarma*, providing additional morphological and taxonomic notes.

Berry (1972) reported it from mangrove swamps along the West coast of Peninsular Malaysia, especially from the middle and upper intertidal zones of the forests. This species have been recorded in the reference collection of Phuket Marine Biological Center (Thailand, Lundoer, 1974), and in an ecological study on the West coast of Peninsular Malaysia (Sasekumar, 1974). In particular, Sasekumar (1974) found *E. singaporense* in the inner portion of the studied mangrove forest (Kapar Mangrove Forest Reserve, Port Klang, Selangor), and near a belt of trees running along the mud-bank top of a river side. These sites were dominated by *Rhizophora mucronata* and *Bruguiera parviflora*, with a substrate of fine sand and silt, and salinity values ranging from brackish water to saltwater (Sasekumar, 1974).

Sivasothi et al. (1993) described *E. singaporense* as a burrowing species, facultative climber during either nocturnal low tide or diurnal high tide. Moreover, these authors reported it as mainly feeding on leaf litter and occasionally scavenging (Sivasothi et al., 1993). Sivasothi (2000) found that, in his studied area, this species was particularly abundant in a *Thalassina anomala* (mud lobster) mound system, compared to the rest of the forest floor, which was instead colonised by other *Episesarma* species. Nordhaus et al. (2009) reported this species as *Neoepisesarma singaporensis* from an estuarine lagoon (Java, Indonesia). This species was found in a mangrove area colonised by sparse *Sonneratia caseolaris*, *S. alba*, *Avicennia alba* and *A. marina*, and abundant shrubs of *Acanthus* spp. and *Derris trifoliata*, and characterised by muddy substrate and brackish salinity conditions. Diele et al. (2013) recorded *E. singaporense*, although in small abundance, in a study on the impact of typhoon disturbance on the mangrove crab community in southern Vietnam.

In a study on the ratio of stable carbon isotopes ($\delta^{13}C$) in plants and animals from mangrove systems and offshore waters in Peninsular Malaysia, Rodelli et al. (1984) included *E. singaporense* among the studied species, and obtained isotopic values close to those of the mangrove leaves and detritus, thus suggesting an herbivorous diet of this species.

Nordhaus et al. (2011) investigated the stomach content, the food preference and the consumption rates of *E. singaporense* from Indonesia. In particular, the stomach contents of this species contained mostly detritus and leaves, and the measured consumption rates were significantly lower than those of other smaller genera (Nordhaus et al., 2011). The studied specimens preferred brown leaves, and chose *Avicennia alba* among the offered mangrove species; during a qualitative feeding experiment, this species was observed to feed on fish, suggesting an occasionally omnivorous diet (Nordhaus et al., 2011).

In a recent study on the stable carbon and nitrogen isotopes fractionation between mangrove leaves and sesarmid crabs, Herbon and Nordhaus (2013) investigated the change in carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotopes ratio in the muscle tissues of *E. singaporense* and *E. versicolor* fed on a *Rhizophora apiculata* diet over 90 days. Moreover, these authors conducted consumption rates experiments, and analysed carbon and nitrogen isotopes ratios from the muscle tissues, hepatopancreas and stomach contents of several specimens collected in the field (Herbon & Nordhaus, 2013). Their results suggested that these species are able to selectively assimilate isotopic heavy carbon compounds, and to recycle their internal nitrogen reserves to fulfill their nitrogen needs. Moreover, higher carbon and nitrogen ratios were found in muscle tissues compared to hepatopancreas, probably due to lower turnover rates in the muscle tissues (Herbon & Nordhaus, 2013).

Sudtongkong et al. (2012) described the morphology of the 4 zoeal stages, and compared their features with those of other sesarmid species.

Figure 3.9: ***Episesarma singaporense.*** Male specimen (Sg.Temburong_151013_site2_2, from the Brunei Bay collection, loc. Sungai Belayang, see Chapter 4). Dorsal (above), frontal (middle) and ventral view (below). Scales in cm. Photo by G. Polgar.

Table 3.11: List of the studies conducted on *Episesarma singaporense.*

Author and Year	Subject of the study	Field	Country
Tweedie 1936	species description as *Sesarma* (*Sesarma*) *singaporensis* (Singapore)	taxonomy	Singapore
Tweedie 1940	as *Sesarma singaporensis*; new distribution records (Singapore; Penang, Peninsular Malaysia); morphological and taxonomic notes	taxonomy	Singapore, Malaysia (Peninsular Malaysia)
Serène & Soh 1967a	diagnostic key and morphological notes on the Malayan *Episesarma* species	taxonomy	Malaysia (Peninsular Malaysia)
Berry 1972	mangrove macrofauna of the West coast of Peninsular Malaysia	spatial ecology	Malaysia (Peninsular Malaysia)
Lundoer 1974	checklist of brachyuran crabs in the reference collection at Phuket Marine Biology Center (Thailand)	distribution record (only)	Thailand
Sasekumar 1974	distribution, abundance and zonation of mangrove macrofauna (polychaetes, gastropods, crustaceans, sipunculids, fishes) in Port Klang (Peninsular Malaysia)	spatial ecology	Malaysia (Peninsular Malaysia)
Rodelli et al. 1984	stable isotope ratio as a carbon tracer in mangrove ecosystems (West coast Peninsular Malaysia)	feeding ecology	Malaysia (Peninsular Malaysia)
Sivasothi et al. 1993	tree climbing and herbivory of mangrove crabs (Singapore)	feeding ecology / tree climbing	Singapore
Sivasothi 2000	diet, distribution and spatial strategy of the tree climbing grapsoid species of Singapore mangroves	feeding ecology	Singapore
Nordhaus et al. 2009	as *Neoepisesarma singaporensis*, spatio-temporal variation of macrobenthic communities in an impacted mangrove-fringed lagoon (Segara Anakan lagoon, Indonesia)	spatial ecology	Indonesia
Nordhaus et al. 2011	feeding ecology, food preferences, stable isotopes, consumption rates, gut contents (Indonesia)	feeding ecology	Indonesia
Sudtongkong et al. 2012	zoeal morphology (Thailand)	ontogenesis	Thailand

Table 3.11, continued.

Diele et al. 2013	impact of typhoon on diversity of key ecosystem engineers (Vietnam)	spatial ecology	Vietnam
Herbon & Nordhaus 2013	stable isotope fractionation between mangrove leaves and crabs (Indonesia)	feeding ecology	Indonesia
Lee et al. 2015	taxonomy of 5 species of *Episesarma* in Singapore	taxonomy	Singapore

3.3.3.5 *Episesarma versicolor* (Tweedie, 1940)

This species has been described as *Sesarma versicolor* from Singapore and Peninsular Malaysia (Penang, Pahang) by Tweedie (1940). Serène and Soh (1967a) provided additional morphological and taxonomic notes and included this species in their diagnostic key of the "*mederi* group" (see Subchapter 3.3.3).

Tweedie (1950a) reported this species from Borneo, from a riverine system, and Lundoer (1974) recorded it in the reference collection of the Phuket Marine Biological Center (Thailand). This species has been reported also from India (Bouillon et al., 2004; Manikantan et al., 2016), Borneo (Sarawak, Ashton et al., 2003b), Hong Kong (Kwok & Tang, 2005), Philippines (Masagca, 2009), Indonesia (Nordhaus et al., 2011), and Vietnam (Diele et al., 2013). Berry (1972) recorded it from the West coast of Peninsular Malaysia, from the middle and upper intertidal zone of the investigated mangrove forests.

E. versicolor has been reported in several ecological studies, including works on the spatial distribution and zonation, feeding ecology, burrowing ecology, and interspecific interactions (e.g. Sasekumar, 1974; Sivasothi, 2000; Thongtham et al., 2008).

Sasekumar (1974) found this species in the same sites of its congeneric *E. singaporense*, i.e. in the landward parts of the studied mangrove forest, and in a belt of trees running along the mud-bank top of the studied river side. Frith et al. (1976) found it instead in the same sites of the congeneric *E. mederi*, i.e. the landward part of the studied forest (western Thailand), on muddy substrate, in saltwater salinity conditions.

Macintosh (1988) considered *E. versicolor* as the representative species of a habitat category called "roots of mangrove trees along creek banks". Moreover, this author noticed that this species commonly performs tree climbing behaviour, as a anti-predatory strategy, "running vertically up tree trunks at great speed" when "chased and disorientated" (Macintosh, 1988).

In a study on the crab diversity of a mangrove system associated with the Negombo estuary (Sri Lanka), Priyadarshani et al. (2008) reported this species from the landward part of the investigated transect (50 m from the shore line), in a *Avicennia* and *Lumnitzera* zone. In contrast, in another study from the same area (Negombo eastuary, Sri Lanka), Dissanayake and Chandrasekara (2014) found *E. versicolor* in the seaward part of the investigated area, in a *Rhizophora* and *Avicennia* zone, while this species was absent from the landward *Lumnitzera* zone.

A few studies on the distribution and abundance of mangrove macrofauna communities reported this species from different kinds of mangrove forests, including pristine forests (East Malaysia, Ashton et al., 2003b), rehabilitated forest reserves, previously exploited for charcoal production or shrimp farming (Thailand and Peninsular Malaysia, Macintosh et al., 2002; Ashton et al., 2003a), and areas still under charcoal production at the time of the study (Peninsular Malaysia, Ashton et al., 2003a).

Sasekumar and Ooi (2005) reported *E. versicolor* from Langkawi (West coast of Peninsular Malaysia) from a riverine mangrove forest dominated by *Rhizophora apiculata* and *Ceriops tagal* trees, 3 to 4 m tall. Nordhaus et al. (2009) reported this species as *Neoepisesarma versicolor* from a mangrove estuarine lagoon (Java, Indonesia). This study recorded this species from an area with sparse *Sonneratia caseolaris*, *S. alba*, *Avicennia alba* and *A. marina*, and abundant shrubs of *Acanthus* spp. and *Derris trifoliata*, on muddy substrate and in brackish salinity conditions (Nordhaus et al., 2009). Leh et al. (2010) collected this species from Selangor (Peninsular Malaysia), from an undisturbed mixed forest, and from an adjoining cleared area, where trees had been almost completely cut.

Figure 3.10: *Episesarma versicolor.* Male specimen (specimen not deposited, personal coll., January 2011, loc: Kuala Selangor). Dorsal (above), ventral (middle) and frontal view (below). CW = 2.88 cm.

Several studies investigated the feeding biology and ecology of *E. versicolor* (e.g. Rodelli et al., 1984; Sivasothi et al., 1993; Bouillon et al., 2002). This species was included in the study on stable carbon isotopes by Rodelli et al. (1984), which found results similar to those of the other congeneric species (see Subchapters 3.3.3.2 and 3.3.3.4, *Episesarma mederi* and *Episesarma singaporense*). Bouillon et al. (2002) analysed the stable carbon isotope ratios of this species from an estuarine mangrove system on the southeastern coast of India, with similar results.

Leh and Sasekumar (1985) studied the gut contents of *E. versicolor* from Selangor (Peninsular Malaysia), which were mainly composed of mangrove plant materials (90% of the gut volumetric composition), and smaller percentages of brachyuran debris (5%), inorganic sediment (3%), and insects (2%).

E. versicolor was included in a study on stomach contents, leaf consumption rates, food preference, and leaf removal rates in sesarmid crabs in Western Thailand (Poovachiranon & Tantichodok, 1991). The stomach content of this species was found to be similar to that of the congeneric *E. mederi*, i.e. mainly composed of vascular plant matter. In the leaf preference experiments, *E. versicolor* showed a preference for green leaves, in contrast with *E. mederi* (Poovachiranon & Tantichodok, 1991).

Sivasothi et al. (1993) described *E. versicolor* as a burrowing species, facultative climber at nocturnal low tide or diurnal high tide. This species was also found to feed mainly at night, on leaf litter, and occasionally scavenging (Sivasothi et al., 1993). Sivasothi (2000) analysed the stomach content of *E. versicolor*, finding it composed mainly of vascular plant material. In this study, this species was recorded in large numbers from the main forest, while it was almost absent in a *Thalassina anomala* mounds system, in contrast with the congeneric *E. singaporense* (Sivasothi, 2000; see also Subchapter 3.3.3.4).

Thongtham and Kristensen (2005) analysed the carbon and nitrogen budgets of experimental individuals fed on a diet of fresh, mature and senescent mangrove leaves. The study measured the ingestion and egestion rates, and the metabolic loss of carbon and nitrogen, and it enumerated the bacterial abundance in different parts of the crab digestive tract (Thongtham & Kristensen, 2005). The results showed that a leaf diet can provide sufficient carbon for maintenance and growth, but not enough nitrogen; these leaf-eating crabs must therefore obtain a nitrogen supply by other means, such as intracellular deposits following occasional ingestion of animal tissue (Thongtham & Kristensen, 2005).

Thongtham et al. (2008) measured the removal rate of mangrove leaves in the field (Thailand) by *E. versicolor*, and they related it to the number of crab burrows and tidal inundation time. Moreover, these authors conducted observations on the feeding behaviour of this species, analysed the gut contents, and conducted leaf consumption and preference experiments (Thongtham et al., 2008). The results revealed that this species feeds mostly at night, mainly on vascular plant material and detritus, and prefers brown senescent leaves. According to the leaf removal rates measured in this study, these sesarmid crabs may remove 70-80% of the leaf litter fall, and ingest 60-70% of the removed litter, therefore playing a significant role in the nutrients recycling within the mangrove ecosystem (Thongtham et al., 2008).

Masagca (2009) conducted field observations on the feeding behaviour of several sesarmid species in different mangrove areas of the Philippines. *E. versicolor* has been observed feeding on mangrove calyxes and leaves, cropping leaf litter material into fragments, and bringing them to the burrows (Masagca, 2009).

Kristensen et al. (2010) investigated the food partitioning in *E. versicolor*, with emphasis on the nitrogen allocation. In this study, feeding experiments were conducted in the laboratory, and carbon and nitrogen stable isotope signatures were measured in the field. The results suggested that this species can meet its nitrogen demand by occasionally feeding on animal tissue, such as fish and crustacean carcasses (Kristensen et al., 2010).

Nordhaus et al. (2011) investigated the gut content of *E. versicolor* from Indonesia, which was found to be mainly composed of detritus, bark and mangrove leaves. These authors compared these results with other studies (Bouillon et al., 2002; Kristensen et al., 2010), and concluded that this species shows opportunistic and omnivorous feeding habits (Nordhaus et al., 2011).

Adachi et al. (2012) investigated the hepatopancreatic cellulase mechanisms involved in the digestive process of the cellulose in several mangrove crabs, including *E. versicolor* and other sesarmid species (see also subchapter 3.3.3.3, *E. palawanense*). The results revealed that these crabs can efficiently digest cellulose and produce faeces which are more easily processed and decomposed by other consumers (Adachi et al., 2012).

E. versicolor was investigated also by Herbon and Nordhaus (2013), which conducted a study on the change in carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotopes ratio in the muscle tissues of specimens fed on a *Rhizophora apiculata* diet over 90 days (see also Subchapter 3.3.3.4 for further details).

In a study on the feeding habits of the eel catfish *Plotosus canius* in a mangrove estuary on the West coast of Peninsular Malaysia, Leh et al. (2012) reported *E. versicolor* as one of the dominant food item in the fish gut contents, especially for the larger catfish size classes.

E. versicolor was included in a study by Kristensen et al. (2017) on the food partitioning of sesarmid and ucidid crabs from several geographic areas worldwide. This study utilised stable isotope signatures to identify discrimination values of carbon and nitrogen which can provide sufficient nutrients for a balanced diet (Kristensen et al., 2017).

Thongtham and Kristensen (2003) conducted a detailed study on the morphology and physico-chemical conditions of *E. versicolor* burrows in the field (Thailand), and investigated how the temporal variations of salinity and temperature in the burrows affect the behaviour of this species. These authors found that the burrow morphology varies considerably, from simple structures with few branches and just one opening when the sediment is relatively compact, to complex, labyrinthine structures with up to five openings in softer sediment areas (Thongtham & Kristensen, 2003). Neighbouring burrows may accidentally fuse, although usually *E. versicolor* shows a territorial behaviour, and the structure complexity may be increased by other associated fauna, such as alpheid shrimps, fiddler crabs and other smaller sesarmid crabs, which excavate small side branches in the shallower parts of the main structure (Thongtham & Kristensen, 2003). This study also revealed that this species is an euryhaline organism, capable of survive in a wide range of salinity conditions. Moreover, experimental individuals tended to avoid extreme temperature conditions, suggesting that burrows can be utilised as a refuge from overheating and desiccation (Thongtham & Kristensen, 2003).

E. versicolor has been included in two studies by Offenberg et al. (2004, 2006), investigating the interspecific interactions among the ant *Oecophylla smaragdina*, the mangrove species *Rhizophora mucronata*, and the sesarmid crabs *Episesarma mederi* and *E. versicolor* (see also Subchapter 3.3.3.2). Offenberg et al. (2006) highlighted how the presence of ants reduced damages on the mangrove leaves by insects. This indirectly decreases the susceptibility to crab feeding, since these animals tend to feed on leaves already attacked by insects. The study illustrates a complex trophic network of indirect interspecific interactions (Offenberg et al., 2006).

Fratini et al. (2005) included *E. versicolor* among the studied species in their phylogenetic study on the evolutionary origin of tree-climbing behaviour within the Grapsoidea (see also Subchapter 3.3.3.2).

Supmee et al. (2012) performed a population genetic analysis of *E. versicolor* from Thailand, where this species has been commercially exploited. This study investigated the genetic population structure, suggesting a northward direction of population expansion of this species in this area, and high correlation among local populations, probably due to exchange of both larvae and postlarvae individuals (Supmee et al., 2012).

Table 3.12: List of the studies conducted on *Episesarma versicolor*.

Author and Year	**Subject of the study**	**Field**	**Country**
Tweedie 1940	species description as *Sesarma versicolor* (Singapore; Penang, Pahang, Peninsular Malaysia)	taxonomy	Singapore, Malaysia (Peninsular Malaysia)
Tweedie 1950a	as *Sesarma versicolor*; new distribution record (Kuching, Sarawak, East Malaysia)	distribution record (only)	Malaysia (East Malaysia)
Serène & Soh 1967a	diagnostic key and morphological notes on the Malayan *Episesarma* species	taxonomy	Malaysia (Peninsular Malaysia)
Berry 1972	mangrove macrofauna of the West coast of Peninsular Malaysia	spatial ecology	Malaysia (Peninsular Malaysia)
Lundoer 1974	checklist of brachyuran crabs in the reference collection at Phuket Marine Biology Center (Thailand)	distribution record (only)	Thailand
Sasekumar 1974	distribution, abundance and zonation of mangrove macrofauna (polychaetes, gastropods, crustaceans, sipunculids, fishes) in Port Klang (Peninsular Malaysia)	spatial ecology	Malaysia (Peninsular Malaysia)

Table 3.12, continued.

Frith et al. 1976	zonation and abundance of mangrove macrofauna on Phuket Island (Thailand)	spatial ecology	Thailand
Rodelli et al. 1984	stable isotope ratio as a carbon tracer in mangrove ecosystems (West coast Peninsular Malaysia)	feeding ecology	Malaysia (Peninsular Malaysia)
Leh & Sasekumar 1985	food composition in the gut contents of Malaysian sesarmid crabs (Selangor, Peninsular Malaysia)	feeding ecology	Malaysia (Peninsular Malaysia)
Macintosh 1988	ecology and physiology of decapods in mangrove swamps	spatial ecology / physiology	IWP
Poovachiranon & Tantichodok 1991	role of sesarmid crabs in the mineralization of mangrove leaf litter (Thailand)	feeding ecology	Thailand
Sivasothi et al. 1993	tree climbing and herbivory of mangrove crabs (Singapore)	feeding ecology / tree climbing	Singapore
Sivasothi 2000	diet, distribution and spatial strategy of the tree climbing grapsoid species of Singapore mangroves	feeding ecology / spatial ecology	Singapore
Macintosh et al. 2002	ecology-conservation, intertidal diversity and mangrove rehabilitation in the Ranong mangrove system (Thailand)	spatial ecology	Thailand
Ashton et al. 2003a	new distribution record (Klong Ngao, Thailand; Matang, Kuala Selangor, Peninsular Malaysia); ecological comparison of the brachyuran crab community structure in differently managed mangrove forests	distribution record (only)	Thailand, Malaysia (Peninsular Malaysia)
Ashton et al. 2003b	ecology and diversity of crab and mollusc macrofaunal community in the Sematan mangrove forest (Sarawak, Malaysia)	spatial ecology	Malaysia (East Malaysia)
Thongtham & Kristensen 2003	physical and chemical characteristics of *Episesarma versicolor* burrows, behavioural response to altered environmental conditions (Thailand)	burrowing ecology	Thailand
Bouillon et al. 2004	resource utilization by epifauna in mangrove forests with different imputs of organic matter (India, Sri Lanka, Kenya)	feeding ecology	India, Sri Lanka, Kenya

Table 3.12, continued.

Offenberg et al. 2004	interspecific interactions, ecological role of ants (*Oecophylla smaragdina*) in protecting mangrove trees from beetles (Chrysomelidae) and crab (*Episesarma versicolor* and *E. mederi*) grazing (Thailand)	behaviour / interspecific interactions	Thailand
Fratini et al. 2005	phylogeny, evolutionary origin of tree-climbing behaviour in grapsoid crabs, convergence, 16S and 12S rRNA genes	phylogeny	world
Kwok & Tang 2005	checklist of the sesarmid crabs of Hong Kong, ecological and taxonomic notes, key to the species	taxonomy / spatial ecology	Hong Kong
Sasekumar & Ooi 2005	as *Sesarma versicolor*; faunal diversity in Langkawi mangrove forests (Peninsular Malaysia)	spatial ecology	Malaysia (Peninsular Malaysia)
Thongtham & Kristensen 2005	feeding ecology, carbon and nitrogen budgets of *Episesarma versicolor* (Thailand) in different diet conditions, bacterial abundance in the digestive tract, nutrient assimilation	feeding ecology	Thailand
Offenberg et al. 2006	interspecific interactions, indirect role of ants (*Oecophylla smaragdina*) in protecting mangrove trees from crab (*Episesarma versicolor*) grazing (Thailand)	behaviour / interspecific interactions	Thailand
Priyadarshani et al. 2008	diversity of mangrove crabs in Negombo estuary (Sri Lanka)	spatial ecology	Sri Lanka
Thongtham et al. 2008	feeding ecology, leaf removal by sesarmid crabs (Phuket, Thailand), feeding behaviour and gut contents of *Episesarma versicolor*	feeding ecology	Thailand
Masagca 2009	feeding ecology, burrowing behaviour and arboreal climbing skills of sesarmid crabs in Luzon (Philippines)	feeding ecology / burrowing ecology / tree climbing	Philippines
Nordhaus et al. 2009	as *Neoepisesarma versicolor*, spatio-temporal variation of macrobenthic communities in an impacted mangrove-fringed lagoon (Segara Anakan lagoon, Indonesia)	spatial ecology	Indonesia

Table 3.12, continued.

Kristensen et al. 2010	feeding ecology of *Episesarma versicolor*, food partitioning and food preferences (Phuket, Thailand)	feeding ecology	Thailand
Leh et al. 2010	biomass and abundance of sesarmid crabs in a natural and disturbed mangrove area in Selangor (Peninsular Malaysia)	spatial ecology	Malaysia (Peninsular Malaysia)
Nordhaus et al. 2011	feeding ecology, food preferences, stable isotopes, consumption rates, gut contents (Indonesia)	feeding ecology	Indonesia
Adachi et al. 2012	cellulase activity in hepatopancreas of mangrove crabs, feeding experiments (Thailand)	feeding ecology	Thailand
Leh et al. 2012	feeding biology of eel catfish *Plotosus canius* in a Malaysian mangrove estuary and mudflat (Selangor, Peninsular Malaysia)	feeding ecology	Malaysia (Peninsular Malaysia)
Supmee et al. 2012	population genetic of *Episesarma versicolor* along the Andaman Sea coast of Thailand	population genetic	Thailand
Diele et al. 2013	impact of typhoon on diversity of key ecosystem engineers (Vietnam)	spatial ecology	Vietnam
Herbon & Nordhaus 2013	stable isotope fractionation between mangrove leaves and crabs (Indonesia)	feeding ecology	Indonesia
Dissanayake & Chandrasekara 2014	effects of mangrove zonation and soil parameters on macrobenthic fauna (Sri Lanka)	spatial ecology	Sri Lanka
Lee et al. 2015	taxonomy of 5 species of *Episesarma* in Singapore	taxonomy	Singapore
Manikantan et al. 2016	occurrence of *E. versicolor* in Tamil Nadu mangrove forests (India)	spatial ecology	India
Kristensen et al. 2017	stable isotopes and food partitioning in leaf-eating mangrove crabs (IWP; *E. versicolor*: Thailand)	feeding ecology	Thailand

3.3.4 Genus *Fasciarma* Shahdadi & Schubart, 2017

The genus *Fasciarma* has been established by Shahdadi and Schubart (2017), to host *Perisesarma fasciatum*, a species previously included in the genus *Perisesarma*. In particular, a few authors have considered this species as an aberrant species within *Perisesarma*, due to incongruence with the diagnostic characters of this genus, and therefore have suggested to remove it from the genus (Campbell, 1967; Davie, 2010; Shahdadi & Schubart, 2015). Campbell (1967) actually removed this species from *Perisesarma*, although this change was not officially accepted until Shahdadi and Schubart (2017) established a new genus to accommodate it.

The only species included in this genus, *F. fasciatum* (Lanchester, 1900), has been recorded from Peninsular Malaysia, Singapore, and/or northern Borneo.

Table 3.13: List of the main studies conducted on the genus *Fasciarma* (including taxonomic studies and reviews of the genus).

Author and Year	Subject of the study
Shahdadi & Schubart 2017	genus description

3.3.4.1 *Fasciarma fasciatum* (Lanchester, 1900)

This species has been described as *Sesarma* (*Parasesarma*) *fasciata* by Lanchester (1900a), from Singapore, from a “marshy ground near the sea”. A few years later, Rathbun (1909) described the same species as *Sesarma* (*Chiromantes*) *siamense*, from Thailand.

Subsequently, a few authors reported the species as *Sesarma* (*Chiromantes*) *siamense* from Thailand and Cambodia, and added morphological and taxonomic notes (Rathbun, 1910a; Kemp, 1918). Tweedie (1936) recorded it as *Sesarma* (*Chiromantes*) *fasciata*, and added new distribution records (Singapore and Peninsular Malaysia). Moreover, this author synonymised *Sesarma* (*Chiromantes*) *siamense* Rathbun, 1909 with *Sesarma* (*Chiromantes*) *fasciata* Lanchester, 1900.

Tweedie (1950a) reported this species as *Sesarma fasciata* from Borneo. Soh (1978) and Kwok and Tang (2005) recorded this species from Hong Kong, while Serène and Moosa (1971) and Pratiwi and Widyastuti (2013) reported it from Indonesia.

Lanchester (1900a) placed this species in the subgenus *Parasesarma*, because the anterolateral tooth is not always clearly defined (see also Subchapter 3.3.10). However, this author noticed that one of the females had "indications of a tooth behind the orbital angle", and Tweedie (1936) states that the "epibranchial tooth is always low and obtuse, often obscure, and in one adult male, scarcely indicated". Campbell (1967) and Davie (2010) included the species in the genus *Perisesarma*, although these authors suggested to remove it from the genus, due to its aberrant characters (in particular, rows of chitinous tubercles instead of the typical pectinated crests on the dorsal face of the male chelar palm). Therefore, Shahdadi and Schubart (2017) established a new genus, *Fasciarma*, to include *F. fasciatum* only.

Berry (1972) included this species in his report on the mangrove macrofauna of the West coast of Peninsular Malaysia, where it was recorded from the middle and upper part of the forest, especially abundant "on higher, dryer, partially cleared sites". In an ecological study on the distribution of mangrove macrofauna (Selangor, Peninsular Malaysia), Sasekumar

(1974) reported *F. fasciatum* from a sandy area, artificially altered by dumping of sand for the construction of a nearby bridge, and colonised by a thick mat of the sedge *Fimbristylis schoenoides*. The measured salinity ranged from brackish water to saltwater conditions (Sasekumar, 1974).

Guerao et al. (2004) described the complete larval and early juvenile morphology of this species, and compared it with other published larval description of *Parasesarma* and *Perisesarma* species. These authors also reported that *F. fasciatum* was observed living "in the upper, often dry, fringes of mangroves on relatively hard and sandy substratum", where it was "repeatedly observed scurrying on mounds of the burrowing decapod *Thalassina* (C. D. Schubart, personal observation)" (Guerao et al., 2004).

Torres et al. (2011) conducted a study on the growth, tolerance to low salinity, and osmoregulation abilities in several decapod larvae, including *F. fasciatum* and other crustacean species.

Figure 3.11: ***Fasciarma fasciatum.*** Male specimen (LK_sg.kilim161113_site1_4, from the Peninsular Malaysia collection, loc. Langkawi, see Chapter 4). Dorsal (above), ventral (middle) and frontal view (below). CW = 1.02 cm.

Table 3.14: List of the studies conducted on *Fasciarma fasciatum.*

Author and Year	Subject of the study	Field	Country
Lanchester 1900a	species description as *Sesarma* (*Parasesarma*) *fasciata* (Singapore)	taxonomy	Singapore
Rathbun 1909	species description as *Sesarma* (*Chiromantes*) *siamense* (Thailand)	taxonomy	Thailand
Rathbun 1910a	as *Sesarma* (*Chiromantes*) *siamense* (Thailand); morphological and taxonomic notes	taxonomy	Thailand

Table 3.14, continued.

Tesch 1917	species included in checklist and in diagnostic key of sesarmid species	taxonomy	IWP
Kemp 1918	as *Sesarma siamense*; new distribution records (Tonle Sap, Cambodia; Patani River, Thailand); morphological and taxonomic notes	taxonomy	Cambodia, Thailand
Tweedie 1936	as *Sesarma* (*Chiromantes*) *fasciata*; new distribution records (Singapore; Johor Strait; Port Swettenham = Port Klang, Peninsular Malaysia); *Sesarma* (*Chiromantes*) *siamensis* Rathbun, 1909 synonimised to *Sesarma* (*Chiromantes*) *fasciata*	distribution record (only)	Singapore, Malaysia (Peninsular Malaysia)
Tweedie 1950a	as *Sesarma fasciata*; new distribution record (Labuan, East Malaysia)	distribution record (only)	Malaysia (East Malaysia)
Campbell 1967	suggestion of removing the species from the genus *Perisesarma*	taxonomy	IWP
Serène & Moosa 1971	as *Perisesarma fasciatum*; new distribution record (Ambon, Indonesia)	distribution record (only)	Indonesia
Berry 1972	as *Perisesarma fasciatum*; mangrove macrofauna of the West coast of Peninsular Malaysia	spatial ecology	Malaysia (Peninsular Malaysia)
Sasekumar 1974	as *Perisesarma fasciatum*; distribution, abundance and zonation of mangrove macrofauna in Port Klang (Peninsular Malaysia)	spatial ecology	Malaysia (Peninsular Malaysia)
Soh 1978	as *Perisesarma fasciatum*; new distribution record (Hong Kong)	distribution record (only)	Hong Kong
Guerao et al. 2004	as *Perisesarma fasciatum*; larval and juvenile morphology (Singapore)	ontogenesis	Singapore
Kwok & Tang 2005	as *Perisesarma fasciatum*; checklist of the sesarmid crabs of Hong Kong, key to the species	distribution record (only)	Hong Kong
Torres et al. 2011	as *Perisesarma fasciatum*; growth, salinity tolerance and osmoregulation in decapod crustacean larvae; review	physiology	IWP
Pratiwi & Widyastuti 2013	as *Perisesarma fasciatum*; distribution and zonation of mangrove crustaceans in Lampung Bay (Indonesia)	spatial ecology	Indonesia

3.3.5 Genus *Haberma* Ng & Schubart, 2002

The genus *Haberma* has been described by Ng and Schubart (2002), and it is characterised by the propodus and dactylus of the first and second ambulatory legs of the adult male forming sub-chelate structures. The general adult features of these crabs are similar to those of juvenile sesarmids, especially with regards to their small size, large eyes, and long, slender legs (Ng & Schubart, 2002).

This genus currently includes three species, recorded from Singapore (Ng & Schubart, 2002), Indonesia (Rahayu & Ng, 2005), and Hong Kong (Cannicci & Ng, 2017). Specimens of this genus have been reported also from Terengganu (Peninsular Malaysia; Taufek, 2013), although this author did not discriminate them at species level.

These species have been recorded from mangrove forests, in different environmental conditions, such as on muddy river banks and hard substrates in the upper intertidal zone (Rahayu & Ng, 2005), in open areas with no leaf cover, and disturbed areas covered by man-made debris (Ng & Schubart, 2002). Cannicci and Ng (2017) recorded specimens of *H. tingkok* at ebbing and low tides, climbing on tree trunks of *Kandelia obovata* and *Aegiceras corniculatus*, at a height of 1.5-1.8 m above the substrate.

Two species have been recorded from Peninsular Malaysia, Singapore, and/or northern Borneo:

- *H. kamora* Rahayu & Ng, 2005
- *H. nanum* Ng & Schubart, 2002

Table 3.15: List of the main studies conducted on the genus *Haberma* (including taxonomic studies and reviews of the genus).

Author and Year	Subject of the study
Ng & Schubart 2002	genus description (Singapore)

3.3.5.1 *Haberma kamora* Rahayu & Ng, 2005

This species has been described from Irian Jaya, Indonesia (Rahayu and Ng, 2005), where it was found on the muddy banks of a river and on hard substrates in the upper intertidal zone of a mangrove forest.

Nordhaus et al. (2009) also reported it from Indonesia, in a study conducted in the Sekara-Anakan lagoon (Java), a mangrove-fringed lagoon heavily affected by human activities (fishing, effluents from agriculture and industry, and deforestation). This species was found on muddy substrate.

This species has been included in this synopsis, because it has been recorded in the surveys conducted in this project (Brunei Bay, see Chapter 4).

Table 3.16: List of the studies conducted on *Haberma kamora.*

Author and Year	Subject of the study	Field	Country
Rahayu & Ng 2005	species description (Papua = Irian Jaya, Indonesia)	taxonomy	Indonesia
Nordhaus et al. 2009	spatio-temporal variation of macrobenthic communities in the mangrove-fringed Segara Anakan lagoon (Indonesia)	distribution record (only)	Indonesia

3.3.5.2 *Haberma nanum* Ng & Schubart, 2002

Haberma nanum has been described from a mangrove forest in Singapore by Ng and Schubart (2002), which recorded it from relatively open habitats with hard dried mud and no leaf cover. These authors reported that this species was more abundant in disturbed areas, such as soil-covered man-made debris around a ruined building (Ng & Schubart, 2002).

Su and Lim (2016) investigated the predator avoidance strategies of *H. nanum* from Singapore. This species exhibited a flight behaviour when exposed to an experimental mudskipper model, and showed a strong predator recognition capability (Su & Lim, 2016).

Table 3.17: List of the studies conducted on *Haberma nanum*.

Author and Year	Subject of the study	Field	Country
Ng & Schubart 2002	species description (Singapore)	taxonomy	Singapore
Su & Lim 2016	antipredatory strategies of *Paracleistostoma depressum* and *Haberma nanum* (Singapore)	behaviour / interspecific interactions	Singapore

3.3.6 Genus *Labuanium* Serène & Soh, 1970

The genus *Labuanium* includes 12 species distributed throughout the Indo-West Pacific region (see Ng et al., 2015b), including records from Madagascar (Cumberlidge et al., 2005), Myanmar (De Man, 1887; Alcock, 1900), Cambodia (Kemp, 1918), Taiwan (Jeng et al., 2003; Ng & Liu, 2003), Indonesia (Ng & Davie, 2010; Ng, 2012), Peninsular Malaysia (Tweedie, 1940), Borneo (Tweedie, 1950a), Australia (see Jeng et al., 2003), Hawaii and Pacific Islands (Ng, 2012), Philippines (Ng et al., 2015b), and Japan (Maenosono & Naruse, 2016).

The genus was described by Serène and Soh (1970), to include species having an antennular basal segment strongly swollen and the antennular fossae nearly circular, the antennae nearly longitudinal, the lateral border of carapace at least slightly convex, the male abdomen narrow, and the dactyli of pereopods 2 - 5 clearly shorter than the propodi (Serène & Soh, 1970). Recently, Ng (2012) and Ng et al. (2015b) pointed out that the genus has to be considered heterogeneous, and it is currently under taxonomic revision. In particular, these authors identified four species groups:

- the first group includes only the type species, *L. politum*, and it is defined by having very short ambulatory propodus and dactyli. This species has been found almost exclusively in association with nipah palms (*Nypa fruticans*);

- the second group includes species allied to *L. gracilipes*, having relatively long ambulatory dactyli that are gently curved and lined with scattered stiff setae;

- the third group includes species allied to *L. rotundatum*, which have relatively shorter ambulatory dactyli that are almost straight, and whose margins are densely lined with short setae. Both the second and third groups include arboreal species, living on inland trees but not far from the sea;

- the fourth group includes *L. trapezoideum* only, which is not arboreal but lives instead on cliff fronts and vertical walls near waterfalls.

Some of these species are known only from their type specimens, and their ecology and biology is almost unknown (*L. cruciatum*, *L. demani*, *L. finni*, *L. schetteii*; see Ng et al., 2015b).

Except for *L. trapezoideum*, the other known species are nocturnal and arboreal, living several meters above the ground in phytotelmic habitats, such as water-filled *Pandanus* leaf axils (Cumberlidge et al., 2005), water-filled tree holes (Ng & Liu, 2003), and fronds of the nipah palm (Ng et al., 2015b).

Only one species, *Labuanium politum* (De Man, 1887), has been reported from Peninsular Malaysia, Singapore, and/or northern Borneo.

Table 3.18: List of the main studies conducted on the genus *Labuanium* (including taxonomic studies and reviews of the genus).

Author and Year	Subject of the study
Serène & Soh 1970	genus description
Cumberlidge et al. 2005	ecological notes (tree climbing; phytotelmic habitats)
Ng et al. 2015b	historical and ecological notes

3.3.6.1 *Labuanium politum* (De Man, 1887)

This species has been reported for the first time by De Man (1887) from the Mergui Archipelago, Myanmar. However, the actual paper describing this species was published only one year later, by the same author (De Man, 1888).

In the following decades, the species has been reported from the same geographic area (Mergui Archipelago, Myanmar; Alcock, 1900; Tesch, 1917), and from Cambodia (Kemp, 1918), Peninsular Malaysia (Tweedie, 1940), Borneo (Tweedie, 1950a; Choy, 1991), and Indonesia (Serène & Moosa, 1971). More recently, Rahayu and Setyadi (2009) and Pratiwi and Rahmat (2015) reported *L. politum* from Papua and Ambon (Indonesia), while Ng et al. (2015b) recorded it from Singapore and the Philippines.

This species is considered an obligate tree climber, since it has been observed living almost exclusively on nipah palms (*Nypa fruticans*), hiding in the bases of the leaf stalks during the day, and coming out at night to feed on the leaves, by using the chelipeds to tear off small leaf pieces (Ng et al., 2015b).

Figure 3.12: *Labuanium politum.* Female specimen, from the reference collection of the Raffles Museum of Biodiversity Research in Singapore (today Lee Kong Chian Natural History Museum, National University of Singapore), visited by the author in 2011-2012. Specimen number: ZRC 2003.0383. Dorsal (above), ventral (middle) and frontal view (below). Scales are in mm.

Table 3.19: List of the studies conducted on *Labuanium politum*.

Author and Year	Subject of the study	Field	Country
De Man 1887	species recorded as *Sesarma polita* (Mergui Archipelago, Myanmar; western part of Indian Archipelago)	distribution record (only)	Myanmar
De Man 1887-88	new distribution records (Mergui Archipelago, Myanmar) and species description	taxonomy	Myanmar
Alcock 1900	new distribution records (Mergui Archipelago, Myanmar); morphological and taxonomic notes	taxonomy	Myanmar
Tesch 1917	new distribution records (Mergui Archipelago, Myanmar); species included in checklist and in diagnostic key of sesarmid species	distribution record (only)	Myanmar
Kemp 1918	new distribution records (Tonle Sap, Cambodia)	distribution record (only)	Cambodia
Tweedie 1940	as *Sesarma polita*; new distribution records (Sedili River, Johor, Peninsular Malaysia); distribution notes	distribution record (only)	Malaysia (Peninsular Malaysia)
Tweedie 1950a	as *Sesarma polita*; new distribution records (Labuan, Borneo); morphological and taxonomic notes	taxonomy	Malaysia (East Malaysia)
Serène & Moosa 1971	new distribution record (Ambon, Indonesia); morphological and taxonomic notes	taxonomy	Indonesia
Choy 1991	checklist of Crustacea of Brunei Darussalam	distribution record (only)	Brunei Darussalam
Rahayu & Setyadi 2009	new distribution records (Papua, Indonesia)	distribution record (only)	Indonesia
Ng et al. 2015b	new distribution records (Singapore, Philippines); review on taxonomy and ecology; association with nipah palm	taxonomy / spatial ecology	Singapore, Philippines
Pratiwi & Rahmat 2015	checklist of brachyuran crabs in the reference collection at the Research Centre for Oceanografi, Indonesian Institute of Sciences (LIPI) collected from 1960 to 1970 (Indonesia)	distribution record (only)	Indonesia

3.3.7 Genus *Nanosesarma* Tweedie, 1950

The genus *Nanosesarma* has been described by Tweedie (1950c), to include species having the distal part of the postero-lateral border of the ambulatory meri spinate or denticulate. Moreover, all the species included in this genus have small adult size (CW usually < 1cm), and almost all the species present one or more fine granular lines on the outer surface of the cheliped (Tweedie, 1950c; Serène & Soh, 1970).

The genus currently comprises 10 species (Ng et al., 2008; Naderloo & Türkay, 2009), widely distributed throughout the Indo-West Pacific region, including the Red Sea (Nobili, 1905a), Madagascar and East Africa (Crosnier, 1965; Vannini & Valmori, 1981), Persian Gulf (Naderloo & Türkay, 2009), India (Kemp, 1915; Ravichandran et al., 2007; Beleem et al., 2014; Trivedi et al., 2015), Myanmar (Alcock, 1900), Thailand (Kemp, 1918), Vietnam (Chertoprud et al., 2012), China and Japan (Shen, 1935; Sakai, 1939; Komai et al., 2004), Korea (Kim & Choe, 1969), Taiwan (Ng et al., 2001), Hong Kong (Kwok & Tang, 2005), Borneo (De Man, 1895; Tweedie, 1950a), Peninsular Malaysia and Singapore (Tweedie, 1936; Tweedie, 1940), and Indonesia (De Man, 1887, 1888, 1890).

Serène and Soh (1970) splitted this genus in two sub-genera, *Nanosesarma* (*Nanosesarma*) and *Nanosesarma* (*Beanium*). However, Holthuis (1977) and Abele (1979) pointed out that *Nanosesarma* (*Beanium*) has to be considered a junior synonym of *Nanosesarma* (*Nanosesarma*). Therefore, the subdivision in sub-genera by Serène and Soh (1970) is currently considered invalid (Ng et al., 2008).

Figure 3.13: Example of *Nanosesarma* specimen, showing the meri of the walking legs, whose postero-lateral border in this genus is spinate or denticulate (see arrows). *N. batavicum*, from the reference collection of the Raffles Museum of Biodiversity Research in Singapore (Lee Kong Chian Natural History Museum, National University of Singapore), visited by the author in 2011-2012. Specimen number: ZRC 1964-9-3-46-56. The picture has been taken under a stereomicroscope.

Nanosesarma species have been recorded in several ecological studies on the diversity and zonation of mangrove macrofauna (e.g. Frith et al., 1976; Ashton et al., 2003b; Ravichandran et al., 2007). Although most of the species have been found in mangrove systems (e.g. Chertoprud et al., 2012; Diele et al., 2013; Varadharajan & Soundarapandian, 2014), a few studies recorded specimens from rocky shores (Naderloo & Türkay, 2009), cobble beaches (Naderloo et al., 2013), and coral reefs (Dong et al., 2015).

Species of this genus have been reported from areas with freshwater and brackish-saltwater conditions (e.g. Frith et al., 1976; Ravichandran et al., 2007), on different kind of substrata (e.g. Naderloo et al., 2013). In particular, within mangrove forests, a few authors pointed out that these crabs have been found mainly inside cavities of decayed wood (Komai et al., 2004), or hiding in rock crevices and among oysters and cirripeds (Chertoprud et al., 2012). De Man (1887-1888) found *N. andersonii* inhabiting burrows of the bivalve *Novaculina*.

Even though *Nanosesarma* species have been recorded from several localities, little is known about their biology and autecology.

The larval morphology has been described for a few species, such as *N. gordoni* (Japan; Terada, 1982), *N. andersonii* (India; Vijayakumar & Kannupandi, 1986), and *N. batavicum* (India; Selvakumar & Haridasan, 2000a). Selvakumar and Haridasan (2000b) studied the toxic effects of heavy metals on zoeal development of *N. batavicum*.

Seven species have been recorded from Peninsular Malaysia, Singapore, and/or northern Borneo:

- *N. andersonii* (De Man, 1888)
- *N. batavicum* (Moreira, 1903)
- *N. edamense* (De Man, 1887)
- *N. minutum* (De Man, 1887)
- *N. nunongi* Tweedie, 1950
- *N. pontianacense* (De Man, 1895)
- *N. tweediei* (Serène, 1967)

Table 3.20: List of the main studies conducted on the genus *Nanosesarma* (including taxonomic studies and reviews of the genus).

Author and Year	Subject of the study
Tweedie 1950c	genus description; key to the Indo-Pacific species (*N. minutum*, *N. gordoni*, *N. vestitum*, *N. batavicum*, *N. edamense*, *N. andersonii*, *N. nunongi*), with distribution, morphological and taxonomic notes
Serène & Soh 1970	taxonomic notes; the genus is split in two subgenera: *Nanosesarma* (*Nanosesarma*) and *Nanosesarma* (*Beanium*)
Holthuis 1977	taxonomic notes; subgenera considered invalid: *Beanium* reunited with *Nanosesarma*
Abele 1979	taxonomic and historical notes

3.3.7.1 *Nanosesarma andersonii* (De Man, 1888)

This species has been described by De Man (1887-1888) from the Mergui Archipelago, Myanmar. In particular, this author recorded his specimens from abandoned burrows of the bivalve *Novaculina* sp., along a river bank (De Man, 1887-1888).

De Man (1887) and Alcock (1900) provided morphological and taxonomic notes, while Kemp (1918) added a new record from the West coast of Thailand. Tweedie (1940) recorded this species from eastern (Pahang) and western (Penang) coast of Peninsular Malaysia, and Tweedie (1950a,c) reported it from Borneo. In particular, Tweedie (1950a) suggested that his previous samples from Penang (Tweedie 1940) were to be attributed to a new undescribed species.

Lundoer (1974) reported *N. andersonii* from the reference collection of the Phuket Marine Biolological Center (Thailand), and stated that the collected samples were found on wood, in mangrove forests. Choy (1991) and Choy and Booth (1994) reported this species from Brunei Darussalam, while Komai et al. (2004) recorded it from Japan, and provided morphological and taxonomic notes, and remarks on its distribution and ecology. In particular, Choy and Booth (1994) recorded this species from an *Avicennia* dominated coastal wetland, while Komai et al. (2004) pointed out that the collected specimens were found in cavities made by wood boring sphaeromatid isopods on decayed wood within the mangrove forest (Komai et al., 2004). In their study on the habitat preference of mangrove macrofauna from Pichavaram forest (India), Ravichandran et al. (2007) found *N. andersonii* from almost all the examined sites within the mangrove forest, i.e. along all the intertidal gradient, in freshwater and saltwater conditions. Vijayakumar and Kannupandi (1986) described the larval morphology of this species, from specimens from India.

Table 3.21: List of the studies conducted on *Nanosesarma andersonii.*

Author and Year	Subject of the study	Field	Country
De Man 1887-1888	species description as *Sesarma andersoni* (Mergui Archipelago, Myanmar)	taxonomy	Myanmar
De Man 1887	as *Sesarma andersoni*: morphological and taxonomic notes	taxonomy	IWP
Alcock 1900	as *Sesarma andersoni*; morphological and taxonomic notes (Mergui Archipelago, Myanmar)	taxonomy	Myanmar
Tesch 1917	species included in checklist and in diagnostic key of sesarmid species	distribution record (only)	IWP
Kemp 1918	as *Sesarma andersoni*; new distribution record (Trang, Thailand)	distribution record (only)	Thailand
Tweedie 1940	as *Sesarma andersoni*; new distribution records (Penang and Pahang, Peninsular Malaysia); distribution notes	distribution record (only)	Malaysia (Peninsular Malaysia)
Tweedie 1950a	as *Sesarma andersoni*; new distribution record (Sarawak, East Malaysia); taxonomic notes	taxonomy	Malaysia (East Malaysia)
Tweedie 1950c	species transferred to the newly established genus *Nanosesarma*; distribution notes	taxonomy	IWP
Lundoer 1974	checklist of brachyuran crabs in the reference collection at Phuket Marine Biology Center (Thailand)	distribution record (only)	Thailand
Vijayakumar & Kannupandi 1986	larval development of *N. andersonii* (India)	ontogenesis	India
Choy 1991	as *Neosesarma andersoni*; checklist of Crustacea of Brunei Darussalam	distribution record (only)	Brunei Darussalam
Choy & Booth 1994	macrofaunal community in a *Avicennia* dominated coastal wetland (Brunei Darussalam) before and after an inundation event	spatial ecology	Brunei Darussalam
Komai et al. 2004	new records from Ryukyu Islands (Japan), taxonomic and ecological notes	taxonomy	Japan
Ravichandran et al. 2007	diversity and habitat preference of crabs in Pichavaram mangrove system (India)	spatial ecology	India

3.3.7.2 *Nanosesarma batavicum* (Moreira, 1903)

This species was first described as *Sesarma barbimana* by De Man (1890) from Batavia (today Jakarta, Indonesia), and subsequently as *Sesarma batavica* by Moreira (1903) from the same locality. Also Cano (1889) described a species with the name *Sesarma barbimana*, which is today considered a synonym of *Nanosesarma minutum* (see Abele, 1979, and Subchapter 3.3.7.4).

Kemp (1915) reported this species as *Sesarma batavicum* from the East coast of India, and provided taxonomic and morphological notes. In this study, the collected specimens were found among clusters of shell of a oyster-bed or in natural cavities of laterite blocks, both in fresh and saltwater conditions (Kemp, 1915). Tweedie (1936) reported this species as *Sesarma batavica* from Singapore, the Johor Strait, and the West coast of Peninsular Malaysia (Selangor), while Tweedie (1940) reported it from the East (Pahang) and West (Penang) coast of Peninsular Malaysia, and added a few morphological notes. In his checklist of the reference collection of the Phuket Marine Biolological Center (Thailand), Lundoer (1974) reported *N. batavicum* from mangrove forests, where it was found on wood. Frith et al. (1976) recorded this species from the West coast of Thailand, from the landward and middle part of the investigated mangrove forest, on muddy substrate, and in saltwater conditions.

Selvakumar and Haridasan (2000a) described the morphology of the five zoeal stages and megalopa of *N. batavicum* from India, while Selvakumar and Haridasan (2000b) investigated the toxic effect of heavy metals on the larval development of this species, which was found to be particularly sensitive to mercury and zinc.

Ashton et al. (2003b) recorded this species as *Beanium batavicum* from Borneo, while Ravichandran et al. (2007) found *N. batavicum* in most of the zones of their studied mangrove forest (India). Dev Roy and Nandi (2008) reported this species as *Beanium batavicum* from a brackish coastal lake on the East coast of India. Chertoprud et al. (2012) and Diele et al. (2013) recorded this species from Vietnam, while Varadharajan and Soundarapandian (2014) found it in several localities along the southeastern coast of India. Leh et al. (2010) collected this species in the 1980s from an upper intertidal mangrove site in Selangor (Peninsular Malaysia), where it was found in a disturbed area, where trees had been cleared a few months before the sampling. In this area, the soil was almost unvegetated and covered by fallen trunks and scattered wooden debris (Leh et al., 2010). Dong et al. (2015) reported this species from a coral reef in Hainan (China).

Fig. 3.14: ***Nanosesarma batavicum.*** Male specimen (PK050314_31, from the Peninsular Malaysia collection, loc. Pulau Kukup, see Chapter 4). Dorsal (above), ventral (middle) and frontal view (below). CW=.0.51 cm. Photos were taken under a stereomicroscope.

Table 3.22: List of the studies conducted on *Nanosesarma batavicum*.

Author and Year	Subject of the study	Field	Country
De Man 1890	species description (as *Sesarma barbimana*) from Batavia (=Jakarta, Indonesia)	taxonomy	Indonesia
Moreira 1903	species description as *Sesarma batavica* (Indonesia)	taxonomy	Indonesia
Kemp 1915	as *Sesarma batavicum*, new distribution records (India); morphological and taxonomic notes	taxonomy	India
Tesch 1917	species included in checklist and in diagnostic key of sesarmid species	distribution record (only)	IWP
Tweedie 1936	as *Sesarma* (*Parasesarma*) *batavica*; new distribution records (Singapore; Johor Straits; Port Swettenham = Port Klang, Selangor)	distribution record (only)	Singapore, Malaysia (Peninsular Malaysia)
Tweedie 1940	as *Sesarma batavica*; new distribution records (Penang, Pahang, Peninsular Malaysia); morphological notes	distribution record (only)	Malaysia (Peninsular Malaysia)
Tweedie 1950c	species transferred to the newly established genus *Nanosesarma*; distribution and morphological notes	taxonomy	IWP
Lundoer 1974	checklist of brachyuran crabs in the reference collection at Phuket Marine Biology Center (Thailand)	distribution record (only)	Thailand
Frith et al. 1976	zonation and abundance of mangrove macrofauna on Phuket Island (Thailand)	spatial ecology	Thailand
Selvakumar & Haridasan 2000a	larval development (India)	ontogenesis	India
Selvakumar & Haridasan 2000b	toxic effect of heavy metals on zoeal development (India)	ontogenesis	India
Ashton et al. 2003b	ecology and diversity of crab and mollusc macrofaunal community in the Sematan mangrove forest (Sarawak, East Malaysia)	spatial ecology	Malaysia (East Malaysia)
Ravichandran et al. 2007	diversity and habitat preference of crabs in Pichavaram mangrove system (India)	spatial ecology	India
Dev Roy & Nandi 2008	diversity of brackish coastal lakes (India)	spatial ecology	India

Table 3.22, continued.

Leh et al. 2010	biomass and abundance of sesarmid crabs in a natural and disturbed mangrove area in Selangor (Peninsular Malaysia)	spatial ecology	Malaysia (Peninsular Malaysia)
Chertoprud et al. 2012	diversity and functional structure of brachyuran crab assemblages of southern Vietnam, ecological notes	spatial ecology	Vietnam
Diele et al. 2013	impact of typhoon on diversity of key ecosystem engineers (Vietnam)	spatial ecology	Vietnam
Varadharajan & Soundarapandian 2014	crab diversity of the South East coast of India	distribution record (only)	India
Dong et al. 2015	macrobenthic community of coral reefs at Hainan (China) (in Chinese)	spatial ecology	China

3.3.7.3 *Nanosesarma edamense* (De Man, 1887)

This species has been described as *Sesarma edamensis* by De Man (1887) from Java, Indonesia. De Man (1888) reported the species from Edam and Sabira Islands (Java, Indonesia), and added morphological and taxonomic notes.

Tweedie (1950a) recorded this species as *Sesarma edamensis* from mangrove forests in Labuan (East Malaysia) and provided additional morphological and taxonomic notes, while Tweedie (1950c) transferred this species to the newly established genus *Nanosesarma*. Serène & Moosa (1971) reported this species from Ambon (Indonesia) and added morphological notes. Serène (1973) and Ng and Richer de Forges (2007) recorded this species from New Caledonia. The former author provided also morphological and taxonomic notes (Serène, 1973).

The biology and autecology of this species are practically unknown.

Figure 3.15: ***Nanosesarma edamense*.** Male specimen (MB_141112_site3_7, from the Peninsular Malaysia collection, loc. Pulau Merambong, see Chapter 4). Dorsal (above), ventral (middle) and frontal view (below). CW=0.48 cm.

Table 3.23: List of the studies conducted on *Nanosesarma edamense*.

Author and Year	Subject of the study	Field	Country
De Man 1887	species description as *Sesarma edamensis* (Java, Indonesia)	taxonomy	Indonesia
De Man 1888	new distribution records (Edam and Noordwatcher = Sabira Island, Indonesia)	distribution record (only)	Indonesia
Tesch 1917	species included in checklist and in diagnostic key of sesarmid species	distribution record (only)	IWP
Tweedie 1950a	as *Sesarma edamensis*; new distribution record (Labuan, East Malaysia); morphological and taxonomic notes	taxonomy	Malaysia (East Malaysia)
Tweedie 1950c	species transferred to the newly established genus *Nanosesarma*; distribution, morphological and taxonomic notes	taxonomy	IWP
Serène & Moosa 1971	new distribution record (Ambon, Indonesia); morphological and taxonomic notes	taxonomy	Indonesia
Serène 1973	new distribution record (New Caledonia); morphological and taxonomic notes	taxonomy	New Caledonia
Ng & Richer de Forges 2007	checklist of brachyuran crabs from New Caledonia	distribution record (only)	New Caledonia

3.3.7.4 *Nanosesarma minutum* (De Man, 1887)

This species has been officially described as *Sesarma minuta* by De Man (1887) from Edam Island (Indonesia). However, this author provided only a few notes and stated that the species would have been described later, on a subsequent work on crustacean samples collected by J. Brock in the same study area. Therefore, the full description of this species appeared only one year later, as *Sesarma minuta*, by De Man (1888). Cano (1889) described this species as *Sesarma barbimana* from Peru, even though Rathbun (1910c) pointed out that this locality is probably incorrect. Later, Abele (1979) stated that the name *S. barbimana* Cano, 1889 has to be considered a junior synonym of *N. minutum*.

Shen (1935) described this species from China, as *Sesarma gordoni*, which is currently considered a synonym of *N. minutum* (see Ng et al., 2008). Later on, Sakai (1939) and Fukui et al. (1989) reported this species as *S. gordoni* from Japan and Taiwan, respectively.

Rathbun (1910a) reported this species as *Sesarma* (*Sesarma*) *minutum* from Thailand and added a few morphological and taxonomic notes. Tweedie (1936) recorded it as *Sesarma* (*Sesarma*) *minuta* from Singapore and Johor (Peninsular Malaysia). Crosnier (1965) reported *N. minutum* from Madagascar, and Lundoer (1974) recorded it from Thailand. Both these authors found this species along rocky shores. Macnae (1968) reported this species living in IWP mangrove forests, among sessile mollusks on tree stems and on the ground.

Berry (1972) included it in his account of the mangrove macrofauna of the West coast of Peninsular Malaysia, where it was collected from the seaward pioneer edge of the investigated forests. Vannini and Valmori (1981) found it in rotten wood partially buried in the mud in mangrove forests of Somalia. Hsueh (1996) recorded *N. minutum* from a coastal wetland in Taiwan, where it was found in the middle intertidal area, in crevices of cobbles or oyster clusters. Ng et al. (2001) and Kwok and Tang (2005) included this species in the checklist of brachyuran crabs from Taiwan and Hong Kong, respectively. Chertoprud et al. (2012) recorded it from Vietnam, and pointed out that this species was found in sheltered rocky intertidal areas, among oysters and cirripeds, and on intertidal and shallow subtidal mudflats in forests of *Rhizophora apiculata* (Chertoprud et al., 2012). Ravichandran et al. (2007) found *N. minutum* in a mangrove area on the south-eastern coast of India, while Beleem et al. (2014) and Trivedi et al. (2015) reported it from the West coast of India.

Karasawa and Kato (2001) included this species in a phylogenetic analysis of the Grapsoidea based on adult morphological characters. *N. minutum* was also included in a study on the antibacterial activity of the heamolymph extracts of selected species of mangrove crabs by Veeruraj et al. (2008). However, the haemolymph of this species did not show any antibacterial activity against the tested pathogenic strains (Veeruraj et al., 2008).

Figure 3.16: *Nanosesarma minutum.* Male specimen (MB_141112_site3_10 from the Peninsular Malaysia collection, loc. Pulau Merambong, see Chapter 4). Dorsal (above), ventral (middle) and frontal view (below). CW=0.39 cm.

Table 3.24: List of the studies conducted on *Nanosesarma minutum*.

Author and Year	Subject of the study	Field	Country
De Man 1887	species description as *Sesarma minuta* (Edam Island, Indonesia)	taxonomy	Indonesia
De Man 1888	new distribution records (Edam Island, Indonesia), detailed description, taxonomic and morphological notes	taxonomy	Indonesia
Cano 1889	species decription as *Sesarma barbimana* (Peru), but most definitely erroneous attribution (see Rathbun 1910c)	taxonomy	Peru (?)
Rathbun 1910a	as *Sesarma* (*Sesarma*) *minutum*; new distribution record (Thailand)	taxonomy	Thailand
Rathbun 1910c	Crustacea of Peru; note about incorrect locality for *Sesarma barbimana* collected by Cano (1889)	distribution record (only)	world
Tesch 1917	species included in checklist and in diagnostic key of sesarmid species	distribution record (only)	IWP
Shen 1935	species decription as *Sesarma gordoni* (China), later synonymised	taxonomy	China
Tweedie 1936	as *Sesarma* (*Sesarma*) *minuta*; new distribution records (Singapore; Johor, Peninsular Malaysia)	distribution record (only)	Singapore, Malaysia (Peninsular Malaysia)
Sakai 1939	new distribution record as *Sesarma gordoni* (Japan)	distribution record (only)	Japan
Tweedie 1950c	species transferred to the newly established genus *Nanosesarma*; distribution notes	taxonomy	IWP
Crosnier 1965	new distribution record (Madagascar); morphological and taxonomic notes	taxonomy	Madagascar
Macnae 1968	floraand fauna of mangrove swamps and forests in IWP region	spatial ecology	IWP
Berry 1972	mangrove macrofauna of the West coast of Peninsular Malaysia	spatial ecology	Malaysia (Peninsular Malaysia)
Lundoer 1974	checklist of brachyuran crabs in the reference collection at Phuket Marine Biology Center (Thailand)	distribution record (only)	Thailand
Abele 1979	S. *barbimana* Cano, 1889 synonimised with *N. minutum*; morphological and taxonomic notes	taxonomy	IWP

Table 3.24, continued.

Vannini & Valmori 1981	checklist of grapsoid species from Somalia	distribution record (only)	Somalia
Fukui et al. 1989	as *N. gordoni*; new distribution record (Taiwan)	distribution record (only)	Taiwan
Hsueh 1996	composition and microhabitats of brachyuran community of Kaomei coastal wetland (Taiwan)	spatial ecology / biodiversity	Taiwan
Karasawa & Kato 2001	paleontology, redefinition of the fossil genus *Miosesarma*, adult morphology-based phylogenetic analysis of 22 living and fossils genera of grapsoid crabs	phylogenesis	world
Ng et al. 2001	checklist of brachyuran crabs from Taiwan	distribution record (only)	Taiwan
Kwok & Tang 2005	checklist of the sesarmid crabs of Hong Kong, ecological and taxonomic notes, key to the species	taxonomy / spatial ecology	Hong Kong
Ravichandran et al. 2007	diversity and habitat preference of crabs in Pichavaram mangrove system (India)	spatial ecology	India
Veeruraj et al. 2008	antibacterial activity of crab haemolymph on clinical pathogens (India)	physiology	India
Chertoprud et al. 2012	new distribution record (Vietnam), ecological and taxonomic notes	taxonomy / spatial ecology	Vietnam
Beleem et al. 2014	crab diversity of the Gulf of Kachchh (Gujarat, India)	distribution record (only)	India
Trivedi et al. 2015	checklist of crustacean fauna of Gujarat (India)	distribution record (only)	India

3.3.7.5 *Nanosesarma nunongi* Tweedie, 1950

N. nunongi has been described by Tweedie (1950c) from the East and West coast of Peninsular Malaysia. Apparently, no other studies have recorded this species since then.

Table 3.25. List of the studies conducted on *Nanosesarma nunongi.*

Author and Year	**Subject of the study**	**Field**	**Country**
Tweedie 1950c	species description (Pahang, Penang, Peninsular Malaysia)	taxonomy	Malaysia (Peninsular Malaysia)

Figure 3.17: ***Nanosesarma nunongi.*** Male specimen (PK_050314_32, from the Peninsular Malaysia collection, loc. Pulau Kukup, see Chapter 4). Dorsal (above), ventral (middle) and frontal view (below). CW= 0.43 cm. Pictures were taken under a stereomicroscope.

3.3.7.6 *Nanosesarma pontianacense* (De Man, 1895)

This species was described as *Sesarma* (*Episesarma*) *pontianacensis* by De Man (1895) from a single female specimen from southern Borneo. Nobili (1903) recorded another female specimen from Samarinda (Kalimantan, Borneo). Tweedie (1940) reported this species as *Sesarma pontianacensis* from Singapore, the West coast of Peninsular Malaysia, and Indonesia, and provided a first description of a male specimen.

Serène and Soh (1970) included this species in the genus *Nanosesarma*, although they pointed out differences from the typical diagnostic characters of this genus. According to Ng et al. (2008), this species should be included in a own monotypic genus, and a revision is ongoing.

Lundoer (1974) reported *N. pontianacense* from the reference collection of the Phuket Marine Biology Center (Thailand). Nordhaus et al. (2009) reported this species on muddy substrate from the Sekara-Anakan lagoon (Java, Indonesia), an estuarine, mangrove-fringed lagoon, which has been heavily impacted (fishing, effluents from agriculture and industry, and deforestation).

Figure 3.18: ***Nanosesarma pontianacense.*** Female specimen (PBedukang_131013_5 from the Brunei Bay collection, loc. Pulau Bedukang, see Chapter 4). Dorsal (above) and ventral view (below). CW= 0.48 cm. Photos were taken on the live specimen.

Table 3.26: List of the studies conducted on *Nanosesarma pontianacense.*

Author and Year	Subject of the study	Field	Country
De Man 1895	species description as *Sesarma* (*Episesarma*) *pontianacensis* (Pontianak, southern Borneo)	taxonomy	Indonesia (Kalimantan)
Nobili 1903	new distribution record (southern Borneo)	distribution record (only)	Indonesia (Kalimantan)
Tesch 1917	species included in checklist and in diagnostic key of sesarmid species	distribution record (only)	IWP

Table 3.26, continued.

Tweedie 1940	as *Sesarma pontianacensis*; new distribution records (Singapore; Penang, Peninsular Malaysia; Karimon Islands, Indonesia), morphological notes; first description of a male specimen	taxonomy	Singapore, Malaysia (Peninsular Malaysia), Indonesia
Lundoer 1974	checklist of brachyuran crabs in the reference collection at Phuket Marine Biology Center (Thailand)	distribution record (only)	Thailand
Nordhaus et al. 2009	spatio-temporal variation of macrobenthic communities in the mangrove-fringed Segara Anakan lagoon (Indonesia)	distribution record (only)	Indonesia

3.3.7.7 *Nanosesarma tweediei* (Serène, 1967)

This species was described from the East coast of Peninsular Malaysia, Singapore, and Vietnam, by Serène (1967). A few years later, Serène and Soh (1970) stated that *N. tweediei* has to be considered a synonym of *N. pontianacense*. However, Ng et al. (2008) considered *N. tweediei* as a valid species.

The biology and autecology of this species is practically unknown.

Table 3.27: List of the studies conducted on *Nanosesarma tweediei.*

Author and Year	**Subject of the study**	**Field**	**Country**
Serène 1967	species description (Mersing, Johor, Peninsular Malaysia; Singapore; Vietnam)	taxonomy	Malaysia (Peninsular Malaysia), Singapore, Vietnam
Serène & Soh 1970	species synonymised with *N. pontianacense* (action considered invalid by Ng et al. 2008)	taxonomy	IWP

3.3.8 Genus *Neosarmatium* Serène & Soh, 1970

The genus has been described by Serène and Soh (1970), to include species characterised by a deeply vaulted, sub-quadrate carapace, the outer surface of the palm usually with a median longitudinal row, and the dorsal surface of the dactyl often bearing spines or blunt teeth (Davie, 1994).

The genus currently includes 19 species (see Ng et al., 2008; Ragionieri et al., 2012), distributed throughout the Indo-West Pacific region, from East and South Africa (Vannini & Valmori, 1981; Micheli et al., 1991; Peer et al., 2014), to Sri Lanka (Dahdouh-Guebas et al., 2011), India (Trivedi et al., 2015), Taiwan and Hong Kong (Ng et al., 2001; Kwok & Tang, 2005), Japan (Islam et al., 2002), Peninsular Malaysia and Borneo (Tweedie, 1940, 1950a), Indonesia (Rahayu & Davie, 2006), Philippines (Schubart & Ng, 2002), Australia (Salgado Kent & McGuinness, 2006, 2008), Fiji Islands (McLay & Ryan, 1990).

Davie (1994) provided a detailed review of the genus, with a diagnostic key and description of the species, including details on the morphology, taxonomy, ecology and distribution. Both Schubart and Ng (2002) and Rahayu and Davie (2006) provided revised keys, and described a few new species from Indonesia. Ragionieri et al. (2009, 2012) conducted a morphological and genetic study on *N. meinerti* from the whole Indo-West Pacific region, and found that this species is actually a species-complex of four different species. These authors provided also a revised diagnostic key of all the species of this genus (Ragionieri et al., 2012).

Crabs of this genus are among the largest sesarmid crabs in the mangroves, and are consumers of a large percentage of the mangrove leaf litter (e.g. Micheli et al., 1991). Most of the studies on the ecology and biology of this genus were conducted on a few species, i.e.

N. meinerti (today considered *N. africanum*, see Ragionieri et al., 2012) and *N. smithi*, mainly from African and Australian mangrove systems. In particular, several studies were conducted on the feeding ecology of these two species (Micheli et al., 1991; Emmerson & McGwynne, 1992; Steinke et al., 1993; Dahdouh-Guebas et al., 1997, 1999; Skov & Hartnoll, 2002; Fratini et al., 2011). Several studies investigated their burrowing ecology (Micheli et al., 1991; Gillikin et al., 2001; Berti et al., 2008; Andreetta et al., 2014), life history and population dynamics (Emmerson, 1994b, 2001), zonation and interspecific ecology (Dahdouh-Guebas et al., 2002; Hartnoll et al., 2002; Bosire et al., 2004; Cannicci et al., 2009; Fratini et al., 2011), physiology (Gillikin et al., 2004), and ontogenetic aspects (Flores et al., 2003; Paula et al., 2003a).

For all the other species, information on the biology and ecology are scarce or unknown.

Four species have been recorded from Peninsular Malaysia, Singapore, and/or northern Borneo:

- *N. asiaticum* Ragionieri, Fratini & Schubart, 2012
- *N. indicum* (A. Milne-Edwards, 1868)
- *N. smithi* (H. Milne-Edwards, 1853)
- *N. spinicarpus* Davie, 1994

Table 3.28: List of the main studies conducted on the genus *Neosarmatium* (including taxonomic studies and reviews of the genus).

Author and Year	Subject of the study
Serène & Soh 1970	genus description
Davie 1994	revision of the genus; description of *N. spinicarpus* and *N. trispinosum*; key of the whole genus
Schubart & Ng 2002	taxonomic notes; description of *N. daviei*; new name combination of *N. tangi* (previously *Chiromantes tangi*); key of the genus
Rahayu & Davie 2006	taxonomic notes; description of *N. bidentatum* and *N. papuense*; key to the Indo-West Pacific species
Ragionieri et al. 2012	revision of *N. meinerti* species complex, with description of 3 new pseudospecies; key of the whole genus

3.3.8.1 *Neosarmatium asiaticum* Ragionieri, Fratini & Schubart, 2012

This species has been recently described by Ragionieri et al. (2012). These authors performed genetic and morphological analyses on a widely distributed species, *Neosarmatium meinerti*, which has been previously recorded throughout the whole Indo-West Pacific region (Ragionieri et al., 2009, 2012). Their results proved *N. meinerti* to be a species-complex, and this species was therefore splitted in 4 species, namely *N. africanum*, *N. asiaticum*, *N. australiense*, and *N. meinerti*.

N. asiaticum has been recorded with different names [*Sesarma meinerti*, *Sesarma tetragona*, *Sesarma* (*Episesarma*) *meinerti*, *Sesarma* (*Sarmatium*) *meinerti*, *Sesarma* (*Sesarma*) *meinerti*, *Neosarmatium meinerti*, *Neosarmatium malabaricum*] from several localities, including the Andaman Islands and India (De Man, 1887; Henderson, 1893; Ortmann, 1894a,b; Alcock, 1900; Hokinawa, 1940; Lin, 1949), Sri Lanka (Dahdouh-Guebas et al., 2011), Peninsular Malaysia and Borneo (Ashton, 2002), Indonesia (De Man, 1895), Philippines (Bürger, 1893; De Man, 1929), China (Dai & Yang, 1991), and Taiwan (Horikawa, 1940; Lin, 1949; Ng et al., 1997).

In particular, Ashton (2002) recorded this species as *Neosarmatium malabaricum* from the mangrove forests of the Merbok Estuary (Kedah, Peninsular Malaysia), where it was found in a *Bruguiera* zone along the river side. Dahdouh-Guebas et al. (2011) included *N. asiaticum* (as *N. meinerti*) in their study on the effects of anthropic habitat alteration (e.g. hydrographic changes) on the behaviour of propagule predators, and their role in the shaping of mangrove vegetation structure. Their study was conducted in a basin and riverine mangrove forest, with very low tidal excursion (Sri Lanka, Dahdouh-Guebas et al., 2011).

Ragionieri et al. (2012) pointed out that the ecology and biology of this species is almost unknown, although the study by Dahdouh-Guebas et al. (2011) confirmed that these crabs are consumers of leaf litter and mangrove propagules. Moreover, the former authors stated that this species can be found in “mangroves and estuaries with grassy banks which are under the influence of tides” (Ragionieri et al., 2012).

Table 3.29: List of the studies conducted on *Neosarmatium asiaticum*.

Author and Year	Subject of the study	Field	Country
De Man 1887	species description as *Sesarma meinerti* (Andaman Islands and India)	taxonomy	Andaman Islands, India
Henderson 1893	as *Sesarma tetragona*, new distribution records (Madras = Chennai, India)	distribution record (only)	India
Bürger 1893	as *Sesarma meinerti*, new distribution records (Philippines)	distribution record (only)	Philippines
De Man 1895	as *Sesarma* (*Episesarma*) *meinerti*, new distribution records (Atjeh, Indonesia); taxonomic and morphological notes, morphometric measurements	taxonomy	Indonesia
Alcock 1900	as *Sesarma meinerti*, new distribution records (Andaman Islands and India); taxonomic and morphological notes	taxonomy	Andaman Islands, India
De Man 1929	as *Sesarma* (*Sarmatium*) *meinerti*, new distribution records (Philippines)	distribution record (only)	Philippines
Horikawa 1940	as *Sesarma meinerti*, new distribution records (Taiwan)	distribution record (only)	Taiwan
Lin 1949	as *Sesarma meinerti*, new distribution records (Taiwan)	distribution record (only)	Taiwan
Dai & Yang 1991	as *Neosarmatium meinerti*, new distribution records (China)	distribution record (only)	China
Ng et al. 1997	as *Neosarmatium meinerti*, new distribution records (Taiwan)	distribution record (only)	Taiwan
Ashton 2002	as *Neosarmatium malabaricum*, as distribution record; paper on feeding ecology, mangrove leaf species and leaf age preferences of *Perisesarma eumolpe* and *P. onychophorum* (Kedah, Peninsular Malaysia)	distribution record (only)	Malaysia (Peninsular Malaysia)
Dahdouh-Guebas et al. 2011	as *Neosarmatiu meinerti*, effect of anthropic hydrographical changes on propagule predation behaviour (Sri Lanka)	feeding ecology	Sri Lanka
Ragionieri et al. 2012	species definition (as pseudocryptic species within *N. meinerti* species complex)	taxonomy	IWP

3.3.8.2 *Neosarmatium indicum* (A. Milne-Edwards, 1868)

This species has been described as *Metagrapsus indicus* by A. Milne-Edwards (1868a) from Sulawesi, Indonesia. As Davie (1994) pointed out, this species must not be confused with *Sesarma indica* H. Milne-Edwards 1837, which corresponds instead to the species currently known as *Tiomanum indicum* (H. Milne-Edwards, 1837) (see also Subchapter 3.3.16.1).

De Man (1887, 1892) provided a few taxonomic notes and morphometric measurements on the species, reported as *Sarmatium indicum*. In his revision of the *Neosarmatium* genus, Davie (1994) pointed out that *N. indicum*, *N. punctatum,* and *N. malabaricum* have been sometimes confused in the early literature. Therefore, this author considered the material identified as *N. punctatum* by Tweedie (1940, 1950a,b) from Aor Island (East coast of Peninsular Malaysia) and Borneo, and by Soh (1978) from Hong Kong, as referable to *N. indicum* (see Davie, 1994).

Yeo et al. (1999) reported *N. indicum* from Tioman Island (East coast of Peninsular Malaysia) and provided taxonomic and morphological notes, and added a few information on the ecology. These authors stated that this species can be found in “habitats ranging from estuaries to mangrove to almost pure freshwaters beyond tidal influence” and it has been observed “some distance away from the nearest water”, being therefore adapted to terrestrial conditions (Yeo et al., 1999). Tweedie (1940) recorded this species [as *Sesarma* (*Sarmatium*) *punctata*] from a brackish swamp on Aor Island (South China Sea), from the banks of a small stream, near its entry into to the sea. Both Tweedie (1940) and Yeo et al. (1999) stated that this species builds deep burrows in soft clay sediment, and it is active at night. Ng et al. (1997, 2001) reported this species from Taiwan, while Schubart and Ng

(2002) recorded it from a stream bank in Philippines.

Islam et al. (2002) and Sarker et al. (2012) reported *N. indicum* from Japan, where it has been found from mangrove stands of *Kandelia candel*. In particular, Islam et al. (2002) provided a description of the zoeal and megalopal morphology, while Sarker et al. (2012) described the embryonic development of the eggs before hatching.

Figure 3.19: ***Neosarmatium indicum.*** Male specimen. From the reference collection of the Raffles Museum of Biodiversity Research in Singapore (Lee Kong Chian Natural History Museum, National University of Singapore), visited by the author in 2011-2012. Specimen number: ZRC 2000-1842. Dorsal (above), ventral (middle) and frontal view (below). Scales are in mm.

Table 3.30: List of the studies conducted on *Neosarmatium indicum*.

Author and Year	Subject of the study	Field	Country
A. Milne-Edwards 1868a	species description as *Metagrapsus indicus* (Celebes = Sulawesi, Indonesia)	taxonomy	Indonesia
De Man 1887	as *Sarmatium indicum* (no new locality); morphological and taxonomic notes	taxonomy	IWP
De Man 1892	as *Sarmatium indicum* (Macassar = Sulawesi, Indonesia); morphometric measurements	distribution record (only)	Indonesia
Nobili 1903b	as *Sarmatium indicum* (Seychelles)	distribution record (only)	Seychelles Islands
Tweedie 1940	as *Sesarma* (*Sarmatium*) *punctata*; new distribution record (Aor Island, Peninsular Malaysia), ecological notes	distribution record (only)	Malaysia (Peninsular Malaysia)
Tweedie 1950a	as *Sesarma indica* and as *Sesarma punctata*; new distribution record (Labuan, East Malaysia); taxonomic notes	taxonomy	Malaysia (East Malaysia)
Tweedie 1950b	as *Sesarma punctata*; new distribution record (Aor Island, Peninsular Malaysia)	distribution record (only)	Malaysia (Peninsular Malaysia)
Soh 1978	as *Neosarmatium punctatum*, new distribution record (Hong Kong)	distribution record (only)	Hong Kong
Ng et al. 1997	new distribution record (Taiwan)	distribution record (only)	Taiwan
Yeo et al. 1999	new distribution record (Tioman Island, Peninsular Malaysia); taxonomic, morphological and ecological notes	taxonomy / spatial ecology	Malaysia (Peninsular Malaysia)
Ng et al. 2001	checklist of the brachyuran crabs from Taiwan	distribution record (only)	Taiwan
Islam et al. 2002	new distribution record (Japan); larval morphology, description of 5 zoeal stages and megalopa	ontogenesis	Japan
Schubart & Ng 2002	new distribution record (Philippines)	distribution record (only)	Philippines
Sarker et al. 2012	description of the embryo development (Japan)	ontogenesis	Japan

3.3.8.3 *Neosarmatium smithi* (H. Milne-Edwards, 1853)

This species has been described as *Sesarma smithi* by H. Milne-Edwards (1853) from South Africa. One year later, the same author provided a further description (H. Milne-Edwards, 1854). A. Milne-Edwards (1868b), Hoffmann (1874) and De Man (1880) reported it from East Africa and Madagascar, and provided additional morphological and taxonomic notes. De Man (1887) added a few notes on the morphology, while Bürger (1893) recorded it from the Philippines, and provided detailed morphological and taxonomic notes, and morphometric measurements.

Subsequently, several works reported this species from a wide range of localities. Rathbun (1910a), Miyake (1936) and Sakai (1939) reported it as *Sesarma* (*Sesarma*) *smithi* from Thailand and Japan. Tweedie (1936) recorded it from Singapore as *Sesarma* (*Sarmatium*) *smithi*, while Barnard (1950) and Chhapgar (1957) added new records from South Africa [as *Sesarma* (*Sesarma*) *smithii*] and India (as *Sesarma oceanica*), respectively. Crosnier (1965) and Vannini and Valmori (1981) reported this species from Madagascar and Somalia. Haig (1984) and Pinto (1984) recorded it from Seychelles and Sri Lanka, respectively. Sakai (1976) and Hirata et al. (1988) reported it from Japan, while Dai and Yang (1991) added a record from China. Marshall and Medway (1976) recorded it from the New Hebrids (South West Pacific).

Figure 3.20: ***Neosarmatium smithi.*** Male specimen. From the reference collection of the Raffles Museum of Biodiversity Research in Singapore (Lee Kong Chian Natural History Museum, National University of Singapore), visited by the author in 2011-2012. Specimen number: ZRC 2012-0276. Dorsal (above), ventral (middle) and frontal view (below). Scales are in mm.

In his review of the genus *Neosarmatium*, Davie (1994) reported this species also from Peninsular Malaysia and Philippines, and added taxonomic and morphological notes. Kwok and Tang (2005) and Trivedi et al. (2015) added new records from Hong Kong and India, respectively. Emmerson (1994a) provided additional notes on the morphology, taxonomy, and ecology of *N. smithi* from South Africa.

As Davie (1994) pointed out, previous works have confused this species with the sister species *N. trispinosum*, which is distributed in the southwestern Pacific region (eastern Australia, New Caledonia, New Guinea, Vanuatu, Fiji). Therefore, several studies citing *N. smithi* are actually referring to *N. trispinosum* (A. Milne-Edwards, 1873; De Man, 1889, 1890; Nobili, 1899; McCulloch, 1913; Giddins et al., 1986; Neilson et al., 1986; Neilson & Richards, 1989). Moreover, also ecological studies conducted in Australia and New Caledonia on *N. smithi* (Smith, 1987; Robertson & Daniel, 1989; Micheli, 1993; Ng & Richer De Forges, 2007) may instead refer to *N. trispinosum*.

Several studies have investigated ecological aspects of *N. smithi*, including its spatial and temporal distribution (Dahdouh-Guebas et al., 2002; Bosire et al., 2004; Priyadarshani et al., 2008; Cannicci et al., 2009; Leh et al., 2010; Dissanayake & Chandrasekara, 2014; Peer et al., 2014), feeding ecology (Masagca, 2009), burrowing ecology (Gillikin et al., 2001; Masagca, 2009; Andreetta et al., 2014), and ecophysiology (Gillikin et al., 2004).

Dahdouh-Guebas et al. (2002) investigated the link between the distribution of particular mangrove tree species and the distribution of certain crab species in Kenya. In particular, *N. smithi* was found in association with the mangrove species *Rhizophora mucronata*, in the seaward part of the studied forest, in contrast with the congeneric *N. meinerti*, which occupied instead an *Avicennia marina* landward zone (Dahdouh-Guebas et al., 2002).

In a study on the recolonisation by crabs and other macrofauna in artificially regenerated mangrove stands (Kenya), Bosire et al. (2004) reported *N. smithi* from open sandy patches in an *Avicennia marina* site, where the forest had been cleared. These areas were characterised by higher salinity (saltwater) and temperature, and lower soil organic contents than the forested areas (Bosire et al., 2004), thus suggesting that this species is able to adapt to extreme environmental conditions found in disturbed areas.

Priyadarshani et al. (2008) studied the distribution of mangrove crabs and their correlation with environmental parameters in a mangrove system in the Negombo Estuary (Sri Lanka). *N. smithi* was recorded both in a *Rhizophora*/*Bruguiera* zone and in an *Avicennia*/*Lumnitzera* zone. It was found to be positively correlated with the soil salinity, soil moisture content, soil organic carbon content, and soil pH, although the correlation was not statistically significant (Priyadarshani et al., 2008).

Cannicci et al. (2009) investigated the differences in macrobenthic patterns between peri-urban mangroves, affected by sewage disposal, and control sites not affected by urban wastewater (East Africa). In particular, these authors found *N. smithi* in both kinds of mangrove sites, particularly abundant in *Rhizophora* zones (Cannicci et al., 2009). Leh et al. (2010) collected this species from a disturbed mangrove area in Selangor (Peninsular Malaysia), where most of the trees had been cut and the soil was partially covered by wooden debris.

Dissanayake and Chandrasekara (2014) studies the influence of mangrove zonation and soil physicochemical parameters on the distribution of macrobenthic fauna (Sri Lanka). These authors recorded *N. smithi* from an *Avicennia* zone, characterised by relatively high soil moisture and organic matter content.

In a study on the temporal variation of brachyuran crabs in the St. Lucia Estuary (South Africa), Peer et al. (2014) pointed out that *N. smithi* has been reported from this system only in 2012, while it has not recorded in previous studies, ranging from 1948 to 2011. In particular, this area hosts a large lake system, which is often isolated from the sea, and therefore experiences periodic fluctuations in physico-chemical parameters, due to flood and drought events. *N. smithi* was found in a mangrove forest at the mouth of the estuary, and along nearby inlets (Peer et al., 2014).

Fratini et al. (2000) investigated the competition and interspecific interaction between *N. smithi* and the gastropod *Terebralia palustris* in a Kenyan mangrove system. Both these species feed on decaying mangrove leaves, and share the same spatial niche and feeding time frame. They compete with each other by utilising different feeding strategies (e.g. crabs store the leaves in burrows, and gastropods crawl onto the leaf *en masse*, to prevent the crabs from removing the leaf).

Masagca (2009) conducted qualitative observations on the feeding and burrowing behaviour of several sesarmid species from the Philippines, including also *N. smithi*. This species was observed feeding mainly on the mangrove litter, composed of decaying *Rhizophora* leaves, seedlings, calyxes and twigs. This author observed this species also feeding on shrimps of the genus *Palaemonetes*, during day time, at flood tide (Masagca, 2009). Moreover, *N. smithi* was found burrowing among *Rhizhophora* roots, and the times of emergence and re-emergence from the burrows were measured (Masagca, 2009).

Gillikin et al. (2001) investigated the occurrence of the semi-terrestrial shrimp *Merguia oligodon* (Hippolytidae) in *N. smithi* burrows from Kenya. These shrimps were found in the horizontal shaft of the burrow, and they were observed consuming *N. smithi* faeces, which were also proven to be a valid dietary supply in a laboratory experiment (Gillikin et al., 2001).

Andreetta et al. (2014) investigated the effects of the macrobenthos burrowing activity on the organic carbon storage in mangrove soils (Kenya). The study involved several crab species, including *N. smithi*, one of the dominant species of leaf-litter consumers and burrowers in the studied area (Andreetta et al., 2014).

Gillikin et al. (2004) conducted physiological tests on the long-term effect of salinity alterations on the bio-energetics of *N. smithi* and *N. meinerti* (today *N. africanum*) in Kenya. The results suggested that both these species would be negatively affected by long-term alterations of mangrove salinity regimes, which were happening in the studied area due to groundwater re-direction (Gillikin et al., 2004). In particular, these authors stated that *N. smithi* occupies the lower *Rhizophora mucronata* zone, usually inundated daily, with salinity ranging from 21‰ to 53‰ (Gillikin et al., 2004).

Table 3.31: List of the studies conducted on *Neosarmatium smithi.*

Author and Year	Subject of the study	Field	Country
H. Milne-Edwards 1853	species description as *Sesarma smithii* (South Africa)	taxonomy	South Africa
H. Milne-Edwards 1854	as *Sesarma smithii*; taxonomic and morphological notes (South Africa)	taxonomy	South Africa
A. Milne-Edwards 1868b	as *Sesarma smithii*; new distribution record (East Africa, Madagascar)	distribution record (only)	East Africa, Madagascar
Hoffmann 1874	as *Sesarma smithi*; new distribution record (Madagascar)	distribution record (only)	Madagascar
De Man 1880	as *Sesarma smithii*, new distribution record (Madagascar)	distribution record (only)	Madagascar
De Man 1887	as *Sesarma smithi*; morphological and taxonomic notes	taxonomy	IWP
Bürger 1893	as *Sesarma smithi*; new distribution record (Philippines), morphological and taxonomic notes, morphometric measurements	taxonomy	Philippines
Rathbun 1910a	as *Sesarma* (*Sesarma*) *smithi*, new distribution record (Thailand)	distribution record (only)	Thailand
Tesch 1917	morphological and taxonomic notes; species included in checklist and in diagnostic key of sesarmid species	taxonomy	IWP
Miyake 1936	as *Sesarma* (*Sesarma*) *smithi*; new distribution record (Japan)	distribution record (only)	Japan
Tweedie 1936	as *Sesarma* (*Sarmatium*) *smithii*; new distribution record (Singapore); *Sesarma* (*Sesarma*) *smithii* transferred to the subgenus *Sesarma* (*Sarmatium*) *smithii*	taxonomy	Singapore
Sakai 1939	as *Sesarma* (*Sesarma*) *smithi*; new distribution record (Japan)	distribution record (only)	Japan
Barnard 1950	as *Sesarma* (*Sesarma*) *smithii*; new distribution record (South Africa)	distribution record (only)	South Africa
Chhapgar 1957	as *Sesarma oceanica*; new distribution record (India)	distribution record (only)	India
Crosnier 1965	as *Sesarma* (*Sesarma*) *smithii*; taxonomy, presentation of the sesarmid and grapsoid species of Madagascar	taxonomy	Madagascar

Table 3.31, continued.

Marshall & Medway 1976	new distribution record (New Hebrids, West Pacific); mangrove community zonation and composition	spatial ecology	New Hebrids
Sakai 1976	new distribution record (Japan)	distribution record (only)	Japan
Vannini & Valmori 1981	checklist of grapsoid species from Somalia	distribution record (only)	Somalia
Haig 1984	as *Sesarma smithi*; new distribution record (Seychelles)	distribution record (only)	Seychelles
Pinto 1984	new distribution record (Sri Lanka)	distribution record (only)	Sri Lanka
Dai et al. 1986	new distribution record (China)	distribution record (only)	China
Smith 1987	feeding ecology, seed predation by grapsoid crabs in mangrove forests (Australia), effects of predation on tree distribution patterns; this study may refer to another species, *N. trispinosum*	feeding ecology	Australia
Hirata et al. 1988	new distribution record (Japan)	distribution record (only)	Japan
Robertson & Daniel 1989	feeding ecology, influence of crabs on mangrove litter processing (Australia); this study may refer to another species, *N. trispinosum*	feeding ecology	Australia
Dai & Yang 1991	new distribution record (China)	distribution record (only)	China
Micheli 1993	feeding ecology, mangrove litter consumption, food preferences, foraging activity (Australia); this study may refer to another species, *N. trispinosum*	feeding ecology	Australia
Davie 1994	new distribution record (Kuala Selangor, Peninsular Malaysia, Philippines); taxonomic, morphological and ecological notes	taxonomy	Malaysia (Peninsular Malaysia), Philippines
Emmerson 1994a	taxonomic notes from South Africa	taxonomy	South Africa
Fratini et al. 2000	competition and interaction between *N. smithi* and *Terebralia palustris* (Gastropoda) foraging on decaying mangrove leaves (Kenya)	feeding ecology	Kenya

Table 3.31, continued.

Gillikin et al. 2001	occurrence of the semi-terrestrial shrimp *Merguia oligodon* in *N. smithi* burrows (Kenya)	burrowing ecology	Kenya
Dahdouh-Guebas et al. 2002	zonation of mangroves species and grapsoid crabs, and mutual relationships (Kenya)	spatial ecology	Kenya
Bosire et al. 2004	ecology, spatial variation in macrobenthos in a post-recolonisation mangrove forest (Kenya)	spatial ecology	Kenya
Gillikin et al. 2004	physiological responses of *N. meinerti* and *N. smithi* exposed to altered salinity regimes (Kenya)	physiology	Kenya
Kwok & Tang 2005	checklist of the sesarmid crabs of Hong Kong, ecological and taxonomic notes, key to the species	taxonomy / spatial ecology	Hong Kong
Ng & Richer De Forges 2007	checklist of brachyuran crabs from New Caledonia; this study may refer to another species, *N. trispinosum*	distribution record (only)	New Caledonia
Priyadarshani et al. 2008	diversity of mangrove crabs in Negombo estuary (Sri Lanka)	distribution record (only)	Sri Lanka
Cannicci et al. 2009	ecology, effect of urban wastewater on mangrove crab and mollusc assemblages of East Africa	spatial ecology	Kenya, Mozambique
Masagca 2009	feeding ecology, burrowing behaviour and arboreal climbing skills of sesarmid crabs in Luzon (Philippines)	feeding ecology / burrowing	Philippines
Leh et al. 2010	biomass and abundance of sesarmid crabs in a natural and disturbed mangrove area in Selangor (Peninsular Malaysia)	spatial ecology	Malaysia (Peninsular Malaysia)
Andreetta et al. 2014	role of burrowing crabs on sediment carbon storage (Kenya)	burrowing ecology	Kenya
Dissanayake & Chandrasekara 2014	effects of mangrove zonation and soil parameters on macrobenthic fauna (Sri Lanka)	spatial ecology	Sri Lanka
Peer et al. 2014	temporal variation of crab diversity in St. Lucia Estuary (South Africa)	spatial ecology	South Africa
Trivedi et al. 2015	checklist of crustacean fauna of Gujarat (India)	distribution record (only)	India

3.3.8.4 *Neosarmatium spinicarpus* Davie, 1994

This species was described by Davie (1994), from Sarawak (Borneo), in his review of the genus *Neosarmatium*.

Tweedie (1940, 1950a) recorded this species as *Sesarma* (*Sarmatium*) *inermis* from a nipah forest in Johor (Peninsular Malaysia), and a freshwater ditch in Sarawak (Borneo), and the first work provided morphometric measurements of the examined specimens. However, Davie (1994) stated that the specimens from Peninsular Malaysia are juveniles, and their identity is not fully certain. The distribution record from this area must therefore be considered as tentative.

Davie (1994) pointed out that *N. inerme* and *N. spinicarpus* are considered aberrant species within the genus *Neosarmatium*, for "having more slender walking legs and by the much shorter, stockier male first pleopod, which has the distal portion short, not strongly narrowed, and only slightly twisted compared with other *Neosarmatium* species" (Davie, 1994, p. 47).

The ecology and biology of this species is practically unknown.

Table 3.32: List of the studies conducted on *Neosarmatium spinicarpus*.

Author and Year	Subject of the study	Field	Country
Tweedie 1940	as *Sesarma* (*Sarmatium*) *inermis*; new distribution records (Johor, Peninsular Malaysia); morphometric measurements	distribution record (only)	Malaysia (Peninsular Malaysia)
Tweedie 1950a	as *Sesarma* (*Sarmatium*) *inermis*; new distribution record (Sarawak, East Malaysia)	distribution record (only)	Malaysia (East Malaysia)
Davie 1994	species description; morphological, historical, ecological notes	taxonomy / spatial ecology	IWP

3.3.9 Genus *Neosesarma* Serène & Soh, 1970

The genus *Neosesarma* has been described by Serène and Soh (1970) to include species characterised by a row of regular dactylar tubercles on the male cheliped, a longitudinal pectinated crest separated from the inner margin on the upper part of male palm, an antero-lateral tooth acute and separated by a deep sulcus from the external orbital angle, and a second smaller tooth clearly marked (Serène & Soh, 1970). Davie (2012) provided a revision of the genus with a diagnostic key to the species, added new distribution records, and described a new species from Australia.

The genus currently includes three species, *N. hirsutum*, *N. gemmiferum* and *N. rectipectinatum*, which have been recorded from mangrove riverine environments in the Peninsular Malaysia (Tweedie, 1936), Borneo (Tweedie, 1950a), Vietnam (Diele et al., 2013), and Australia (Davie, 2012). Two species previously included in the genus *Neosesarma*, namely *N. aequifrons* and *N. laeve*, have been trasferred to the genus *Neosarmatium* (Davie, 1994).

Two species have been recorded from Peninsular Malaysia, Singapore, and/or northern Borneo:

- *N. gemmiferum* (Tweedie, 1936)
- *N. rectipectinatum* (Tweedie, 1950)

Table 3.33: List of the main studies conducted on the genus *Neosesarma* (including taxonomic studies and reviews of the genus).

Author and Year	Subject of the study
Serène & Soh 1970	genus description
Davie 2012	genus revision, key to the species, description of a new species

3.3.9.1 *Neosesarma gemmiferum* (Tweedie, 1936)

This species has been described by Tweedie (1936) as *Sesarma* (*Sesarma*) *gemmifera* from the Johor Strait, Singapore, and the West coast of Peninsular Malaysia (Port Swettenham = Port Klang, Selangor). In particular, this author collected his samples from mangrove swamps, estuarine and riverine environments.

Later, Tweedie (1950a) reported the species as *Sesarma gemmifera* from a river system in Sarawak (Borneo). More recently, *N. gemmiferum* has been reported from a *Rhizophora apiculata* mangrove forest in Vietnam, by Diele et al. (2013). In his revision of the genus, Davie (2012) reported that this species has been found in mangrove areas, in soft muddy areas, and often associated with crevices in trees and fallen logs.

Table 3.34: List of the studies conducted on *Neosesarma gemmiferum*.

Author and Year	**Subject of the study**	**Field**	**Country**
Tweedie 1936	species description as *Sesarma* (*Sesarma*) *gemmifera* from Johor Strait; Singapore; Port Klang, Selangor, Peninsular Malaysia	taxonomy	Malaysia (Peninsular Malaysia), Singapore
Tweedie 1950a	as *Sesarma gemmifera*; new distribution record (Sarawak, East Malaysia)	distribution record (only)	Malaysia (East Malaysia)
Davie 2012	revision of genus; re-description of the species, ecological notes	taxonomy	Singapore
Diele et al. 2013	impact of typhoon on diversity of key ecosystem engineers (Vietnam)	spatial ecology	Vietnam

Figure 3.21: ***Neosesarma gemmiferum.*** Male specimen. From the reference collection of the Raffles Museum of Biodiversity Research in Singapore (Lee Kong Chian Natural History Museum, National University of Singapore), visited by the author in 2011-2012. Specimen number: ZRC 2000.1966. Dorsal (above), ventral (middle) and frontal view (below). Scales are in mm.

3.3.9.2 *Neosesarma rectipectinatum* (Tweedie, 1950)

This species has been described as *Sesarma rectipectinata* by Tweedie (1950a) from Labuan (East Malaysia). More recently, Rahayu and Setyadi (2009) reported this species from Indonesia, and Davie (2012) recorded it from Singapore and Australia.

Davie (2012) noted that *N. rectipectinatum* has been found in mangrove forests, in soft muddy areas, often associated with crevices in trees and fallen logs. It has been observed in burrows and on open substrate among *Avicennia* pneumatophores; it has been found also in burrows in steep eroding banks, and it prefers zones inundated by most tides, in the lower and middle part of estuaries (Davie, 2012).

Table 3.35: List of the studies conducted on *Neosesarma rectipectinatum*.

Author and Year	Subject of the study	Field	Country
Tweedie 1950a	species description (as *Sesarma rectipectinata*) from Labuan (East Malaysia)	taxonomy	Malaysia (East Malaysia)
Rahayu & Setyadi 2009	new distribution records (Papua, Indonesia)	distribution record (only)	Indonesia
Davie 2012	revision of genus; re-description of the species, ecological notes, new distribution records (Singapore, Australia)	taxonomy	Singapore, Australia

Figure 3.22: ***Neosesarma rectipectinatum.*** Male specimen. From the reference collection of the Raffles Museum of Biodiversity Research in Singapore (Lee Kong Chian Natural History Museum, National University of Singapore), visited by the author in 2011-2012. Specimen number: ZRC 2000.1974. Dorsal (above), ventral (middle) and frontal view (below). Scales are in mm.

3.3.10 Genus *Parasesarma* De Man, 1895

The genus *Parasesarma* De Man, 1895 currently includes 58 species (see review of the genus by Shahdadi & Schubart, 2017, and new species by Shahdadi et al., 2017, 2018a), distributed through the whole IWP region.

The genus has been described by De Man (1895), as *Sesarma* (*Parasesarma*), thus considered a subgenus of the genus *Sesarma*. This author also provided a key to the species included in the subgenus at that time, namely *Sesarma* (*Parasesarma*) *picta*, *S*. (*P.*) *leptosoma*, *S*. (*P.*) *quadrata*, *S*. (*P.*) *calypso*, *S*. (*P.*) *erythrodactyla*, *S*. (*P.*) *lenzii*, *S*. (*P.*) *bataviana*, *S*. (*P.*) *moluccensis*, and *S*. (*P.*) *melissa* (De Man, 1895).

Subsequently, Serène and Soh (1970) elevated this subgenus to the generic level. The genus was initially characterised by the absence of an anterolateral tooth, and the presence of dactylar tubercles and pectinated crests on the palm of the male chelipeds (De Man, 1895; Serène & Soh, 1970).

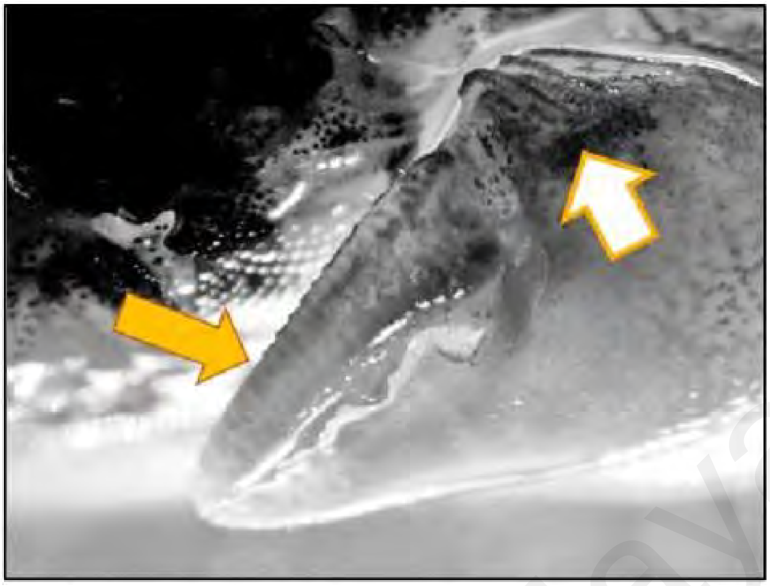

Figure 3.23. Example of *Parasesarma* specimen showing the detail of the cheliped. Preserved specimen of *P. batavianum* from the reference collection from Tanjung Tuan (Negeri Sembilan). The arrows show the dactylar tubercles (*filled arrow*) and the pectinated crests on the propodus (*empty arrow*). Pictures has been taken under a stereomicroscope.

Several authors have pointed out that the taxonomy of this genus is one of the most complex among sesarmid crabs, with many of the species being poorly known and insufficiently described (e.g. Koller et al., 2010; Rahayu & Ng, 2010; Rahayu & Li, 2013).

One species, *Parasesarma lanchesteri* (Tweedie, 1936), has been erroneously included in the genus *Perisesarma* by Ng et al. (2008). In his revision of this genus, Davie (2010) rectified the mistake and placed this species again in the genus *Parasesarma.*

Recently, a taxonomic and molecular study by Shahdadi and Schubart (2017) reviewed the closely allied genera *Parasesarma* and *Perisesarma*, and discussed the use of the anterolateral tooth as a diagnostic character. The results prompted these authors to transfer to *Parasesarma* 18 of the species previously included in *Perisesarma* (Shahdadi & Schubart, 2017).

Most of the species of this genus have been reported from mangrove ecosystems, although a few species have been found on rocky substrates (under rocks in river banks, *P. cognatum*, Rahayu & Li, 2013; on rocky walls along a freshwater river estuary, *P. liho*, Koller et al., 2010).

Within mangrove forests, *Parasesarma* species are generally found along the whole intertidal gradient, from the pioneer shore to the high forest (e.g. Sasekumar, 1974; Ashton et al., 2003a,b; Ravichandran et al., 2007). Some of the species have been observed to be active burrowers (Stieglitz et al., 2000), and they largely contribute to the leaf litter processing (Lee, 1989; Lee & Kwok, 2002; Gillikin & Schubart, 2004). However, the biology and ecology of many of the species are almost unknown (Rahayu & Li, 2013; see also Subchapters 3.3.10.1-3.3.10.15).

The larval morphology has been described for several species, including *P. acis* (Terada, 1976), *P. bidens* (Fukuda & Baba, 1976), *P. catenata* (Pereyra Lago, 1987; Flores et al., 2003), *P. erythrodactyla* (Greenwood & Fielder, 1988), *P. guttatum* (Pereyra Lago, 1993; Flores et al., 2003), *P. leptosoma* (Flores et al., 2003), *P. messa* (Greenwood & Fielder, 1988), *P. pictum* (Pasupathi & Kannupandi, 1987), *P. plicatum* (Fukuda & Baba, 1976; Selvakumar, 1999). More recently, Guerao et al. (2004) provided a review of larval and juvenile morphological characters of *Parasesarma*, and compared them with other species of the genus *Perisesarma*, which is considered systematically very close (Fratini et al., 2005).

Sixteen species have been recorded from Peninsular Malaysia, Singapore, and/or northern Borneo:

- *P. batavianum* (De Man, 1890)
- *P. calypso* (De Man, 1895)
- *P. eumolpe* (De Man, 1895)
- *P. indiarum* (Tweedie, 1940)
- *P. kuekenthali* (De Man, 1902)
- *P. lanchesteri* (Tweedie, 1936)
- *P. lenzii* (De Man, 1894)
- *P. lepidum* (Tweedie, 1950)
- *P. melissa* (De Man, 1887)
- *P. onychophorum* (De Man, 1895)
- *P. peninsulare* Shahdadi, Ng & Schubart, 2018
- *P. plicatum* (Latreille, 1803)
- *P. raouli* Rahayu & Ng, 2009
- *P. rutilimanum* (Tweedie, 1936)
- *P. semperi* (Bürger, 1893)
- *P. ungulatum* (H. Milne Edwards, 1853)

Table 3.36: List of the main studies conducted on the genus *Parasesarma* (including taxonomic studies and reviews of the genus).

Author and Year	Subject of the study
De Man 1895	genus description as subgenus *Sesarma* (*Parasesarma*); key to the species [*S.* (*P.*) *picta*, *S.* (*P.*) *leptosoma*, *S.* (*P.*) *quadrata*, *S.* (*P.*) *calypso*, *S.* (*P.*) *erythrodactyla*, *S.* (*P.*) *lenzii*, *S.* (*P.*) *bataviana*, *S.* (*P.*) *moluccensis*, *S.* (*P.*) *melissa*]
Serène and Soh 1970	subgenus *Sesarma* (*Parasesarma*) moved to genus level (*Parasesarma*)
Guerao et al. 2004	comparison of larval and juvenile morphology of *Perisesarma* and *Parasesarma*
Shahdadi & Schubart 2017	systematic review of the genera *Parasesarma* and *Perisesarma*

3.3.10.1 *Parasesarma batavianum* (De Man, 1890)

This species was described as *Sesarma bataviana* by De Man (1890) from Jakarta (Indonesia). De Man (1895) included it in the newly established subgenus *Sesarma* (*Parasesarma*), while Tesch (1917) cited it in his synopsis of the Indo-West Pacific species of sesarmid crabs, as *Sesarma* (*Parasesarma*) *bataviana*, and added a new record from the northern coast of Java (Indonesia).

Tweedie (1936) recorded this species as *Sesarma* (*Parasesarma*) *bataviana* from a riverine environment in Singapore and from the Johor Strait (Peninsular Malaysia). More recently, Pratiwi and Rahmat (2015) reported this species from the reference collection of the Research Centre for Oceanografi, Indonesian Institute of Sciences (LIPI), collected from 1960 to 1970 (Indonesia).

The ecology and biology of this species are practically unknown.

Figure 3.24: ***Parasesarma batavianum.*** Male specimen (TT_260912_siteB_8 from the Peninsular Malaysia collection, loc. Tanjung Tuan, see Chapter 4). Dorsal (above), ventral (middle) and frontal view (below). CW= 1.02 cm.

Table 3.37: List of the studies conducted on *Parasesarma batavianum*.

Author and Year	Subject of the study	Field	Country
De Man 1890	species description (as *Sesarma bataviana*) from Batavia (today Jakarta, Indonesia)	taxonomy	Indonesia
De Man 1895	species transferred to the newly established subgenus *Sesarma* (*Parasesarma*)	taxonomy	Indonesia
Tesch 1917	examination of De Man 1890 specimens (Batavia) and other specimens (northern coast of Java); species included in checklist and in diagnostic key of sesarmid species	taxonomy	Indonesia
Tweedie 1936	as *Sesarma* (*Parasesarma*) *bataviana*; new distribution records (Singapore; Johor Strait)	distribution record (only)	Singapore, Malaysia (Peninsular Malaysia)
Pratiwi & Rahmat 2015	checklist of brachyuran crabs in the reference collection at the Research Centre for Oceanografi, Indonesian Institute of Sciences (LIPI) collected from 1960 to 1970 (Indonesia)	distribution record (only)	Indonesia

3.3.10.2 *Parasesarma calypso* (De Man, 1895)

This species has been described by De Man (1895), as *Sesarma* (*Parasesarma*) *calypso*, from Aceh (Sumatra, Indonesia). Nobili (1900) added a few morphological and taxonomic notes, while Lanchester (1900a,b) recorded it as *Sesarma calypso* from Malacca (Peninsular Malaysia) and Borneo. However, some of these specimens have later been considered as a new species, *Parasesarma calypso* var. *kükenthali*, by De Man (1902), which also added morphological and taxonomic notes (see also Subchapter 3.3.10.5). Tweedie (1936) reported this species from the Simalur Island (West coast of Sumatra).

The ecology and biology of this species are practically unknown.

Table 3.38: List of the studies conducted on *Parasesarma calypso*.

Author and Year	Subject of the study	Field	Country
De Man 1895	species description [as *Sesarma* (*Parasesarma*) *calypso*] from Atjeh (today Aceh, Sumatra, Indonesia)	taxonomy	Indonesia
Lanchester 1900a	new distribution records (Malacca, Peninsular Malaysia); morphological and taxonomic notes	taxonomy	Malaysia (Peninsular Malaysia)
Lanchester 1900b	new distribution records (Sarawak, Borneo)	distribution record (only)	Malaysia (East Malaysia)
Nobili 1900	taxonomic and morphological notes	taxonomy	Indonesia
De Man 1902	morphological and taxonomic notes, some of the specimens transferred to a new species (*P. kuekentali*)	taxonomy	Indonesia, Malaysia
Tesch 1917	examination of the Leiden Museum collection (co-types De Man 1895); species included in checklist and in diagnostic key of sesarmid species	taxonomy	Indonesia, Malaysia
Tweedie 1936	as *Sesarma* (*Parasesarma*) *calypso*; new distribution records (Sumatra, Indonesia)	distribution record (only)	Indonesia

3.3.10.3 *Parasesarma eumolpe* (De Man, 1895)

This species has been described as *Sesarma* (*Perisesarma*) *eumolpe* by De Man (1895), from Penang (Peninsular Malaysia). Tesch (1917) and Tweedie (1936) reported it as *Sesarma* (*Chiromantes*) *eumolpe* and added new records from western Indonesia, Singapore, and the West coast of Peninsular Malaysia.

Although included into the genus *Perisesarma* until very recently, a taxonomic and molecular study by Shahdadi and Schubart (2017) transferred it to the genus *Parasesarma*. Moreover, in their paper on the new species *Parasesarma peninsulare* (see Subchapter 3.3.10.11), Shahdadi et al. (2018a) provided a description and taxonomic remarks for *P. eumolpe*. These authors also stated that this species may actually be a species-complex, and it will be therefore revised (Shahdadi et al., 2018a).

This species has been recorded in several studies on mangrove biodiversity and ecology from Thailand (Lundoer, 1974; Frith et al., 1976; Poovachiranon & Tantichodok, 1991; Thongtham et al., 2008), Singapore and Peninsular Malaysia (Berry, 1972; Sasekumar, 1974; Zakaria & Sasekumar, 1994; Ashton, 2002; Ashton et al., 2003a; Boon et al., 2008; Taufek, 2013), Borneo (Choy, 1991; Choy & Booth, 1994; Ashton et al., 2003b), Philippines (Masagca, 2009), and Indonesia (Pratiwi & Widyastuti, 2013).

Berry (1972) included *P. eumolpe* in his account on the mangrove macrofauna of the West coast of Peninsular Malaysia, where it was collected from the middle and upper part of the forest, and from the banks of tidal creeks and rivers. Sasekumar (1974) reported this species from the landward zone of an estuarine mangrove forest (Selangor, Peninsular Malaysia), in an area dominated by *Bruguiera parviflora* and *Rhizophora mucronata* tree species. Frith et al. (1976) found *P. eumolpe* in the landward area of their investigated mangrove forest (Thailand), in saltwater salinity conditions, on muddy substrate. The site was previously disturbed by burning and cutting activities, and subsequently colonised by sparse *Nypa fruticans* and *Phoenix paludosa* palms. *P. eumolpe* was also reported from a survey conducted on the macroinvertebrates of a *Bruguiera parviflora* and *Rhizophora* spp. forest in Selangor (Peninsular Malaysia) by Zakaria and Sasekumar (1994). This species was collected both from the intact portion of the forest, and from an adjacent area where the forest had been cleared (Zakaria & Sasekumar, 1994). Choy and Booth (1994) recorded this species from an *Avicennia* dominated coastal wetland.

Ashton et al. (2003a) recorded this species from mangrove forests in Peninsular Malaysia under different management systems: the partially managed Merbok estuary (Kedah), the heavily exploited Matang forest reserve (Perak), and the nature reserve of Kuala Selangor Nature Park (Selangor). *P. eumolpe* was found to be one of the dominant crab species in term of abundance and biomass in two studies on the abundance and diversity of mangrove macrofauna in the Sematan estuary (Sarawak, Borneo; Ashton et al., 2003b), and in the Setiu coastal lagoon (Terengganu, Peninsular Malaysia; Taufek, 2013).

Leh and Sasekumar (1985) investigated the gut contents, the leaf consumption and faeces excretion rates of this species, which was found to feed mainly on mangrove plant materials (91% of the volumetric gut composition), and in smaller percentages on mineral debris (4%), brachyuran debris (2%), and insects (1%). In a study on the role of sesarmid crabs on the mineralization of mangrove leaf litter (Thailand), Poovachiranon and Tantichodok (1991) investigated the gut contents of *P. eumolpe*, which were mainly composed of vascular plants and sediment.

Ashton (2002) conducted feeding experiments in the field and in laboratory on two sesarmid species, *P. eumolpe* and *P. onychophorum* (Peninsular Malaysia). In particular, this author conducted food preference experiments, in which fresh and senescent leaves of different mangrove species were offered to the crabs. The results showed no difference in mangrove species when senescent leaves were offered, while significantly more *Avicennia officinalis* leaves were consumed when the leaves were fresh, by both crab species. Moreover, *P. onychophorum* fed significantly more on *Bruguiera parviflora* than did *P. eumolpe* (Ashton 2002). The field experiments also found that crab distribution was related to the preferred tree species, suggesting that tree species and crab species distributions are related and may be mutually influenced (Ashton, 2002).

Boon et al. (2008) investigated the feeding ecology of *P. eumolpe* and *P. indiarum* (today considered *P. peninsulare*, see Subchapter 3.3.10.11) from Singapore, through field and laboratory experiments on leaf species preferences, leaf age preferences, and feeding rates on leaves. Their results suggested that both species are mainly sediment grazers, but they also feed on mangrove leaves, roots, and occasionally animal matter (Boon et al., 2008). Moreover, both species prefer *Avicennia alba* leaves to other mangrove species, and there is no significant preference for leaves of different ages (Boon et al., 2008).

In a study on the feeding, burrowing and tree climbing behaviour of sesarmid crabs (Philippines), Masacga (2009) reported that *P. eumolpe* was observed feeding on mangrove litter, composed of fallen *Rhizophora* leaves, seedlings, calyx and twigs. Additionally, this author classified this species as a burrowing, non-climbing species (Masagca, 2009).

Sasekumar and Ooi (2005) reported this species as *Chiromantes eumolpe* from Langkawi (Peninsular Malaysia), from riverine mangrove stands dominated by *Rhizophora mucronata* mature trees, or *Rhizophora apiculata* and *Ceriops tagal* younger trees. Sasekumar and Moh (2010) recorded this species from Kelantan (Peninsular Malaysia), from estuarine mangrove patches, in an area heavily reclaimed for prawn aquaculture. In particular, *P. eumolpe* has been collected from *Rhizophora apiculata* stands under sustainable management, on muddy soil with mud lobsters mounds, from an artificial brackish lagoon with small stands of *Sonneratia alba* seedlings and *Avicennia marina* trees, and from an estuary temporarily closed by a sand bar, dominated by *Nypa fruticans*, *Hibiscus*, *Intsia* and *Casuarina* species (Sasekumar & Moh, 2010). Leh et al. (2010) collected *P. eumolpe* from a mangrove site in Selangor (Peninsular Malaysia), from both an undisturbed forest area and from a cleared area, rich in fallen trunks and debris.

Figure 3.25: ***Parasesarma eumolpe.*** Male specimen (KS_boleo_091113_8, from the Peninsular Malaysia collection, loc. Kuala Selangor, see Chapter 4). Dorsal (above), ventral (middle) and frontal view (below). Scale is in cm.

A few studies investigated the colouration of the facial bands of this species (Huang et al., 2008; Todd et al., 2011; Wang & Todd, 2012), which are characteristic of both male and female specimens of *P. eumolpe* and *P. indiarum* (today partly considered *P. peninsulare*, see Subchapter 3.3.10.11).

Huang et al. (2008) first determined quantitatively the relationship between sex, size and facial colour, using a low-cost photographic technique. These authors found significant differences in the colouration both between sexes and among different sizes; these results suggested a role of the facial bands in intraspecific sexual recognition, and as a indicator of the crab maturity (Huang et al., 2008).

Todd et al. (2011) studied the role of the facial bands in communication and intraspecific interactions, through choice experiments. In particular, they found that facial bands brightness and saturation changed with the nutritional status, and that an artificial manipulation of the facial bands had significant effects on the crabs interactions (Todd et al., 2011). In the choice experiments, male crabs consistently chose females with natural colour compared to females with the facial band blacked out; moreover, male crabs defending burrows responded differently to male con-specific intruders with blacked out facial bands compared to non-blacked out controls (Todd et al., 2011).

Wang and Todd (2012) extracted and analysed the facial bands tissues, in order to investigate the presence of carotenoids, as possible responsible pigment for the colouration. Their results confirmed the presence of carotenoids in the facial bands of this species, which can be obtained from dietary sources (Wang & Todd, 2012).

A few authors reported or investigated the acoustic behavior of this species (Tweedie, 1954; Boon et al., 2009; Chen et al., 2014, 2017). Tweedie (1954) presented a review on visual and acoustic signalling by grapsoid crabs through stridulation. This author reported for the first time the stridulation behaviour in a male specimen of *P. eumolpe*, which was observed in the field, rubbing the dactylar tubercles of the chelipeds against each other, after a successful confrontation with another male, possibly a victory display (Tweedie, 1954).

Boon et al. (2009) investigated the sound production and reception in *P. eumolpe* and *P. indiarum* (today considered as *P. peninsulare*, see Subchapter 3.3.10.11) from Singapore. This study found that only male crabs display acoustically, and only during agonistic interactions. Moreover, the results revealed key species-specific differences in the morphology of the stridulatory organs, stridulatory movements and resulting sounds produced. These findings suggested a role of the acoustic signalling in the social behaviour of mangrove sesarmid crabs (Boon et al., 2009).

Chen et al. (2014) conducted an ethological study to investigate whether the acoustic stridulations performed by *P. eumolpe* are post-contest victory displays, as suggested by a previous author (Tweedie, 1954). Their results showed that such displays were generally performed by winners and after fights, and stridulation was observed only during contests, suggesting that stridulation in this species is likely to be a victory display (Chen et al., 2014).

Chen et al. (2017) investigated the function of victory displays in this species, by testing whether the performance of such displays by winning specimens affects the time of fight re-initiation by the losing specimens. Their results suggested that victory displays actually discourage losers from restarting a fight, therefore allowing winners to reduce the potential costs of future contests (Chen et al., 2017).

Table 3.39: List of the studies conducted on *Parasesarma eumolpe*.

Author and Year	Subject of the study	Field	Country
De Man 1895	species description as *Sesarma* (*Perisesarma*) *eumolpe* (Penang, Peninsular Malaysia)	taxonomy	Malaysia (Peninsular Malaysia)
Tesch 1917	as *Sesarma* (*Chiromantes*) *eumolpe*; examination of the Leiden Museum collection; new distribution records (Batavia = Jakarta, North coast of Java, Indonesia); morphological and taxonomic notes; species included in checklist and in diagnostic key of sesarmid species	taxonomy	Indonesia
Tweedie 1936	as *Sesarma* (*Chiromantes*) *eumolpe*; new distribution records (Singapore and neighbouring islands; Johor Strait; Port Swettenham = Port Klang, Peninsular Malaysia)	distribution record (only)	Malaysia (Peninsular Malaysia), Singapore
Tweedie 1954	acoustic and visual signalling in grapsoid crabs (Peninsular Malaysia)	behaviour / social interactions	Malaysia (Peninsular Malaysia)
Berry 1972	mangrove macrofauna of the West coast of Peninsular Malaysia	spatial ecology	Malaysia (Peninsular Malaysia)
Lundoer 1974	as *Chiromantes eumolpe*; checklist of brachyuran crabs in the reference collection at Phuket Marine Biology Center (Thailand)	distribution record (only)	Thailand
Sasekumar 1974	as *Sesarma* (*Chiromantes*) *eumolpe*; distribution, abundance and zonation of mangrove macrofauna (polychaetes, gastropods, crustaceans, sipunculids, fishes) in Port Klang (Peninsular Malaysia)	spatial ecology	Malaysia (Peninsular Malaysia)
Frith et al. 1976	zonation and abundance of mangrove macrofauna on Phuket Island (Thailand)	spatial ecology	Thailand
Leh & Sasekumar 1985	food composition in the gut contents of Malaysian sesarmid crabs (Selangor, Peninsular Malaysia)	feeding ecology	Malaysia (Peninsular Malaysia)
Choy 1991	as *Chiromantes eumolpe*; checklist of Crustacea of Brunei Darussalam	distribution record (only)	Brunei Darussalam
Poovachiranon & Tantichodok 1991	role of sesarmid crabs in the mineralization of mangrove leaf litter (Thailand)	feeding ecology	Thailand

Table 3.39, continued.

Choy & Booth 1994	macrofaunal community in a *Avicennia* dominated coastal wetland (Brunei Darussalam) before and after an inundation event	spatial ecology	Brunei Darussalam
Zakaria & Sasekumar 1994	macroinvertebrate fauna in cleared and intact mangrove forests in Selangor (Peninsular Malaysia)	spatial ecology	Malaysia (Peninsular Malaysia)
Ashton 2002	feeding ecology, mangrove leaf species and leaf age preferences of *Perisesarma eumolpe* and *P. onychophorum* (Kedah, Peninsular Malaysia)	feeding ecology	Malaysia (Peninsular Malaysia)
Ashton et al. 2003a	new distribution records (Merbok; Matang; Kuala Selangor); brachyuran community structure in four mangrove sites under different management systems (Malaysia, Thailand)	spatial ecology	Malaysia (Peninsular Malaysia, Thailand
Ashton et al. 2003b	ecology and diversity of crab and mollusc macrofaunal community in the Sematan mangrove forest (Sarawak, East Malaysia)	spatial ecology	Malaysia (East Malaysia)
Sasekumar & Ooi 2005	as *Chiromanthes eumolpe*; faunal diversity in Langkawi mangrove forests (Peninsular Malaysia)	spatial ecology	Malaysia (Peninsular Malaysia)
Boon et al. 2008	feeding ecology, mangrove leaf species and leaf age preferences of *Perisesarma eumolpe* and *P. indiarum* (today *P. peninsulare*), feeding rates, field and laboratory experiments (Singapore)	feeding ecology	Singapore
Huang et al. 2008	inter- and intraspecific variation in the facial colours of *Perisesarma eumolpe* and *P. indiarum* (today *P. peninsulare*) (Singapore)	anatomy / morphology	Singapore
Boon et al. 2009	acoustic communication, sound production and reception in *Perisesarma eumolpe* and *P. indiarum* (today *P. peninsulare*) (Singapore)	behaviour / social interactions	Singapore
Masagca 2009	feeding ecology, burrowing behaviour and arboreal climbing skills of sesarmid crabs in Luzon (Philippines)	feeding ecology / burrowing	Philippines
Leh et al. 2010	biomass and abundance of sesarmid crabs in a natural and disturbed mangrove area in Selangor (Peninsular Malaysia)	spatial ecology	Malaysia (Peninsular Malaysia)
Sasekumar & Moh 2010	flora and fauna diversity of Bachok mangrove forest (Kelantan, Peninsular Malaysia)	spatial ecology	Peninsular Malaysia

Table 3.39, continued.

Todd et al. 2011	function of colourful facial bands in intraspecific communication and mate choice in *Perisesarma eumolpe* and *P. indiarum* (today *P. peninsulare*)	behaviour / social interactions	Singapore
Wang & Todd 2012	carotenoid pigments in facial bands of *Perisesarma eumolpe* and *P. indiarum* (today *P. peninsulare*) (Singapore)	physiology / anatomy	Singapore
Taufek 2013	crab community structure in Setiu lagoon (Terengganu, Peninsular Malaysia)	spatial ecology	Malaysia (Peninsular Malaysia)
Chen et al. 2014	use of post-contest stridulation as a victory display in *P. eumolpe* (Singapore)	behaviour / social interactions	Singapore
Pratiwi & Widyastuti 2013	distribution and zonation of mangrove crustaceans in Lampung Bay (Indonesia)	spatial ecology	Indonesia
Chen et al. 2017	function of the victory display in *P. eumolpe* (Singapore)	behaviour / social interactions	Singapore
Shahdadi & Schubart 2017	systematic review of the genera *Parasesarma* and *Perisesarma*; *P. eumolpe* transferred to *Parasesarma*	taxonomy / systematics	IWP
Shahdadi et al. 2018a	taxonomic redescription and remarks	taxonomy / systematics	IWP

3.3.10.4 *Parasesarma indiarum* (Tweedie, 1940)

This species was first described as *Sesarma bidens* var. *indica*, a subspecies of *Sesarma bidens*, by De Man (1902), from the Maluku Islands (Indonesia). Tesch (1917) added new distribution records (New Guinea, Java) and provided additional taxonomic notes. Tweedie (1936, 1940) reported it from Singapore, Peninsular Malaysia, and Sumatra. The latter study provided also a new name for the taxon, *Sesarma bidens indiarum*, and added morphological and taxonomic notes. Subsequently, this species has been included in the genera *Chiromantes* or *Perisesarma* until very recently, when Shahdadi and Schubart (2017) transferred it to *Parasesarma*, on the base of morphological and molecular data.

Tweedie (1950a), Choy (1991) and Choy and Booth (1994) recorded it from Borneo (as *Sesarma bidens indiarum*, and *Chiromantes indiarum*, respectively). Lundoer (1974) and Pratiwi and Rahmat (2015) reported it from Thailand (as *Chiromantes indiarum*), and Indonesia (as *Perisesarma indiarum*), respectively.

Shahdadi et al. (2018a) recently re-examined numerous specimens of *P. indiarum* from different geographic areas (Peninsular Malaysia, Indonesia, Thailand, Singapore), and established a new species (*P. peninsulare*, see Subchapter 3.3.10.11) for all these specimens, except the ones from Ambon (Indonesia). These authors also stated that the specimens collected from Borneo (not included in their analysis) will need to be re-examined, and they may probably belong to a new undescribed species.

P. indiarum has been reported from several studies on the distribution of mangrove macrofauna (as *Chiromantes indiarum*, Frith et al., 1976; Frith, 1977; as *Perisesarma indiarum*, Ashton et al., 2003b; Kon et al., 2010), feeding ecology (as *Perisesarma indiarum*, Boon et al., 2008), interspecific interactions (as *Perisesarma indiarum*, Kon et al., 2009), visual and acoustic behaviour (as *Perisesarma indiarum*, Huang et al., 2008; Boon et al., 2009; Todd et al., 2011; Wang & Todd, 2012). However, according to the distribution area stated by Shahdadi et al. (2018) for this species, most of these studies are probably referring to *P. peninsulare*.

Choy and Booth (1994) reported this species in an *Avicennia* dominated coastal wetland (Brunei Darussalam). Ashton et al. (2003b) recorded it from a plot of their transects (Sarawak), containing a large *Sonneratia alba* tree, a few dead *Bruguiera gymnorrhiza* trees, and numerous *Rhizophora* saplings and seedlings (see also Ashton & Macintosh, 2002).

Figure 3.26: ***Parasesarma indiarum.*** Male specimen (Muara_011213_7, from the Brunei Bay collection, loc. Pemburongunan Creek, see Chapter 4). Dorsal (above), ventral (middle) and frontal view (below). CW = 1.53 cm.

Table 3.40: List of the studies conducted on *Parasesarma indiarum*.

Author and Year	Subject of the study	Field	Country
De Man 1902	species description as *Sesarma bidens* var. *indica*, subspecies of *S. bidens* (from Amboina = Ambon and Ternate, Indonesia)	taxonomy	Indonesia
Tesch 1917	as *Sesarma* (*Chiromantes*) *bidens indica*; morphological and taxonomic notes; species included in checklist and in diagnostic key of sesarmid species	taxonomy	Indonesia
Tweedie 1950a	as *Sesarma bidens indiarum*; new distribution record (Labuan, East Malaysia); morphological notes	taxonomy	Malaysia (East Malaysia)
Choy 1991	as *Chiromantes indiarum*; checklist of Crustacea of Brunei Darussalam	distribution record (only)	Brunei Darussalam
Choy & Booth 1994	macrofaunal community in a *Avicennia* dominated coastal wetland (Brunei Darussalam) before and after an inundation event	spatial ecology	Brunei Darussalam
Ashton et al. 2003b	ecology and diversity of crab and mollusc macrofaunal community in the Sematan mangrove forest (Sarawak, East Malaysia)	spatial ecology	Malaysia (East Malaysia)
Pratiwi & Rahmat 2015	checklist of brachyuran crabs in the reference collection at the Research Centre for Oceanografi, Indonesian Institute of Sciences (LIPI) collected from 1960 to 1970 (Indonesia)	distribution record (only)	Indonesia
Shahdadi & Schubart 2017	systematic review of the genera *Parasesarma* and *Perisesarma* ; *P. indiarum* transferred to *Parasesarma*	taxonomy / systematics	IWP
Shahdadi et al. 2018a	specimens from several localities (Peninsular Malaysia, West Indonesia, Thailand, Singapore) transferred to a new species (*P. peninsulare*, see Subchapter 3.3.10.11)	taxonomy	IWP

3.3.10.5 *Parasesarma kuekenthali* (De Man, 1902)

This species has been described as *Sesarma* (*Parasesarma*) *calypso* var. *kükenthali* by De Man (1902) from Halmahera (Maluku Islands, Indonesia) and from a freshwater environment in Soah Konorah (Maluku Islands, Indonesia). This author included also several specimens previously considered as *Sesarma* (*Parasesarma*) *calypso*, collected from Malacca (Peninsular Malaysia) and Borneo by Lanchester (1900a,b), Aceh (Indonesia) by De Man (1895). De Man (1902) stated that these species has been found in Malacca (Peninsular Malaysia) by Nobili (1900), even though this author stated instead that his sample locality was unknown.

Serène and Moosa (1971) reported this species from Ambon (Indonesia), and provided a few taxonomic and morphological notes. Marshall and Medway (1976) recorded *P. kuekenthali* from a *Rhizophora* spp. forest in the New Hebrids (South West Pacific).

The biology and ecology of this species are practically unknown.

Table 3.41: List of the studies conducted on *Parasesarma kuekenthali.*

Author and Year	Subject of the study	Field	Country
De Man 1895	as *Sesarma* (*Parasesarma*) *calypso*, distribution record from Atjeh (today Aceh, Sumatra, Indonesia), morphological and taxonomic notes	taxonomy	Indonesia
Lanchester 1900a	new distribution records (Malacca, Peninsular Malaysia)	distribution record (only)	Malaysia (Peninsular Malaysia)
Lanchester 1900b	as *Sesarma* (*Parasesarma*) *calypso*, new distribution records (Sarawak, East Malaysia)	distribution record (only)	Malaysia (East Malaysia)
Nobili 1900	as *Sesarma* (*Parasesarma*) *calypso*, taxonomic and morphological notes, no new locality	taxonomy	-

Table 3.41, continued.

De Man 1902	species description as *Sesarma* (*Parasesarma*) *calypso* var. *kükenthali* (Maluku Islands, Indonesia; Malacca, Peninsular Malaysia; Aceh, Indonesia; Borneo)	taxonomy	Malaysia (Peninsular Malaysia and East Malaysia), Indonesia
Tesch 1917	as *Sesarma* (*Parasesarma*) *calypso* var. *kükenthali*; species included in checklist and in diagnostic key of sesarmid species	taxonomy	IWP
Serène & Moosa 1971	new distribution record (Ambon, Indonesia); morphological and taxonomic notes	taxonomy	Indonesia
Marshall & Medway 1976	new distribution record (New Hebrids, West Pacific); mangrove community zonation and composition	spatial ecology	New Hebrids

3.3.10.6 *Parasesarma lanchesteri* (Tweedie, 1936)

This species has been described by Tweedie (1936) as *Sesarma* (*Parasesarma*) *calypso lanchesteri*, a subspecies of *Sesarma* (*Parasesarma*) *calypso*, from a mangrove swamp in Singapore.

Tweedie (1950a) reported it from a riverine environment in Sarawak (Borneo), added morphological and taxonomic notes, and considered it as a distinct species, *Sesarma lanchesteri*. This species has been erroneously placed in the genus *Perisesarma* by Ng et al. (2008), while Davie (2010) rectified the mistake and transferred it again to *Parasesarma*.

The ecology and biology of *P. lanchesteri* are practically unknown.

Table 3.42: List of the studies conducted on *Parasesarma lanchesteri*.

Author and Year	Subject of the study	Field	Country
Tweedie 1936	species description as *Sesarma* (*Parasesarma*) *calypso lanchesteri* (from Singapore)	taxonomy	Singapore
Tweedie 1950a	as *Sesarma lanchesteri*; new distribution records (Sarawak, East Malaysia); morphological and taxonomic notes; subspecies [*Sesarma* (*Parasesarma*) *calypso lanchesteri*] elevated to species level (*Sesarma lanchesteri*)	taxonomy	Malaysia (East Malaysia)

3.3.10.7 *Parasesarma lenzii* (De Man, 1895)

This species has been described as *Sesarma* (*Parasesarma*) *lenzii* by De Man (1895) from Aceh (Indonesia) and Penang (Peninsular Malaysia). De Man (1902) added a new distribution record from Halmahera (Indonesia) and provided further morphological and taxonomic notes, and morphometric measurements.

Tesch (1917) included this species in his synopsis of the IWP sesarmid crabs, and suggested that some of the specimens from the Fiji Islands, previously collected by De Man (1889) and attributed to *Sesarma melissa*, are instead *P. lenzii*. This data has been confirmed later by McLay and Ryan (1990), in their review on the state of knowledge of the grapsid crabs of the Fiji Islands. Crosnier (1965) reported this species as *Sesarma* (*Parasesarma*) *lenzii* from Madagascar, and provided morphological and taxonomic notes for his specimens.

Macintosh et al. (2002) recorded this species in an ecological study from the West coast of Thailand. In this study, this species was found to be particularly abundant in an upstream area of a natural, mixed, mature mangrove forest that has been protected for over 40 years. In particular, this site was characterised by large earth mounds of the mud lobster

Thalassina anomala throughout the forest, which influenced this site to have a higher average shore level (Macintosh et al., 2002).

Ashton et al. (2003a) reported this species as *Sesarma lenzii* from the West coast of Thailand and Peninsular Malaysia, in an ecological study on the brachyuran communities of several study sites under different management systems. In particular, this species was found both in a natural mangrove forest and in monotypic *Rhizophora* spp. mangrove plantations (Ashton et al., 2003a).

This species was recorded as *Parasesarma lenzii* from Sarawak (Borneo) by Ashton et al. (2003b), in an ecological study on the macrofaunal communities of an estuarine mangrove forest reserve. In particular, this species was found both in an upstream and in a downstream area along the Sematan River, in plots with brackish salinity conditions, and mixed vegetation (*Bruguiera cylindrica*, *B. gymnorrhiza*, *Rhizophora apiculata*, *Xylocarpus granatum*, *Ceriops tagal*, *Pandanus odoratissimus*, *Acanthus ilicifolius*). The area was also colonised by mounds of the mud lobster *Thalassina anomala* (Ashton et al., 2003b; see also Ashton & Macintosh, 2002).

Tab. 3.43: List of the studies conducted on *Parasesarma lenzii.*

Author and Year	Subject of the study	Field	Country
De Man 1895	species description [as *Sesarma* (*Parasesarma*) *lenzii*] from Atjeh (today Aceh, Indonesia) and Penang (Peninsular Malaysia)	taxonomy	Indonesia, Malaysia (Peninsular Malaysia)
De Man 1902	morphological and taxonomic notes; new distribution records (Halmahera, Indonesia); morphometric measurements	taxonomy	Indonesia
Tesch 1917	new distribution record (Fiji Islands); species included in checklist and in diagnostic key of sesarmid species	distribution record (only)	Fiji Islands
Crosnier 1965	as *Sesarma lenzi*, new distribution record (Madagascar); morphological and taxonomic notes	taxonomy	Madagascar
McLay & Ryan 1990	review on the state of knowledge on sesarmid crabs in Fiji Islands	distribution record (only)	Fiji Islands
Macintosh et al. 2002	ecology-conservation, intertidal diversity and mangrove rehabilitation in the Ranong mangrove system (Thailand)	spatial ecology	Thailand
Ashton et al. 2003a	new distribution records (Klong Ngao, Thailand; Merbok, Peninsular Malaysia); brachyuran community structure in four mangrove sites under different management systems	spatial ecology	Thailand, Malaysia (Peninsular Malaysia)
Ashton et al. 2003b	ecology and diversity of crab and mollusc macrofaunal community in the Sematan mangrove forest (Sarawak, East Malaysia)	spatial ecology	Malaysia (East Malaysia)

3.3.10.8 *Parasesarma lepidum* (Tweedie, 1950)

This species has been described as *Sesarma lepida* by Tweedie (1950a) from Labuan (East Malaysia). In his description, Tweedie (1950a) considered this species as belonging to the "group (*Parasesarma*)", although he did not formally move it to this subgenus.

Serène and Moosa (1971) recorded this species as *Parasesarma lepidium* from Ambon (Indonesia) and provided a few morphometric measurements. Lundoer (1974) reported this species in his checklist of the brachyuran species in the reference collection at Phuket Marine Biology Center (Thailand), collected from a mangrove forest area.

The ecology and biology of this species are practically unknown.

Table 3.44: List of the studies conducted on *Parasesarma lepidum*.

Author and Year	Subject of the study	Field	Country
Tweedie 1950a	Species description as *Sesarma lepida* (Labuan, East Malaysia)	taxonomy	Malaysia (East Malaysia)
Serène & Moosa 1971	new distribution record (Ambon, Indonesia); morphometric measurements	taxonomy	Indonesia
Lundoer 1974	checklist of brachyuran crabs in the reference collection at Phuket Marine Biology Center (Thailand)	distribution record (only)	Thailand

Figure 3.27: ***Parasesarma lepidum***. Male specimen. From the reference collection of the Raffles Museum of Biodiversity Research in Singapore (Lee Kong Chian Natural History Museum, National University of Singapore), visited by the author in 2011-2012. Specimen number: ZRC 1964-9-3-466-487. Dorsal (above), ventral (middle) and frontal view (below left), and detail of the cheliped (below right). The specimen has been preserved for several years (collected in 1964), therefore the original colouration has completely disappeared. Scales are in mm.

3.3.10.9 *Parasesarma melissa* (De Man, 1887)

This species was described from the Mergui Archipelago (Myanmar) by De Man (1887), as *Sesarma melissa*. De Man (1888, 1895) reported this species from the Mergui Archipelago (Myanmar) and Penang (Peninsular Malaysia), and added morphological and taxonomic notes, and morphometric measurements. In particular, De Man (1895) included the species in the subgenus *Sesarma* (*Parasesarma*). Tesch (1917) cited the species as *Sesarma* (*Parasesarma*) *melissa* in his synopsis of the IWP species of sesarmid crabs.

Tweedie (1936) reported this species from Singapore and the Johor Strait, and Port Swettenham (today Port Klang, Peninsular Malaysia), while Lundoer (1974) recorded it from a mangrove forest area in Thailand. Berry (1972) recorded it as *Sesarma melissum* from mangrove systems on the West coast of Peninsular Malaysia, where it was collected from “the sides of streams flowing through the forest”.

Sasekumar (1974) reported this species as *Sesarma* (*Parasesarma*) *melissum* from an estuarine mangrove forests in Selangor (West coast of Peninsular Malaysia), where it was found in forest areas with fine sand/silty substrate and brackish to saltwater salinity conditions. The vegetation was dominated by *Bruguiera parviflora* and *Rhizophora mucronata*, with few *Bruguiera gymnorhiza* and *Xylocarpus granatum* (Sasekumar, 1974).

Leh et al. (2010) reported it from a upper intertidal mangrove area in Selangor (Peninsular Malaysia). In particular, these authors collected their specimens in the 1980s, from an unvegetated area of the forest where trees had been cut a few months before (Leh et al., 2010).

Figure 3.28: ***Parasesarma melissa.*** Male specimen (LK_ayer-hangat151113_site1_6 from the Peninsular Malaysia collection, loc. Langkawi, see Chapter 4). Dorsal (above), ventral (middle) and frontal view (below). CW= 1.18 cm.

Table 3.45: List of the studies conducted on *Parasesarma melissa*.

Author and Year	Subject of the study	Field	Country
De Man 1887	species description as *Sesarma melissa* (from Mergui Archipelago, Myanmar)	taxonomy	Myanmar
De Man 1888	as *Sesarma melissa*; new distribution records (Mergui Archipelago, Myanmar)	distribution record (only)	Myanmar
De Man 1895	as *Sesarma* (*Parasesarma*) *melissa*; new distribution records (Penang, Peninsular Malaysia); morphological and taxonomic notes; morphometric measurements	taxonomy	Malaysia (Peninsular Malaysia)
Tesch 1917	species included in checklist and in diagnostic key of sesarmid species	taxonomy	IWP
Tweedie 1936	as *Sesarma* (*Parasesarma*) *melissa*; new distribution records (Singapore; Johor Strait; Port Swettenham = Port Klang, Selangor, Peninsular Malaysia)	distribution record (only)	Singapore, Malaysia (Peninsular Malaysia)
Berry 1972	mangrove macrofauna of the West coast of Peninsular Malaysia	spatial ecology	Malaysia (Peninsular Malaysia)
Lundoer 1974	checklist of brachyuran crabs in the reference collection at Phuket Marine Biology Center (Thailand)	distribution record (only)	Thailand
Sasekumar 1974	distribution, abundance and zonation of mangrove macrofauna in Port Klang (Peninsular Malaysia)	spatial ecology	Malaysia (Peninsular Malaysia)
Leh et al. 2010	biomass and abundance of sesarmid crabs in a natural and disturbed mangrove area in Selangor (Peninsular Malaysia)	spatial ecology	Malaysia (Peninsular Malaysia)

3.3.10.10 *Parasesarma onychophorum* (De Man, 1895)

This species has been first described as *Sesarma livida* by De Man (1888), from Myanmar. A few years later, De Man (1895) described the same taxon as *Sesarma* (*Perisesarma*) *onychophora*, from Penang (Peninsular Malaysia), Aceh (Indonesia), and Borneo.

Lanchester (1900a) recorded it as *Sesarma onychophora* from Singapore, and Tesch (1917) added a new record from Sumatra (Indonesia). Tweedie (1936) reported this species as *Sesarma* (*Chiromantes*) *onychophora* from Peninsular Malaysia and Lundoer (1974) recorded it as *Chiromantes onychophorum* from Thailand. More recently, this species have been considered as belonging to the genus *Perisesarma* (see Davie, 2010), until a morphological and molecular study by Shahdadi and Schubart (2017) transferred it to the genus *Parasesarma*.

The ecology of *P. onychophorum* has been investigated in a few studies on the distribution and zonation of mangrove macrofauna (Berry, 1972; Sasekumar, 1974; Macintosh et al., 2002; Ashton et al., 2003a,b), and on the mangrove foodwebs and feeding ecology (Malley, 1978; Rodelli et al., 1984; Ashton, 2002).

Berry (1972) included this species in his account on the mangrove macrofauna of the West coast of Peninsular Malaysia, where it was found in the seaward eroding bank, in the middle portion of the forest, and along the banks of creeks and river crossing the forest. Sasekumar (1974) reported it from most of his study area, hosting an estuarine mangrove forest consisting mainly of *Bruguiera* and *Rhizophora* spp. trees, on a sandy-muddy substrate, in brackish to saltwater salinity conditions (Selangor, Peninsular Malaysia).

Macintosh et al. (2002) conducted a study on the intertidal macrofaunal diversity in the Ranong Biosphere Reserve (Thailand). These authors reported *P. onychophorum* from an abandoned shrimp farm area, which had been recently rehabilitated by planting four mangrove species (*Rhizophora apiculata*, *R. mucronata*, *Bruguiera cylindrica* and *Ceriops tagal*). Ashton et al. (2003a) recorded this species from all their investigated sites (Thailand and Peninsular Malaysia), which were undergoing different management conditions, namely a recently rehabilitated forest reserve, a partially exploited forest, an heavily exploited forest, and a nature park. Ashton et al. (2003b) found *P. onychophorum* in a few plots of their study area (Sarawak, Borneo), with a mixed vegetation composition (*Bruguiera* spp., *Rhizophora* spp., *Xylocarpus* spp., *Avicennia* spp.), on muddy substrate (see also Ashton & Macintosh, 2002). Leh et al. (2010) reported this species in a study from an upper intertidal mangrove site in Selangor (Peninsular Malaysia), where it was collected both from a undisturbed area of the forest, and from an unvegetated area, where trees had been cleared a few months before the sampling sessions.

Malley (1978) analysed the gut contents of *P. onychophorum* from Penang (Peninsular Malaysia), in order to elucidate the role of this species in the breakdown of mangrove leaf litter to detrital-sized particles. The results suggested that this species consumes fallen leaves or their fragments, incompletely digests them, and returns them to the environment as faecal matter in a more finely-divided state, thus contributing to the mangrove leaf degradation to litter detritus (Malley, 1978).

Rodelli et al. (1984) conducted a study on the ratio of stable carbon isotopes ($\delta^{13}C$) in plants and animals from Malaysian mangrove swamps, coastal inlets, and offshore waters, in order to explore the trophic position of the different taxa, and the dynamics of the mangrove foodweb. In particular, *P. onychophorum* isotopic values were relatively close to those of the mangrove leaves and detritus, therefore suggesting an herbivorous diet of this species (Rodelli et al., 1984).

Leh and Sasekumar (1985) investigated the gut contents of several species of sesarmid crabs from Selangor (Peninsular Malaysia), including also *P. onychophorum*. This species was found to be primarily vegetarian, feeding mainly on mangrove plant material (83% of the gut volumetric composition), and in smaller percentage on mineral and brachyuran debris, and insects (17%) (Leh & Sasekumar, 1985). These authors also conducted experiments on leaf consumption and faeces excretion on this species, and calculated daily consumption rates (Leh & Sasekumar, 1985).

Ashton (2002) investigated the food preference in the field and in laboratory of two sesarmid species, *P. eumolpe* and *P. onychophorum* in Peninsular Malaysia (see also Subchapter 3.3.10.3).

Macintosh (1988) provided information on several ecological and physiological aspects. In particular, *P. onychophorum* was considered as the representative species for the habitat category of "open habitats within mixed forest up to MHWS (mean high water level at spring tide)", and it was observed utilising hollow tree trunks, fallen logs and debris as alternative refuges (Macintosh, 1988). Moreover, this author reported this species as having a relatively high tolerance to low salinity values, which allows it to inhabit the middle and upper intertidal zones. This species was also found to follow a lunar frequency in the breeding activity, regulating the larval release endogenously to coincide with the highest spring tides (Macintosh, 1988).

Figure 3.29: ***Parasesarma onychophorum.*** Male specimen (PK_261212_17, from the Peninsular Malaysia collection, loc. Pulau Kukup, see Chapter 4). Dorsal (above), ventral (middle) and frontal view (below). CW = 2.25 cm.

Table 3.46: List of the studies conducted on *Parasesarma onychophorum*.

Author and Year	Subject of the study	Field	Country
De Man 1888	species description as *Sesarma livida* (Mergui Archipelago, Myanmar)	taxonomy	Myanmar
De Man 1895	species description as *Sesarma* (*Perisesarma*) *onychophora* (Penang, Peninsular Malaysia; Atjeh = Aceh, Indonesia; Pontianak, Kalimantan, Indonesia)	taxonomy	Malaysia (Peninsular Malaysia), Indonesia
Lanchester 1900a	new distribution records as *Sesarma onychophora* (Singapore)	distribution record (only)	Singapore
Tesch 1917	as *Sesarma* (*Chiromantes*) *onychophora*; new distribution record (Sumatra, Indonesia); species included in checklist and in diagnostic key of sesarmid species	distribution record (only)	Indonesia
Tweedie 1936	as *Sesarma* (*Chiromantes*) *onychophora*; new distribution records (Port Swettenham = Port Klang, Penang, Peninsular Malaysia)	distribution record (only)	Malaysia (Peninsular Malaysia)
Berry 1972	mangrove macrofauna of the West coast of Peninsular Malaysia	spatial ecology	Malaysia (Peninsular Malaysia)
Lundoer 1974	checklist of brachyuran crabs in the reference collection at Phuket Marine Biology Center (Thailand)	distribution record (only)	Thailand
Sasekumar 1974	distribution, abundance and zonation of mangrove macrofauna in Port Klang (Peninsular Malaysia)	spatial ecology	Malaysia (Peninsular Malaysia)
Malley 1978	feeding ecology, degradation of mangrove leaf litter, gut contents (Penang, Peninsular Malaysia)	feeding ecology	Malaysia (Peninsular Malaysia)
Rodelli et al. 1984	stable isotope ratio as a carbon tracer in mangrove ecosystems (West coast Peninsular Malaysia)	feeding ecology	Malaysia (Peninsular Malaysia)
Leh & Sasekumar 1985	food composition in the gut contents of Malaysian sesarmid crabs (Selangor, Peninsular Malaysia)	feeding ecology	Malaysia (Peninsular Malaysia)
Macintosh 1988	ecology and physiology of decapods in mangrove swamps	spatial ecology	IWP

Table 3.46, continued.

Ashton 2002	feeding ecology, mangrove leaf species and leaf age preferences of *Perisesarma eumolpe* and *P. onychophorum* (Kedah, Peninsular Malaysia)	feeding ecology	Malaysia (Peninsular Malaysia)
Macintosh et al. 2002	ecology-conservation, intertidal diversity and mangrove rehabilitation in the Ranong mangrove system (Thailand)	spatial ecology	Thailand
Ashton et al. 2003a	new distribution records (Klong Ngao, Thailand; Merbok, Matang, Kuala Selangor, Peninsular Malaysia); brachyuran community structure in four mangrove sites under different management systems	spatial ecology	Thailand, Malaysia (Peninsular Malaysia)
Ashton et al. 2003b	ecology and diversity of crab and mollusc macrofaunal community in the Sematan mangrove forest (Sarawak, East Malaysia)	spatial ecology	Malaysia (East Malaysia)
Leh et al. 2010	biomass and abundance of sesarmid crabs in a natural and disturbed mangrove area in Selangor (Peninsular Malaysia)	spatial ecology	Malaysia (Peninsular Malaysia)
Shahdadi & Schubart 2017	systematic review of the genera *Parasesarma* and *Perisesarma*; *P. onychophorum* transferred to *Parasesarma*	taxonomy / systematics	IWP

3.3.10.11 *Parasesarma peninsulare* Shahdadi, Ng & Schubart, 2018

This species has been recently described by Shahdadi et al. (2018a), to accommodate specimens previously included in *P. indiarum*. In particular, these authors conducted morphological and molecular analyses on specimens from several localities across South East Asia, and stated that most of the previous records of *P. indiarum* (from Peninsular Malaysia, Thailand, west Indonesia) have to be considered as belonging to a new species, *P. peninsulare* (Shahdadi et al., 2018a). The distribution range of *P. indiarum* is instead limited to Ambon (Indonesia).

In this study, we recorded *P. indiarum* both from the Peninsular Malaysia and Borneo (see Chapter 4). However, taxonomic discrimination of the specimens was made before Shahdadi et al. (2018a) described their new species. Moreover, these authors did not include specimens from Borneo in their analysis, and they also stated that samples from Bornean assemblages will need to be re-examined, since they may belong to a new undescribed species. Therefore, both *P. indiarum* and *P. peninsulare* were included in this synopsis.

Several studies reporting *P. indiarum* are most likely referring to *P. peninsulare* (Frith et al., 1976; Frith, 1977; Ashton et al., 2003b; Boon et al., 2008, 2009; Huang et al., 2008; Kon et al., 2009, 2010; Boon et al., 2009; Todd et al., 2011; Adachi et al., 2012; Wang & Todd, 2012).

Frith et al. (1976) found this species (as *Chiromantes indiarum*) in a landward fringe of a mangrove forest (Thailand), on a muddy substrate, in saltwater salinity conditions. The area was previously disturbed by burning and cutting activities, and subsequently recolonised by sparse *Nypa fruticans* and *Phoenix paludosa* palms (Frith et al., 1976).

Frith (1977) recorded this species (as *Chiromantes indiarum*) from the landward zone of the investigated mangrove forest (Thailand), on sandy substrate, in a relatively open area with a few *Bruguiera gymnorhiza* trees, and from a dense forest of *B. gymnorhiza* mixed with a few *Rhizophora mucronata* trees.

P. peninsulare was one of the main species investigated in a study on the impacts of canopy shade and root structure on physical environment (temperature, moisture and grain size of the substrate), benthic faunal distribution, and food resource availability (recorded as *Perisesarma indiarum*, Thailand, Kon et al., 2010).

In a study on the feeding ecology of *P. eumolpe* and *P. indiarum* (today considered *P. peninsulare*) from Singapore, Boon et al. (2008) found similar results for both the investigated species (see also Subchapter 3.3.10.3). In particular, both species were found to be mainly sediment grazers, but they also feed on mangrove leaves, roots, and occasionally animal matter. They also prefer *Avicennia alba* leaves to other mangrove species, and they exhibit no significant preference for leaves of differing ages (Boon et al., 2008).

Kon et al. (2009) chose this species (as *Perisesarma indiarum*) to investigate the role of mangrove root structures as shelter from predators for benthic animals. In particular, these authors studied the impact of predation on benthic faunal communities in a mangrove forest through a predator exclusion experiment, and the uses of mangrove root structures by benthic animals through a laboratory experiment (Kon et al., 2009).

A few studies investigated the visual and acoustic interactions of this species (reported as *Perisesarma indiarum*; Huang et al., 2008; Boon et al., 2009; Todd et al., 2011; Wang & Todd, 2012). In particular, these studies focused on the role of the colourful facial bands of this species and the congeneric *P. eumolpe* on the intraspecific visual interactions, and on the function of the palm pectinated crests and dactylar tubercles on the acoustic communication (see also Subchapter 3.3.10.3).

In a study on the hepatopancreatic cellulase mechanisms involved in the digestive process of the cellulose, Adachi et al. (2012) investigated the endogenous cellulase activity in this species (referred as *Perisesarma indiarum*) and other mangrove and marsh crabs. Their results suggested that *P. peninsulare* is able to endogenously digest cellulose, in contrast with other marsh crab species (Adachi et al., 2012).

Table 3.47: List of the studies conducted on *Parasesarma peninsulare.*

Author and Year	Subject of the study	Field	Country
Tesch 1917	as *Sesarma* (*Chiromantes*) *bidens indica*; new distribution records (New Guinea; South coast of Java, Indonesia); morphological and taxonomic notes; species included in checklist and in diagnostic key of sesarmid species	taxonomy	Papua New Guinea, Indonesia
Tweedie 1936	as *Sesarma* (*Chiromantes*) *bidens indica*; new distribution records (Singapore)	distribution record (only)	Singapore
Tweedie 1940	as *Sesarma bidens indiarum*; new distribution records (Singapore; Pahang, Penang, Peninsular Malaysia; Sumatra, Indonesia); morphological and taxonomic notes; new name *Sesarma bidens indiarum* for the species previously known as *Sesarma bidens indica*	taxonomy	Singapore, Malaysia (Peninsular Malaysia), Indonesia
Lundoer 1974	as *Chiromantes indiarum*; checklist of brachyuran crabs in the reference collection at Phuket Marine Biology Center (Thailand)	distribution record (only)	Thailand
Frith et al. 1976	as *Chiromantes indiarum*; zonation and abundance of mangrove macrofauna on Phuket Island (Thailand)	spatial ecology	Thailand
Frith 1977	as *Chiromantes indiarum*; distribution of benthic macrofauna of a mangrove, mudflat and sandflat at Koh Surin Nua Island (Thailand)	spatial ecology	Thailand
Boon et al. 2008	as *Perisesarma indiarum*; feeding ecology, mangrove leaf species and leaf age preferences of *Perisesarma eumolpe* and *P. indiarum*, feeding rates, field and laboratory experiments (Singapore)	feeding ecology	Singapore
Huang et al. 2008	as *Perisesarma indiarum*; inter- and intraspecific variation in the facial colours of *Perisesarma eumolpe* and *P. indiarum* (Singapore)	anatomy/ morphology	Singapore
Boon et al. 2009	as *Perisesarma indiarum*; acoustic communication, sound production and reception in *Perisesarma eumolpe* and *P. indiarum* (Singapore)	behaviour/ social interactions	Singapore
Kon et al. 2009	as *Perisesarma indiarum*; role of mangrove root structures to shelter benthic macrofauna (*P. indiarum*, *Uca bengali*) against predators (*Periophthalmus argentilineatus*), laboratory and field experiments (Thailand)	spatial ecology	Thailand

Table 3.47, continued.

Kon et al. 2010	as *Perisesarma indiarum*; effects of mangrove canopy shade and root structure on physical environment, benthic faunal distribution, and food resource availability (Thailand)	spatial ecology	Thailand
Todd et al. 2011	as *Perisesarma indiarum*; function of colourful facial bands in intraspecific communication and mate choice in *Perisesarma eumolpe* and *P. indiarum* (Singapore)	behaviour/ social interactions	Singapore
Adachi et al. 2012	as *Perisesarma indiarum*; cellulase activity in hepatopancreas of mangrove crabs, feeding experiments(Thailand)	physiology	Thailand
Wang & Todd 2012	as *Perisesarma indiarum*; carotenoid pigments in facial bands of *Perisesarma eumolpe* and *P. indiarum* (Singapore)	physiology/ anatomy	Singapore
Pratiwi & Rahmat 2015	as *Perisesarma indiarum*; checklist of brachyuran crabs in the reference collection at the Research Centre for Oceanografi, Indonesian Institute of Sciences (LIPI) collected from 1960 to 1970 (Indonesia)	distribution record (only)	Indonesia
Shahdadi et al. 2018a	species description, from specimens previously attributed to *P. indiarum* (see Subchapter 3.3.10.4)	taxonomy	IWP

3.3.10.12 *Parasesarma plicatum* (Latreille, 1803)

This species has been object of several taxonomic changes and nomenclature confusion, which has been recently reviewed by Rahayu and Ng (2010). It has been initially described as *Cancer quadratus* by Fabricius (1798), from East India. However, this author used this name twice for two different species, in 1787 and 1798. *Cancer quadratus* Fabricius, 1787 (type locality Jamaica) is now known to be a synonym of *Ocypode quadratus* (Ocypodidae) and it is an Atlantic taxon. The name *Cancer quadratus* Fabricius, 1798 (type locality East India) was instead used for a sesarmid crab, which is today *P. plicatum* (Fabricius, 1787, 1798; Rahayu & Ng, 2010).

Latreille (1803) realised that the same name had been utilised for two different species, and proposed a new name for the sesarmid species, *Ocypode plicatum*. Although almost all authors cited the author and year for *Parasesarma plicatum* as "(Latreille, 1806)", the valid authorship for this taxon is "(Latreille, 1803)", which first used this name (as *Ocypode plicatum*) with a proper description.

Before Rahayu and Ng (2010) revision, this species was thought to be distributed throughout the whole IWP region, with records from East Africa (Hilgendorf, 1878; Lenz & Richters, 1881; De Man, 1889; Borradaile, 1907; Crosnier, 1965; Flores et al., 2003), the Persian Gulf (see Apel, 2001), India (Dev Roy & Nandi, 2008), the Eastern Indian Ocean and Andaman Sea (Latreille, 1803; Bosc, 1802; H. Milne Edwards, 1837, 1853; Miers, 1879; Müller, 1887; Henderson, 1893; Alcock, 1900; Nobili, 1903b; Lundoer, 1974; Frith et al., 1976; Frith, 1977), Peninsular Malaysia and Borneo (White, 1847; Lanchester, 1900a,b, 1902; Choy, 1991; Choy & Booth, 1994), Indonesia (De Man, 1892, 1895, 1902), New Caledonia (Ng & Richer De Forges, 2007), Cambodia (Kemp, 1918), East Asia (White, 1847; Fukuda & Baba, 1976; Dai & Yang, 1991; Ng et al., 2001; Kwok & Tang, 2005; Chen & Ye, 2008).

In their revision, Rahayu and Ng (2010) redefined the species, and separated it from *P. affine* and *P. ungulatum*, which had been previously synonymised to *P. plicatum*. Therefore, the specimens previously recorded as *P. plicatum* from South East Asia and East Asia are currently considered as *P. affine* or *P. ungulatum*, while those from Indonesia and New Caledonia are considered as *P. ungulatum*. Moreover, a recent work by Naderloo and Schubart (2010) re-described the specimens from the Persian Gulf and East Africa as a new species, *P. persicum*. Therefore, the actual distribution of *P. plicatum* is considered to be the Indian Ocean and the Andaman Sea, while *P. affine* is distributed in East Asia, and *P.*

ungulatum ranges from Indonesia and Malaysia to East Asia (Rahayu & Ng, 2010).

A few authors recently reported *P. plicatum* from West India (Shukla et al., 2013; Beleem et al., 2014; Trivedi et al., 2015), Vietnam (Diele et al., 2013) and Indonesia (Pratiwi & Widyastuti, 2013). Following the current distribution of the species, these records are probably referring to *P. persicum*, *P. affine*, or *P. ungulatum*, even though a taxonomic re-examination of the specimens would be necessary to clarify the identity.

However, during the sampling sessions conducted during this project in the Brunei (see Chapter 4), a specimen which morphologically corresponds to *P. plicatum* (*sensu* Rahayu & Ng, 2010) was collected. Moreover, Taufek (2013) reported this species from an ecological study in Terengganu (Peninsular Malaysia). Therefore, *P. plicatum* has been included in this synopsis.

This species has been reported from several studies on the ecology of the mangrove macrofauna, in particular regarding the diversity and zonation of benthic fauna (Frith et al., 1976; Frith, 1977; Ravichandran et al., 2007; Taufek, 2013; Varadharajan et al., 2013; Varadharajan & Soundarapandian, 2014; Kamalakkannan, 2015), and the feeding ecology (Bouillon et al., 2004; Dahdouh-Guebas et al., 2011).

Frith et al. (1976) found this species in Phuket Island (Thailand), on prop roots and tree trunks, in a mangrove forest dominated by *Rhizophora apiculata* and characterised by muddy substrate and saltwater conditions (samples collected from ground water at 20 cm depth). Frith (1977) recorded this species from a dense forest of *Rhizophora mucronata*, mixed with a few *R. apiculata* trees, in the seaward mangrove zone of Koh Surin Nua Island (Thailand). This species was found in a sandy to muddy area, on prop roots and lower trunks of *Rhizophora* spp., associated with abundant dead wood (Frith, 1977).

Ravichandran et al. (2007) reported this species as *Sesarma plicatum* from an estuarine mangrove forest on the South East coast of India, from all the sampling stations investigated in their study. In particular, these authors stated that *P. plicatum* was found in both a *Rhizophora* zone and a *Avicennia* zone, on muddy substrate (Ravichandran et al., 2007).

Taufek (2013) recorded *P. plicatum* from a coastal lagoon on the East coast of Peninsular Malaysia, and found this species to be abundant in most of the investigated sites. Varadharajan et al. (2013) and Varadharajan and Soundarapandian (2014) conducted a study on the crab diversity of the South East coast of India, by collecting samples at different fish landing centers, or using a net from a boat. Both these studies reported *P. plicatum*, although they did not provide information on the habitat conditions of the studied sites (Varadharajan et al., 2013; Varadharajan & Soundarapandian, 2014). Kamalakkanan (2015) recorded this species from an *Avicennia marina* zone in a mangrove forest in Pondicherry (South East coast of India).

Bouillon et al. (2004) conducted a study on the patterns of resource utilisation by mangrove macrofauna in different mangrove forests (Kenya, East India, Sri Lanka) with contrasting inputs of organic matter (locally produced vs imported from the aquatic environment). These authors recorded juvenile specimens of *P. plicatum* from the East Indian forest, and they measured the $\delta^{13}C$ and $\delta^{15}N$ stable isotope ratios. Their results suggested that this species feeds mainly on microphytobenthos, at least in its juvenile stages (Bouillon et al., 2004).

Dahdouh-Guebas et al. (2011) investigated how anthropic hydrographical changes affects the propagule predation behaviour of mangrove grapsoid crabs (Sri Lanka), including *P. plicatum* amongst the studied species. This study was conducted in a basin and riverine mangrove forest, with very low tidal excursion (Dahdouh-Guebas et al., 2011).

Selvakumar (1999) described the larval morphology of *P. plicatum* from East India, comprising five zoeal and a megalopal stages, and compared them with other known sesarmid species. Ganapiriya et al. (2017) described the structure of accessory glands in male specimens of *P. plicatum* from India.

Figure 3.30: *Parasesarma plicatum.* Male specimen (Muara011213_14, from the Brunei Bay collection, loc. Pemburongunana Creek, see Chapter 4). Dorsal (above), ventral (middle) and frontal view (below). Scales are in mm.

Table 3.48: List of the studies conducted on *Parasesarma plicatum*.

Author and Year	Subject of the study	Field	Country
Fabricius 1798	species description as *Cancer quadratus* (East India)	taxonomy	India
Bosc 1802	as *Ocypode quadrata* (East India)	distribution record (only)	India
Latreille 1803	attribution of a new name *Ocypode plicata* to the species described as *Cancer quadratus* by Fabricius 1798	taxonomy	India
H. Milne-Edwards 1837	as *Sesarma quadrata* (Pondicherry = Puducherry, India); morphological and taxonomic notes	taxonomy	India
H. Milne-Edwards 1853	as *Sesarma quadrata* (India); morphological and taxonomic notes	taxonomy	India
Heller 1865	as *Sesarma aspera* (Nicobars; Sri Lanka; Madras, India)	distribution record (only)	Nicobars, Sri Lanka, India
Miers 1879	as *Sesarma quadratum* (Rodriguez, Mauritius Islands)	distribution record (only)	Mauritius Islands
De Man 1887	as *Sesarma quadrata*; description of the type specimen of Fabricius; morphological and taxonomic notes	taxonomy	IWP
Müller 1887	as *Sesarma aspera* (Sri Lanka)	distribution record (only)	Sri Lanka
Henderson 1893	as *Sesarma quadrata* (India)	distribution record (only)	India
Alcock 1900	as *Sesarma quadratum* (India, Sri Lanka, Andaman and Nicobar Islands); morphological and taxonomic notes	taxonomy	India, Sri Lanka, Andaman and Nicobars Islands
Nobili 1903b	as *Sesarma quadrata* (Pondicherry = Puducherry, India); morphological and taxonomic notes; morphometric measurements	taxonomy	India
Tesch 1917	as *Sesarma* (*Parasesarma*) *plicata*; morphological and taxonomic notes; species included in checklist and in diagnostic key of sesarmid species	taxonomy	IWP
Serène 1968	as *Sesarma* (*Parasesarma*) *plicatum*; checklist of the brachyuran species of the Indo Pacific region	distribution record (only)	IWP

Table 3.48, continued.

Lundoer 1974	checklist of brachyuran crabs in the reference collection at Phuket Marine Biology Center (Thailand)	distribution record (only)	Thailand
Frith et al. 1976	zonation and abundance of mangrove macrofauna on Phuket Island (Thailand)	spatial ecology	Thailand
Frith 1977	distribution of benthic macrofauna of a mangrove, mudflat and sandflat at Koh Surin Nua Island (Thailand)	spatial ecology	Thailand
Selvakumar 1999	larval morphology (India)	ontogenesis	India
Bouillon et al. 2004	resource utilization by epifauna in mangrove forests with different imputs of local vs imported organic matter (India, Sri Lanka, Kenya)	feeding ecology	India, Sri Lanka, Kenya
Ravichandran et al. 2007	diversity and habitat preference of crabs in Pichavaram mangrove system (India)	spatial ecology	India
Dev Roy & Nandi 2008	diversity of brackish coastal lakes (India)	spatial ecology	India
Rahayu & Ng 2010	taxonomy, revision of the *Parasesarma plicatum* species-group (IWP)	taxonomy	IWP
Dahdouh-Guebas et al. 2011	effect of anthropic hydrographical changes on propagule predation behaviour (Sri Lanka)	feeding ecology	Sri Lanka
Taufek 2013	crab community structure in Setiu lagoon (Terengganu, Peninsular Malaysia)	spatial ecology	Malaysia (Peninsular Malaysia)
Varadharajan et al. 2013	crab diversity of Puducherry (India)	distribution record (only)	India
Varadharajan & Soundarapandian 2014	crab diversity of the South East coast of India	distribution record (only)	India
Kamalakkanan 2015	habitat distribution and diversity of mangrove crabs in Pondicherry (today Puducherry, India)	spatial ecology	India
Ganapiriya et al. 2017	description of the structure of accessory glands in male specimens of *P. plicatum* (India)	anatomy	India

3.3.10.13 *Parasesarma raouli* Rahayu & Ng, 2009

This species was described by Rahayu and Ng (2009), from Sungai Melayu, Johor (Peninsular Malaysia). In particular, these authors based their description on a series of specimens collected by Raoul Serène in the 1960s, who temporarily labelled them as *Sesarma* (*Parasesarma*) *melayuensis*. This author did not described the species, even though this name was cited in a catalogue of material by Yang (1979; see Rahayu & Ng, 2009).

Recently, *P. raouli* was reported from Indonesia by Widyastuti and Rahayu (2016), from a mangrove area in the Riau Archipelago, where it was found "crawling on the base of a mangrove tree in an environment dominated by *Sonneratia alba* on a sand substrate" (Widyastuti & Rahayu, 2016).

The ecology and biology of this species are practically unknown.

Table 3.49: List of the studies conducted on *Parasesarma raouli.*

Author and Year	Subject of the study	Field	Country
Yang 1979	as *Sesarma* (*Parasesarma*) *melayuensis*; list of brachyurans in the Zoological Reference Collection of the National University of Singapore	distribution record (only)	Singapore
Rahayu & Ng 2009	species description (Sungai Melayu, Johor, Peninsular Malaysia)	taxonomy	Malaysia (Peninsular Malaysia)
Widyastuti & Rahayu 2016	new distribution record (Riau Archipelago, Indonesia)	distribution record (only)	Indonesia

3.3.10.14 *Parasesarma rutilimanum* (Tweedie, 1936)

This species was described as *Sesarma* (*Parasesarma*) *rutilimana* by Tweedie (1936) from Singapore and Johor (Sedili River, East coast of Peninsular Malaysia), from riverine environments and a small island. Tweedie (1950a) reported it as *Sesarma rutilimana* from Labuan (East Malaysia).

Choy (1991) reported this species in the checklist of Crustacea of Brunei Darussalam, while Choy and Booth (1994) found it in an *Avicennia marina* dominated coastal wetland in Brunei Darussalam. Ashton et al. (2003b) recorded it in an ecological study on the macrofaunal community of an estuarine mangrove forest (Sarawak, Borneo). In particular, *P. rutilimanum* was found in most of the sampling plots, in both upstream and downstream sampling stations, in a mixed mangrove forest, in brackish salinity conditions. Some of these plots were also occupied by mounds of the mud lobster *Thalassina anomala* (Ashton et al., 2003b; see also Ashton & Macintosh, 2002).

Pratiwi and Rahmat (2015) reported *P. rutilimanum* in their review of the reference collection (1960-1970) of the Research Centre for Oceanografi, Indonesian Institute of Sciences (LIPI, Indonesia). In particular, *P. rutilimanum* has been recorded from one of the Krakatau Islands, in the Sunda Strait, from mangrove systems, swamp and estuarine environments, on sandy and muddy substrates (Pratiwi & Rahmat, 2015).

Figure 3.31: ***Parasesarma rutilimanum.*** Male specimen. From the reference collection of the Raffles Museum of Biodiversity Research in Singapore (Lee Kong Chian Natural History Museum, National University of Singapore), visited by the author in 2011-2012. Specimen number: ZRC 2000.1907. Dorsal (above), ventral (middle) and frontal view (below). Scales are in mm.

Table 3.50: List of the studies conducted on *Parasesarma rutilimanum*.

Author and Year	Subject of the study	Field	Country
Tweedie 1936	species description as *Sesarma* (*Parasesarma*) *rutilimana* (from Pulau Senang and Jurong river, Singapore; Kuala Sedili, Johor, Peninsular Malaysia)	taxonomy	Singapore, Malaysia (Peninsular Malaysia)
Tweedie 1950a	as *Sesarma rutilimana*; new distribution record (Labuan, East Malaysia)	distribution record (only)	Malaysia (East Malaysia)
Choy 1991	checklist of Crustacea of Brunei Darussalam	distribution record (only)	Brunei Darussalam
Choy & Booth 1994	macrofaunal community in a *Avicennia* dominated coastal wetland (Brunei Darussalam) before and after an inundation event	spatial ecology	Brunei Darussalam
Ashton et al. 2003b	ecology and diversity of crab and mollusc macrofaunal community in the Sematan mangrove forest (Sarawak, East Malaysia)	spatial ecology	Malaysia (East Malaysia)
Pratiwi & Rahmat 2015	new distribution record (Sunda strait, Indonesia); checklist of brachyuran crabs in the reference collection at the Research Centre for Oceanografi, Indonesian Institute of Sciences (LIPI) collected from 1960 to 1970	distribution record (only)	Indonesia

3.3.10.15 *Parasesarma semperi* (Bürger, 1893)

This species was described as *Sesarma semperi* by Bürger (1893), from Philippines. De Man (1902) provided a description of the co-type, as *Sesarma* (*Perisesarma*) *semperi*, adding taxonomic and morphological notes, and morphometric measurements.

Subsequently, this species has been reported from Borneo (Tweedie, 1950a; Ashton et al., 2003b), Thailand (Frith et al., 1976), Indonesia (Rahayu & Davie, 2002; Nordhaus et al., 2011; Murniati, 2017), Australia (Salgado Kent & McGuinness, 2006, 2008), and Japan (Komai et al., 2004).

P. semperi has been included in the genus *Perisesarma* until very recently (see Davie, 2010), when Shahdadi and Schubart (2017) moved it to *Parasesarma*, on the base of morphological and molecular data.

Frith et al. (1976) found this species in a *Rhizophora apiculata* mangrove forest, in saltwater conditions, and on a muddy substrate. Ashton et al. (2003b) reported this species from a few of their investigated plots, characterised by brackish salinity conditions, and a mixed plant assemblage (*Rhizophora mucronata*, *Bruguiera gymnorrhiza*, *Xylocarpus granatum*, *Avicennia alba*, see also Ashton & Macintosh, 2002). Some of these plots were also colonised by mounds of the mud lobster *Thalassina anomala* (Ashton et al., 2003b; see also Ashton & Macintosh, 2002). Murniati (2017) recorded this species from Lombok (Indonesia), from a small island covered by mangrove forests, on a muddy substrate.

Salgado Kent and McGuinness (2006) provided a comparison of methods to estimate the abundance of grapsoid crabs (*P. semperi* and other sesarmid and grapsoid species), including visual counts, pitfall traps, photography, and excavation.

Salgado Kent and McGuinness (2008) investigated the food preference of *P. semperi* and other sesarmid species from Australia. In particular, they conducted choice experiments, by offering the crabs leaves and propagules of different mangrove species, in different conditions (fresh, senescent, decayed). *P. semperi* was found to prefer decayed leaves of *Rhizophora stylosa*, and *Avicennia marina* propagules (Salgado Kent & McGuinness, 2008).

Nordhaus et al. (2011) conducted a study on the diet, food preference, and consumption rates of *P. semperi* and other sesarmid species from Java (Indonesia). In particular, their results showed that *P. semperi* has an omnivorous diet, mainly composed of detritus, mangrove litter and bark, and a small amount of roots, algae and animal matter. This species preferred brown leaves of *Rhizophora apiculata* and *Sonneratia caseolaris*, and green leaves of *Avicennia alba*. These authors found that the preferred leaves were characterized by a high amount and/or freshness of nitrogenous compounds, and their biochemical composition was significantly different from that of disliked leaves, thus suggesting that the nitrogen compound composition may explain the crabs food preference (Nordhaus et al., 2011).

Shahdadi et al. (2018b) conducted a study on the systematics and phylogeography of *P. semperi* and *P. longicristatum*, on the base of morphological and molecular data. These authors re-confirmed these two species as belonging to the genus *Parasesarma*, and they examined specimens from the whole distribution area of the species, conducting genetic, morphometric and morphological analyses (Shahdadi et al., 2018b). Their findings confirmed these species as close sister taxa, forming reciprocally monophyletic groups (Shahdadi et al., 2018b).

Figure 3.32: ***Parasesarma semperi.*** Male specimen (P.Bedukang131013_37, from the Brunei Bay collection, loc. Pulau Bedukang, see Chapter 4). Dorsal (above), ventral (middle) and frontal view (below). CW = 1.18 cm.

Table 3.51: List of the studies conducted on *Parasesarma semperi*.

Author and Year	Subject of the study	Field	Country
Bürger 1893	species description as *Sesarma semperi* (Philippines)	taxonomy	Philippines
De Man 1902	description of co-type as *Sesarma* (*Perisesarma*) *semperi*; morphological and taxonomic notes; morphometric measurements	taxonomy	Philippines
Tesch 1917	as *Sesarma* (*Chiromantes*) *semperi*; species included in checklist and in diagnostic key of sesarmid species	distribution record (only)	IWP
Tweedie 1950a	as *Sesarma semperi*; new distribution record (Labuan, East Malaysia); morphological and taxonomic notes	taxonomy	Malaysia (East Malaysia)
Frith et al. 1976	zonation and abundance of mangrove macrofauna on Phuket Island (Thailand)	spatial ecology	Thailand
Rahayu & Davie 2002	new distribution record from Indonesia	distribution record (only)	Indonesia
Ashton et al. 2003b	ecology and diversity of crab and mollusc macrofaunal community in the Sematan mangrove forest (Sarawak, East Malaysia)	spatial ecology	Malaysia (East Malaysia)
Komai et al. 2004	new distribution record from Ryukyu Islands (Japan), taxonomic and ecological notes	taxonomy / spatial ecology	Japan
Salgado Kent & McGuinness 2006	comparison of methods for estimating relative abundance of grapsoid crabs (Australia)	sampling methodology	Australia
Salgado Kent & McGuinness 2008	feeding ecology, food preferences of sesarmid crabs in Darwin Harbour (Australia), influences of environmental conditions	feeding ecology	Australia
Nordhaus et al. 2011	feeding ecology, food preferences, stable isotopes, consumption rates, gut contents (Indonesia)	feeding ecology	Indonesia
Murniati 2017	brachyuran communities of mangrove systems of the Local Marine Conservation Areas of Lombok (Indonesia)	spatial ecology	Indonesia
Shahdadi & Schubart 2017	systematic review of the genera *Parasesarma* and *Perisesarma*; *P. semperi* transferred to *Parasesarma*	taxonomy / systematics	IWP
Shahdadi et al. 2018b	systematics and phylogeography of *P. semperi* and *P. longicristatum*, based on morphological and molecular data (IWP)	systematics / molecular phylogenetics	IWP

3.3.10.16 *Parasesarma ungulatum* (H. Milne Edwards, 1853)

This species has been described as *Sesarma ungulata* by H. Milne Edwards (1853) from Sulawesi (Indonesia). A few years later, De Man (1887-1888) considered this species to be conspecific with *Parasesarma affinis* (De Haan, 1837) and *Sesarma quadrata* Fabricius, 1898 (now *Parasesarma plicatum* Latreille, 1803). This synonymy has been accepted until Rahayu and Ng (2010) revised *P. plicatum*, and re-established *P. ungulatum* as a valid species.

Therefore, a number of studies recorded *P. ungulatum* under different names, such as *Sesarma quadrata* (from New Caledonia, Indonesia, Singapore, Borneo; White, 1847; A. Milne Edwards, 1873; Thallwitz, 1891; De Man, 1892; Lanchester, 1900a,b; Schenkel, 1902) or *Sesarma* (*Parasesarma*) *quadrata* (from Peninsular Malaysia; Lanchester, 1902), *Sesarma* (*Parasesarma*) *plicatum* (from Micronesia and Indonesia; Rathbun, 1907, 1910b), *Sesarma* (*Parasesarma*) *quadrata* var. *affinis* (from Indonesia; De Man, 1902), *Parasesarma plicatum* (from Brunei Darussalam; Choy, 1991; Choy & Booth, 1994).

Lanchester (1900a) provided some ecological notes, stating that his specimens were collected from "under decayed logs of wood on marshy ground at short distance from the sea". Choy and Booth (1994) recorded this species from an *Avicennia marina* dominated coastal wetland.

More recently, *P. ungulatum* has been reported from southern Vietnam (Chertoprud et al., 2012). These authors found this species on sandy substrates in the upper intertidal zone "over tangle of fully grown *Rhizophora stylosa* and in belts of grassy halophile *Sesuvium portulacastrum*", and "on muddy coarse-grained sands in saltwater ponds bordered by mangrove with *Lumnitzera racemosa* and *Aegiceras* sp." (Chertoprud et al., 2012).

Figure 3.33: ***Parasesarma ungulatum.*** Male specimen (Muara_011213_29, from the Brunei Bay collection, loc. Pemburongunan Creek, see Chapter 4). Dorsal (above), ventral (middle) and frontal view (below). CW= 1.22 cm.

Table 3.52: List of the studies conducted on *Parasesarma ungulatum*.

Author and Year	Subject of the study	Field	Country
White 1847	as *Sesarma quadrata*; new distribution record (Borneo)	distribution record (only)	Borneo
H. Milne Edwards 1853	species description as *Sesarma ungulata* (Sulawesi, Indonesia)	taxonomy	Indonesia
A. Milne Edwards 1873	as *Sesarma quadrata* (New Caledonia); new distribution record	distribution record (only)	New Caledonia
De Man 1887-1888	species synonymised with with *Parasesarma affinis* (de Haan, 1837) and *Sesarma quadrata* Fabricus 1898 (now *Parasesarma plicatum* Latreille, 1803)	taxonomy	IWP
Thallwitz 1891	as *Sesarma quadrata* (Aru Islands, Indonesia); new distribution record	distribution record (only)	Indonesia
De Man 1892	as *Sesarma quadrata* (Macassar, Sulawesi, Indonesia); new distribution record	distribution record (only)	Indonesia
Lanchester 1900a	as *Sesarma quadrata* (Singapore); new distribution record, brief notes on the environmental conditions	distribution record (only)	Singapore
Lanchester 1900b	as *Sesarma quadrata* (Sarawak, East Malaysia); new distribution record	distribution record (only)	Malaysia (East Malaysia)
Lanchester 1902	as *Sesarma* (*Parasesarma*) *quadrata* (Terengganu, Peninsular Malaysia); new distribution record	distribution record (only)	Peninsular Malaysia)
Schenkel 1902	as *Sesarma quadrata* (Macassar, Sulawesi, Indonesia); new distribution record	distribution record (only)	Indonesia
De Man 1902	as *Sesarma* (*Parasesarma*) *quadrata* var. *affinis* (Ternate, Maluku Islands, Indonesia)	distribution record (only)	Indonesia
Rathbun 1907	as *Sesarma* (*Parasesarma*) *plicatum* (Caroline Islands, Micronesia); new distribution record	distribution record (only)	Micronesia
Rathbun 1910b	as *Sesarma* (*Parasesarma*) *plicatum* (Macassar, Sulawesi, Indonesia); new distribution record	distribution record (only)	Indonesia
Choy 1991	as *Parasesarma plicatum*; checklist of Crustacea of Brunei Darussalam	distribution record (only)	Brunei Darussalam
Choy & Booth 1994	as *Parasesarma plicatum*; macrofaunal community in a *Avicennia* dominated coastal wetland (Brunei Darussalam) before and after an inundation event	spatial ecology	Brunei Darussalam
Rahayu & Ng 2010	species considered valid again, after De Man (1888) synonymised it with *P. affinis* and *P. plicatum*	taxonomy	IWP
Chertoprud et al. 2012	new distribution record (Vietnam); morphological and ecological notes	spatial ecology	Vietnam

3.3.11 Genus *Perisesarma* De Man, 1895

The genus *Perisesarma* De Man, 1895 currently includes only one species, *P. dussumieri*. However, this genus used to include 25 species, until a recent revision by Shahdadi and Schubart (2017) transferred most of them to the genus *Parasesarma*, or to the newly established genera *Fasciarma* and *Guinearma.* The genus is characterised by having two rows of transverse pectinated crests on the dorsal part of the male chelar carpus, and dactylar tubercles on the upper border of the dactylus (Campbell, 1967; Guerao et al., 2004; Naderloo & Schubart, 2010; Shahdadi & Schubart, 2015).

The genus has undergone several taxonomic and systematic changes. It has been first described as *Sesarma* (*Perisesarma*) by De Man (1895), which considered it a subgenus of *Sesarma* Say, and included 7 species [*S.* (*Perisesarma*) *bidens*, *S.* (*Perisesarma*) *dussumieri*, *S.* (*Perisesarma*) *eumolpe*, *S.* (*Perisesarma*) *guttata*, *S.* (*Perisesarma*) *haswelli*, *S.* (*Perisesarma*) *livida*, *S.* (*Perisesarma*) *onychophorum*]. Rathbun (1909) altered the name of this subgenus in *Sesarma* (*Chiromantes*) Gistel, due to nomenclature reason (see also Tesch, 1917). Campbell (1967) provided a review of the genus as *Sesarma* (*Chiromanthes*) and described three new species, i.e. *S.* (*Chiromanthes*) *brevicristatum*, *S.* (*Chiromanthes*) *darwinensis*, *S.* (*Chiromanthes*) *messa*, and a new subspecies, *S.* (*Chiromanthes*) *semperi longicristatum*. Moreover, this author included in the subsgenus the previously described *Sesarma bidens* var. *indiarum* and *Sesarma semperi*. Holthuis (1977) transferred the species previously included in the subgenus *Sesarma* (*Chiromantes*) sensu Rathbun (1909) again to the genus *Perisesarma*, while considering *Chiromantes* as the correct name for the species previously included in *Holometopus* H. Milne Edwards, 1853.

More recently, several new species have been described from the IWP region, including *P. maipoense*, *P. cricotum*, *P. foresti*, *P. bengalense*, *P. samawati*, *P. tuerkayi* (Soh, 1978; Rahayu & Davie, 2002; Davie, 2003; Gillikin & Schubart, 2004; Shahdadi et al., 2017). Ng et al. (2008) included also *P. fasciatum* and *P. lanchesteri* in the genus, and the three West African species, *P. alberti*, *P. huzardi*, and *P. kamermani*. However, these authors suggested that these latter species should be transferred to a separate genus (Ng et al., 2008).

A recent revision of the genus has been conducted by Davie (2010), which described a new species from Australia (*P. holthuisi*) and provided also a key to the Indo West Pacific species. This author excluded *P. lanchesteri* from the genus, and suggested to also exclude *P. fasciatum*; moreover, he suggested *P. foresti* as a junior synonym of *P. indiarum* (Davie, 2010). Shahdadi and Schubart (2015) presented a review of key morphological characters utilised to discriminate the species of *Perisesarma*, in particular the number and shape of dactylar tubercles and the pectinated crests on the male palm. A few years later, the same authors (Shahdadi & Schubart, 2017) transferred all the species but *P. dussumieri* to the genus *Parasesarma* and to the new genera *Guinearma* (including the West African species) and *Fasciarma* (including the aberrant species *P. fasciatum*).

The type species is currently considered *Sesarma dussumieri* A. Milne-Edwards 1853, designated by Campbell (1967). Rathbun (1918) designated *S. bidens* (De Haan) as type species, which is considered invalid because this species was not originally included in *Perisesarma* by De Man. Subsequently, Holthuis (1977) designated *Sesarma* (*Perisesarma*) *eumolpe* as type species, which is considered invalid, since Campbell (1967) action has priority.

The only species currently included in this genus, *P. dussumieri* (H. Milne Edwards, 1853) has been recorded in Peninsular Malaysia, Singapore, and/or northern Borneo.

Table 3.53: List of the main studies conducted on the genus *Perisesarma* (including taxonomic studies and reviews of the genus).

Author and Year	Subject of the study
De Man 1895	genus description as subgenus *Sesarma* (*Perisesarma*)
Campbell 1967	review of the genus; *Sesarma dussumieri* A. Milne-Edwards 1853 designated as type species
Holthuis 1977	taxonomic notes; establishment of the genus *Perisesarma*
Guerao et al. 2004	comparison of larval and juvenile morphology of *Perisesarma* and *Parasesarma*
Davie 2010	key of the IWP species of the genus
Shahdadi & Schubart 2015	morphological characters and diagnostic value of the cheliped
Shahdadi & Schubart 2017	systematic review of the genera *Parasesarma* and *Perisesarma*

3.3.11.1 *Perisesarma dussumieri* (H. Milne Edwards, 1853)

This species was described as *Sesarma dussumieri* by H. Milne Edwards (1853), from Bombay (today Mumbai, West coast of India). Subsequently, several authors reported it from Peninsular Malaysia and Singapore (Targioni-Tozzetti, 1877; De Man, 1895; Tweedie, 1936), Myanmar (De Man, 1887-1888), Thailand (Ortmann, 1894a; Lundoer, 1974; Frith et al., 1976; Takeda et al., 1996), Sri Lanka (Dahdouh-Guebas et al., 2011), and Indonesia (Pratiwi & Widyastuti, 2013). Alcock (1900) synonymised this species with *Sesarma bidens* (today *Perisesarma bidens*), although this action was considered invalid by Tesch (1917), who refused the synonymy due to taxonomic differences in the sizes of the male abdomens.

P. dussumieri was included in a few ecological studies on zonation of mangrove macrofauna (Frith et al., 1976) and foodwebs (Dahdouh-Guebas et al., 2011). In particular, Frith et al. (1976) recorded this species from a muddy landward fringe of a mangrove forest (Thailand), on muddy substrate, and in saltwater salinity conditions. The area had been previously disturbed by burning and cutting activities, and consequently colonised by sparse *Nypa fruticans* and *Phoenix paludosa* palms. Dahdouh-Guebas et al. (2011) conducted a study on the effect of human hydrographical changes on the propagule predation in two mangrove forests (Sri Lanka). These authors stated that *P. dussumieri* was one of the dominant species in both sites, although they did not specify in which part of the forests this species was found.

Takeda et al. (1996) conducted a study on the variation of the branchial formula of intertidal and supratidal crabs (including *P. dussumieri* and other grapsoid and ocypodid crabs), in order to investigate the physiological adaptations to the semiterrestrial environment.

Figure 3.34: ***Perisesarma dussumieri.*** Male specimen. From the reference collection of the Raffles Museum of Biodiversity Research in Singapore (Lee Kong Chian Natural History Museum, National University of Singapore), visited by the author in 2011-2012. Specimen number: ZRC 1987-558-559-1. Dorsal (above), ventral (middle) and frontal view (below left), and detail of the cheliped (below right). Scales are in mm.

Table 3.54: List of the studies conducted on *Perisesarma dussumieri.*

Author and Year	Subject of the study	Field	Country
H. Milne Edwards 1853	species description as *Sesarma dussumieri* (from Bombay = Mumbai, India)	taxonomy	India
Targioni- Tozzetti 1877	new distribution records (Penang, Peninsular Malaysia; Singapore); morphological and taxonomic notes; morphometric measurements	taxonomy	Malaysia (Peninsular Malaysia), Singapore
De Man 1887	as *Sesarma dussumieri*; distribution notes (India, Peninsular Malaysia, Mergui Archipelago)	distribution record (only)	India, Malaysia (Peninsular Malaysia), Myanmar
De Man 1887-1888	new distribution records (Mergui Archipelago, Myanmar)	distribution record (only)	Myanmar
Ortmann 1894a	new distribution records (Salanga Island = Phuket, Thailand)	distribution record (only)	Thailand
De Man 1895	new distribution records as *Sesarma* (*Perisesarma*) *dussumieri* (Penang, Peninsular Malaysia); morphological and taxonomic notes; morphometric measurements	taxonomy	Malaysia (Peninsular Malaysia)
Alcock 1900	*S. dussumieri* synonymised with *Sesarma bidens*	taxonomy	IWP
Tesch 1917	as *Sesarma* (*Chiromantes*) *dussumieri*; Alcock's synonymy not accepted; species included in checklist and in diagnostic key of sesarmid species	taxonomy	IWP
Tweedie 1936	as *Sesarma* (*Chiromantes*) *dussumieri*; new distribution records (Singapore)	distribution record (only)	Singapore
Lundoer 1974	checklist of brachyuran crabs in the reference collection at Phuket Marine Biology Center (Thailand)	distribution record (only)	Thailand
Frith et al. 1976	zonation and abundance of mangrove macrofauna on Phuket Island (Thailand)	spatial ecology	Thailand
Takeda et al. 1996	variation in branchial formula of ocypodoid and grapsoid crabs in relation to physiological adaptation to the environment (Thailand)	physiology / anatomy	Thailand
Dahdouh-Guebas et al. 2011	effect of anthropic hydrographical changes on propagule predation behaviour (Sri Lanka)	feeding ecology	Sri Lanka
Pratiwi & Widyastuti 2013	distribution and zonation of mangrove crustaceans in Lampung Bay (Sumatra, Indonesia)	spatial ecology	Indonesia

3.3.12 Genus *Pseudosesarma* Serène & Soh, 1970

The genus *Pseudosesarma* has been established by Serène and Soh (1970), in their review on the IWP sesarmid genera. In particular, it includes species having a frontal anterior margin with a shallow but marked median concavity, the anterior border of the cheliped with a subdistal triangular process, the gastric and cardiac regions well delimited by a groove, an antero-lateral tooth well marked, and the carapace length shorter than the width (measured between the external orbital angle) (Serène & Soh, 1970).

Serène and Soh (1970) stated that the genus *Pseudosesarma* corresponded roughly to two groups of species defined as "*edwardsii* group" and "*intermedium* group". The first group was including *Sesarma edwardsii* De Man 1887, and its varieties (*S. edwardsii* var. *crassimanum* De Man 1887, *S. edwardsii* var. *brevipes* De Man 1889, *S. edwardsii* var. *laevimanum* Zehtner 1894, *S. edwardsii* var. *philippinensis* Rathbun 1914). The second group was including *S. intermedium* De Haan 1835, *S. sinensis* H. Milne-Edwards 1853, *S. moeschi* De Man 1888, and *S. johorensis* Tweedie 1940.

In particular, Serène and Soh (1970) considered *Pseudosesarma* as including:

- the already defined "*edwardsii* group", including the previously mentioned species (except *S. edwardsii* var. *brevipes* and *S. edwardsii* var. *philippinensis*, which were moved to the genus *Bresedium*), plus *S. bocourti* and *S. modestum*;
- a new group called "*moeschi* group", which included two species of the "*intermedium* group", i.e. *S. moeschi*, and *S. johorensis*.

These authors distinguished the *edwardsii* group by having an acute flattened process at inner angle of carpus of cheliped, which is much less developed on the *moeschi* group (Serène & Soh, 1970). These authors therefore included 7 species in this genus: *Pseudosesarma bocourti*, *P. edwardsii*, *P. edwardsii laevimanum*, *P. crassimanum*, *P. modestum*, *P. moeschi*, and *P. johorensis*. A few years later, Soh (1978) added to this genus a newly described species, *P. patshuni*, from Hong Kong.

Serène and Soh (1970) also stated that this genus shares several characters with the genus *Sesarmops* and the separation of the two genera need to be further clarified. Moreover, they suggested that a further new genus should be established, giving priority to the shape of the male pleopod, in order to group *P. bocourti* with the species of *Sesarmops* having the same type of male pleopod (Serène & Soh, 1970). These authors also considered the species *P. moeschi* and *P. johorensis* aberrant within the genus *Pseudosesarma*, due to their smooth shining carapace and other characters (Serène & Soh, 1970). Later, Ng et al. (2008) stated in a note that these two species are probably congeneric with *Chiromantes dehaani*, and they therefore may be transferred to a separate genus. In conclusion, the taxonomy and systematic of this genus have gone through several changes and readjustments (see Serène & Soh, 1970), and they are currently still under revision (Ng et al., 2008). Recently, three new species have been described from Sri Lanka (*P. anteactum*, Ng & Schubart, 2017), southwest India (*P. glabrum*, Ng et al., 2017), Myanmar (*P. brehieri*, Ng, 2018).

Pseudosesarma species have been recorded from the whole IWP region, including India and Sri Lanka (Alcock, 1900; Dahdouh-Guebas et al., 2011; Ng & Schubart, 2017), Myanmar (De Man, 1887-1888; Ng, 2018), Peninsular Malaysia and Singapore (Tweedie, 1936, 1940; Yeo et al., 1999), Borneo (De Man, 1895; Nobili, 1900; Tweedie, 1950a; Ng, 1995), Indonesia (De Man, 1892, 1902), Thailand (Kemp, 1918), Vietnam (De Man, 1895), Hong Kong (Soh, 1978; Kwok & Tang, 2005), and Japan (Targioni-Tozzetti, 1877).

These species are usually associated with freshwater conditions, and inhabit mangrove and other coastal and riverine forests, such as nipah forests (Tweedie, 1940; McLauglin et al., 1996), peat swamps (Ng, 1995), freshwater swamps (Tweedie, 1940), "tidal freshwaters beyond the limits of the mangrove" (Yeo et al., 1999), and terrestrial ecosystems, where they have been observed ''several hundred metres from the nearest water source'' (Ng, 1995). *Pseudosesarma* species exposed to a wide range of external salinities have been documented to have strong osmotic abilities (McLauglin et al., 1996), which are typical of semi-terrestrial crabs of the family Sesarmidae (Schubart & Diesel, 1998).

A few species of this genus are also commercially exploited, especially in South East Asia, and they can be commonly found in the aquarium trade, (e.g. *Pseudosesarma bocourti* and *P. moeschi*, see Guerao et al., 2007).

The larval morphology have been described for three of the *Pseudosesarma* species, i.e. *P. crassimanum* (Cuesta et al., 2006), *P. bocourti* and *P. moeschi* (Guerao et al., 2007).

Seven species have been recorded until now from Peninsular Malaysia, Singapore, and/or northern Borneo:

- *P. bocourti* (A. Milne Edwards, 1869)
- *P. crassimanum* (De Man, 1887)
- *P. edwardsii* (De Man, 1888)
- *P. granosimanum* (Miers, 1880)
- *P. johorense* (Tweedie, 1940)
- *P. laevimanum* (Zehntner, 1894)
- *P. moeschi* (De Man, 1888)

Table 3.55: List of the main studies conducted on the genus *Pseudosesarma* (including taxonomic studies and reviews of the genus).

Author and Year	Subject of the study
Serène & Soh 1970	genus description
Guerao et al. 2007	larval morphology; taxonomic, ecological and historical notes on the genus

3.3.12.1 *Pseudosesarma bocourti* (A. Milne Edwards, 1869)

This species was described from Thailand by A. Milne-Edwards (1869), as *Sesarma bocourti*. A few years later, Targioni-Tozzetti (1877) described a new sesarmid species from Japan, *Sesarma cheiragona*, which was later synonymised with *S. bocourti* by De Man (1887). However, the locality of this record has been subsequently considered incorrect, according to Tweedie (1940; see also Guerao et al., 2007a).

A few authors recorded this species as *Sesarma bocourti* from Borneo (De Man, 1880, 1895; Miers, 1880; Zehntner, 1894; Nobili, 1899, 1900), and Indonesia (Nobili, 1900; Roux, 1933). Tesch (1917) provided detailed taxonomic notes, morphometric measurements, and drawings; moreover, this author added a new distribution record from East Borneo.

Tweedie (1940) reported this species from a freshwater swamp in Johor (Peninsular Malaysia), and provided additional taxonomic notes. Later, Ng (1995) included *P. bocourti* in the checklist of the Bako National Park (Sarawak, Borneo), and Yeo et al. (1999) cited this species in a checklist of freshwater and terrestrial decapod crustaceans of Pulau Tioman (East coast of Peninsular Malaysia). Both these studies provided a few ecological notes on the habitats from which their specimens were obtained, which ranged “from true mangal areas to what appear to be tidal freshwaters beyond the inland limits of the mangroves” (Yeo et al., 1999). Ng (1995) stated that this species was found on a peat substrate, where it was digging burrows, often among roots and debris. The crabs were observed emerging "only late at night to feed on dead leaves and other vegetable matter", and they were collected several hundred metres from the nearest water source (Ng, 1995).

Guerao et al. (2007) described the morphology of the larval stages of *P. bocourti* and *P. moeschi*, consisting of four zoeal stages and a megalopa, and they compared their results with the data available for other sesarmid species. Guerao (2008) conducted a study on the resistance to starvation and salinity tolerance of the first zoea of this species and of *P. moeschi*. Their results suggested that the larval stages in these species tolerate freshwater conditions, and can resist to starvation (high endotrophic potential), especially for *P. bocourti*.

Table 3.56: List of the studies conducted on *Pseudosesarma bocourti.*

Author and Year	Subject of the study	Field	Country
A. Milne-Edwards 1869	species description as *Sesarma bocourti* (Bangkok, Thailand)	taxonomy	Thailand
Targioni-Tozzetti 1877	species description as *Sesarma cheirogona* (Yokohama, Japan: erroneous locality, see Guerao et al. 2007)	taxonomy	Japan (but erroneous locality)
De Man 1880	new distribution records (East Malaysia)	distribution record (only)	Malaysia (East Malaysia)
Miers 1880	new distribution records (East Malaysia)	distribution record (only)	Malaysia (East Malaysia)
Zehntner 1894	new distribution records (Sarawak, East Malaysia); morphological notes, morphometric measurements	distribution record (only)	Malaysia (East Malaysia)
De Man 1895	new distribution records as *Sesarma* (*Episesarma*) *bocourti* (Sarawak, East Malaysia); morphological and taxonomic notes; morphometric measurements	taxonomy	Malaysia (East Malaysia)

Table 3.56, continued.

Nobili 1900	new distribution records (Siboga, Padang, Indonesia; Sarawak, East Malaysia); morphological and taxonomic notes	taxonomy	Indonesia, Malaysia (East Malaysia)
Tesch 1917	examination of specimens in Leiden Museum (East Malaysia); morphological and taxonomic notes; species included in diagnostic key of sesarmid species	taxonomy	Malaysia (East Malaysia)
Roux 1933	as *Sesarma bocourti*; new distribution records (Sumatra, Indonesia)	distribution record (only)	Indonesia
Tweedie 1940	as *Sesarma bocourti*; new distribution records (Kota Tinggi, Johor, Peninsular Malaysia), morphological and taxonomic notes	taxonomy	Malaysia (Peninsular Malaysia)
Ng 1995	checklist of freshwater decapods of Bako National Park (Sarawak, East Malaysia); ecological notes	spatial ecology	Malaysia (East Malaysia)
Yeo et al. 1999	checklist of freshwater and terrestrial decapod fauna of Tioman Island (Peninsular Malaysia); taxonomic and ecological notes	taxonomy / spatial ecology	Malaysia (Peninsular Malaysia)
Guerao et al. 2007	larval morphology of *Pseudosesarma bocourti* and *P. moeschi* (Indo-West Pacific)	ontogenesis	IWP
Guerao 2008	Resistance to starvation and salinity tolerance in first zoeal stages of *P. bocourti* and *P. moeschi*	ontogenesis	IWP

Figure 3.35: ***Pseudosesarma bocourti.*** Male specimen (Temburong_28-30mar2014, from the Brunei Bay collection, loc. Sungai Labu, see Chapter 4). Dorsal (above), ventral (middle) and frontal view (below). Scales are in cm. Pictures by G. Polgar.

3.3.12.2 *Pseudosesarma crassimanum* (De Man, 1887)

This species was described as *Sesarma edwardsii* var. *crassimana* by De Man (1887-1888), from India. Subsequently, it has been recorded from Myanmar (De Man, 1888), Borneo (Zehntner, 1894; De Man, 1895; Tweedie, 1950a), Peninsular Malaysia (Lanchester, 1900a; Tweedie, 1940), and Sri Lanka (Dahdouh-Guebas et al., 2011).

Tweedie (1940) reported this species from a riverine area colonised by nipah palms (*Nypa fruticans*), and provided additional taxonomic notes. In particular, this author upgraded this taxon to the specific level, from the previously defined *Sesarma edwardsii* var. *crassimana* to *Sesarma crassimana.* Dahdouh-Guebas et al. (2011) recorded this species in an ecological study on the propagule feeding behaviour of the grapsoid crabs, relatively to human hydrographical changes. The study was conducted in a basin and riverine mangrove forest, with very low tidal excursion (Sri Lanka, Dahdouh-Guebas et al., 2011).

Ng et al. (2008) pointed out that an ongoing investigation with molecular and morphological data has shown that *P. crassimanum* is actually congeneric with another species, *Sesarma dehaani* H.Milne Edwards, 1853, currently placed in the genus *Chiromantes*. Ng and Schubart (2017) re-examined the taxonomy of this species, providing a re-description and a comparison with the congeneric *P. edwardsii*. Cuesta et al. (2006) described the first zoeal stage of *P. crassimanum*.

Figure 3.36: ***Pseudosesarma crassimanum.*** Male specimen. From the reference collection of the Raffles Museum of Biodiversity Research in Singapore (Lee Kong Chian Natural History Museum, National University of Singapore), visited by the author in 2011-2012. Specimen number: ZRC 1999.0957. Dorsal (above), ventral (middle) and frontal view (below). Scales are in mm.

Table 3.57: List of the studies conducted on *Pseudosesarma crassimanum.*

Author and Year	**Subject of the study**	**Field**	**Country**
De Man 1887-1888	species description as *Sesarma edwardsii* var. *crassimana* (Bay of Bengal, India)	taxonomy	India
De Man 1888	as *Sesarma edwardsi* var. *crassimana*; new distribution records (Mergui Archipelago, Myanmar)	distribution record (only)	Myanmar
Zehntner 1894	as *Sesarma edwardsi* var. *crassimana*; new distribution records (Sarawak, East Malaysia); morphological notes, morphometric measurements	distribution record (only)	Malaysia (East Malaysia)
De Man 1895	new distribution records as *Sesarma* (*Episesarma*) *edwardsi* var. *crassimana* (Pontianak, Kalimantan, Indonesia); morphometric measurements	distribution record (only)	Indonesia
Lanchester 1900a	as *Sesarma edwardsi* var. *crassimana*; new distribution records (Malacca, Peninsular Malaysia)	distribution record (only)	Malaysia (East Malaysia)
Tesch 1917	as *Sesarma* (*Sesarma* s.s.) *edwardsi crassimana*; examination of Leiden Museum specimens; species included in checklist and in diagnostic key of sesarmid species	distribution record (only)	IWP
Tweedie 1940	as *Sesarma crassimana*; new distribution records (Sedili River, Johor, Peninsular Malaysia), morphological and taxonomic notes; *Sesarma edwardsii* var. *crassimana* upgraded to species level (*Sesarma crassimana*)	taxonomy	Malaysia (Peninsular Malaysia)
Tweedie 1950a	as *Sesarma crassimana*; new distribution record (Sarawak, East Malaysia); morphological and taxonomic notes	taxonomy	Malaysia (East Malaysia)
Cuesta et al. 2006	larval morphology of 11 species of Sesarmidae from Indo-West Pacific; description of first zoea	ontogenesis	IWP
Dahdouh-Guebas et al. 2011	effect of anthropic hydrographical changes on propagule predation behaviour (Sri Lanka)	feeding ecology	Sri Lanka
Ng & Schubart 2017	clarification on the taxonomy and systematic status	taxonomy	IWP

3.3.12.3 *Pseudosesarma edwardsii* (De Man, 1887)

This species was described in a short note by De Man (1887), as *Sesarma edwardsii*, from the Bengal Bay (India). However, one year later De Man (1887-1888) provided an official description, based on samples from Myanmar.

A few years later, Alcock (1900) reported it from Sri Lanka, India, Myanmar, and the Andaman Islands. Moreover, this species has also been recorded from Peninsular Malaysia (Lanchester, 1900a), Indonesia and Papua New Guinea (Tesch, 1917), Thailand (Kemp, 1918), and Singapore (Tweedie, 1936). In particular, Lanchester (1900a) found his specimens inside the stomach of a monitor lizard (*Varanus salvator*). Kemp (1918) stated that his specimens were collected in freshwater conditions, while Tweedie (1936) reported this species from small islands. More recently, Dev Roy and Nandi (2008) reported this species from a coastal brackish lake on the West coast of India, while Paul et al. (2012) investigated the occurrence and seasonal abundance of this species from the Hugli-Matla Estuary (Bengal Bay, India).

Ng and Schubart (2017) provided a re-description of the species, and compared it with *P. crassimanum* and a newly described species, *P. anteactum*. Kannupandi and Pasupathi (1994) described the four zoeal stages and the megalopa of this species from specimens obtained from mangrove forests (India).

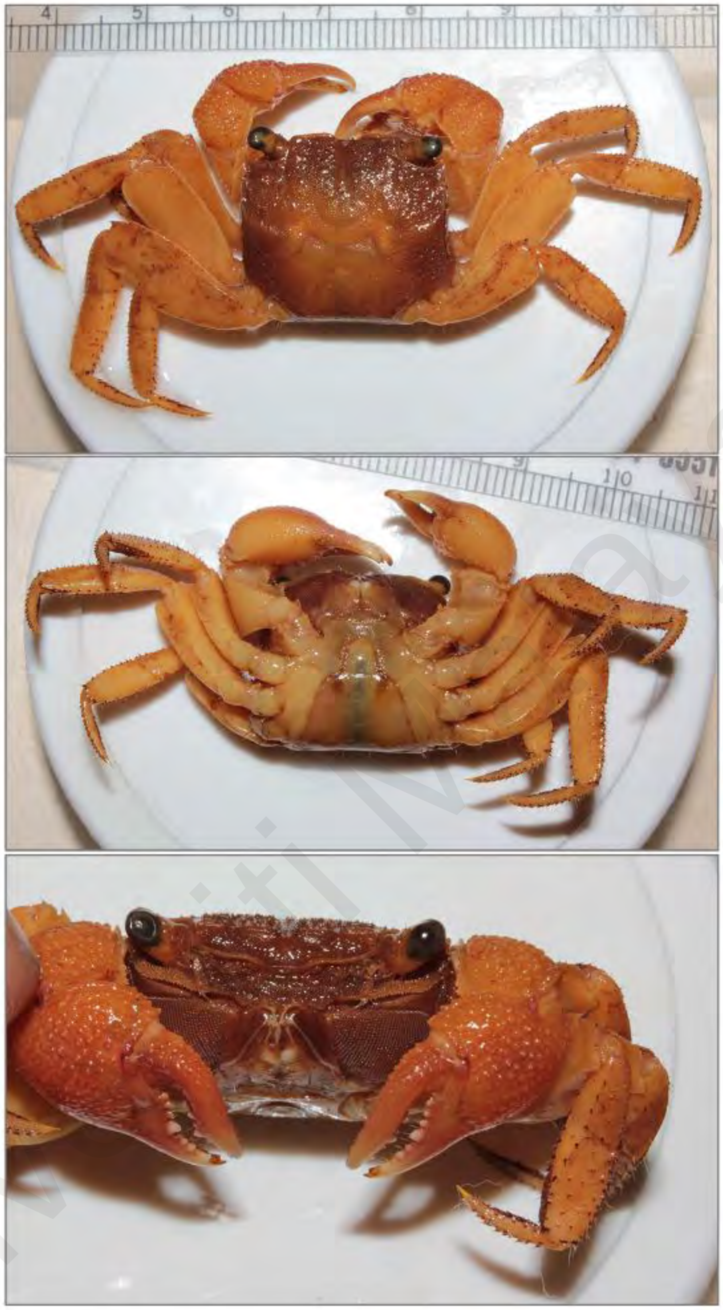

Figure 3.37: ***Pseudosesarma edwardsii.*** Male specimen. From the reference collection of the Raffles Museum of Biodiversity Research in Singapore (Lee Kong Chian Natural History Museum, National University of Singapore), visited by the author in 2011-2012. Specimen number: ZRC 2003.0084. Dorsal (above), ventral (middle) and frontal view (below). Scales are in mm.

Table 3.58: List of the studies conducted on *Pseudosesarma edwardsii*.

Author and Year	Subject of the study	Field	Country
De Man 1887	as *Sesarma edwardsii* (Bay of Bengal, India), pre-description of the species	taxonomy	India
De Man 1887-1888	official description, as *Sesarma edwardsi*; new distribution records (Mergui Archipelago, Myanmar)	taxonomy	Myanmar
Alcock 1900	as *Sesarma edwardsi* (Burmah coast, Myanmar; Ganges-delta, India; Andamans and Sri Lanka); morphological and taxonomic notes	taxonomy	Myanmar, India, Andaman Islands, Sri Lanka
Lanchester 1900a	new distribution records (Malacca, Peninsular Malaysia)	distribution record (only)	Malaysia (Peninsular Malaysia
Tesch 1917	examination of Leiden Museum specimens (New Guinea; Java, Celebes, Indonesia); species included in checklist and in diagnostic key of sesarmid species	distribution record (only)	Papua New Guinea, Indonesia
Kemp 1918	new distribution records (Patani River, Thailand)	distribution record (only)	Thailand
Tweedie 1936	as *Sesarma* (*Sesarma*) *edwardsii*; new distribution records (Singapore)	distribution record (only)	Singapore
Kannupandi & Pasupathi 1994	description of zoeal and megalopal stages (India)	ontogenesis	India
Dev Roy & Nandi 2008	diversity of brackish coastal lakes (India)	spatial ecology	India
Paul et al. 2012	occurrence and seasonal abundance in the Hugli-Matla Estuary (Bengal, India)	spatial ecology	India
Ng & Schubart 2017	clarification on the taxonomy and systematic status	taxonomy	IWP

3.3.12.4 *Pseudosesarma granosimanum* (Miers, 1880)

This species was described by Miers (1880) as *Sesarma granosimana*, from the "Indo-Malayan Seas". De Man (1887) added a few morphological notes, while De Man (1895) recorded it as *Sesarma* (*Sesarma*) *granosimana* from Borneo, and provided taxonomic notes and morphometric measurements.

Roux (1933) reported this species from Indonesia, while Tweedie (1940) collected it in Johor (Peninsular Malaysia), from freshwater swamps and among nipah palms (*Nypa fruticans*). Tweedie (1950a) recorded this species in Borneo, and provided a taxonomic comparison between *P. crassimanum* and *P. granosimanum*. The biology and ecology of this species are practically unknown.

Table 3.59: List of the studies conducted on *Pseudosesarma granosimanum*.

Author and Year	Subject of the study	Field	Country
Miers 1880	species description as *Sesarma granosimana* (from Indo-Malayan seas)	taxonomy	"Indo-Malayan Seas"
De Man 1887	as *Sesarma granosimana*; no new locality, morphological notes	taxonomy	"Indo-Malayan Seas"
De Man 1895	new distribution records as *Sesarma* (*Sesarma*) *granosimana* (Pontianak, Kalimantan); morphological and taxonomic notes; morphometric measurements	taxonomy	Indonesia
Tesch 1917	as *Sesarma* (*Holometopus*) *granosimana;* species included in checklist and in diagnostic key of sesarmid species	distribution record (only)	IWP
Roux 1933	new distribution records (Palembang, Sumatra, Indonesia)	distribution record (only)	Indonesia
Tweedie 1940	as *Sesarma granosimana*; new distribution records (Sedili River, Johor, Peninsular Malaysia); distribution notes	distribution record (only)	Malaysia (Peninsular Malaysia)
Tweedie 1950a	as *Sesarma granosimana*; new distribution record (Sarawak, East Malaysia); morphological and taxonomic notes	taxonomy	Malaysia (East Malaysia)

3.3.12.5 *Pseudosesarma johorense* (Tweedie, 1940)

This species has been described by Tweedie (1940), as *Sesarma johorensis*, from a mangrove swamp near the Pendas River (Johor, Peninsular Malaysia). This author provided a detailed description and morphometric measurements, and a taxonomic comparison with the closely related *P. moeschi*. Moreover, he referred to the diagnostic key of Tesch (1917), placing the new species in the key, according to its taxonomic characters. Tweedie (1950a) reported this species from Labuan (East Malaysia), and added a short taxonomic note.

The biology and ecology of this species are practically unknown.

Table 3.60: List of the studies conducted on *Pseudosesarma johorense.*

Author and Year	Subject of the study	Field	Country
Tweedie 1940	species description as *Sesarma johorensis* (Pendas River, Johor, Peninsular Malaysia)	taxonomy	Malaysia (Peninsular Malaysia)
Tweedie 1950a	as *Sesarma johorensis*; new distribution record (Labuan, East Malaysia); morphological notes	taxonomy	Malaysia (East Malaysia)

3.3.12.6 *Pseudosesarma laevimanum* (Zehntner, 1894)

This species was described by Zehntner (1894) as *Sesarma edwardsii* var. *laevimana* from Sarawak (Borneo). This author reported this species from freshwater conditions, even though he did not provide other information on the habitat.

More recently, this species has been reported from Indonesia, in a study on the spatio-temporal variation of macrobenthic communities of a mangrove-fringed lagoon (Nordhaus et al., 2009). These authors found *P.* cf. *laevimanum* in the central area of the lagoon, which had muddy substrate, and brackish salinity conditions. At the time of the study, this area was receiving high sediment imput due to unsustainable human land use upland, and was also subjected to deforestation. The area was colonised by sparse trees of *Sonneratia caseolaris*, *S. alba*, *Avicennia alba* and *A. marina*, and densely covered with the shrubs *Acanthus* spp. and *Derris trifoliata* (Nordhaus et al., 2009).

Table 3.61: List of the studies conducted on *Pseudosesarma laevimanum*.

Author and Year	**Subject of the study**	**Field**	**Country**
Zehntner 1894	species description as *Sesarma edwardsii* var. *laevimana* (Indonesia; Sarawak, East Malaysia)	taxonomy	Indonesia, Malaysia (East Malaysia)
Nordhaus et al. 2009	spatio-temporal variation of macrobenthic communities in an impacted mangrove-fringed lagoon (Segara Anakan lagoon, Indonesia)	spatial ecology	Indonesia

3.3.12.7 *Pseudosesarma moeschi* (De Man, 1892)

This species was first included by De Man (1887-1888) in the previously described species *Sesarma intermedia* De Haan, 1835, which included samples from Hong Kong, China, Japan, Indonesia, and Myanmar. A few year later, the same author (De Man, 1892) considered the specimens from Myanmar and Indonesia as a new distinct species, and described it as *Sesarma moeschi*. Alcock (1900) recorded this species as *Sesarma intermedia* from Myanmar, while Tesch (1917) included it in his key as *Sesarma moeschi*, and added a distribution record from Sulawesi (Indonesia). Tweedie (1940) reported it as *Sesarma moeachii* from Johor (Peninsular Malaysia), where he found a specimen among the nipah palms (*Nypa fruticans*) along the Sedili River.

McLaughlin et al. (1996) conducted a physiological study on the osmotic and ions regulation of this species, which were found to possess strong osmotic abilities (hypo- and hyper-regulation) over a wide range of salinity conditions. Moreover, these authors reported a personal communication by Prof. P. Naiyanetr, who found this species burrowing in nipah forests beside mangrove areas in the lower tract of estuaries, with average water salinities of 20-28 (McLaughlin et al., 1996).

Guerao et al. (2007) described the complete larval development (four zoeal stages and a megalopa) of this species and the congeneric *P. bocourti* (see also Subchapter 3.3.12.1). Guerao (2008) investigated the resistance to starvation and different salinity conditions in the first zoea of this species and of *P. bocourti*. Zoeal stages were found to tolerate freshwater conditions, and showed relatively high resistance to starvation (high endotrophic potential). Brösing (2014) described the structure of the foregut of this species, from freshly moulted exuviae.

Table 3.62: List of the studies conducted on *Pseudosesarma moeschi.*

Author and Year	Subject of the study	Field	Country
De Man 1887-88	specimens included in *Sesarma intermedia* De Haan, 1835 (Mergui Archipelago, Myanmar; Indonesia)	distribution record (only)	Myanmar, Indonesia
De Man 1892	species description as *Sesarma moeschii* (Sumatra, Indonesia; Mergui Archipelago, Myanmar)	taxonomy	Indonesia, Myanmar
Alcock 1900	new distribution records (Mergui Archipelago, Myanmar)	distribution record (only)	Myanmar
Tesch 1917	new distribution record (Celebes = Sulawesi, Indonesia); species included in checklist and in diagnostic key of sesarmid species	distribution record (only)	Indonesia
Tweedie 1940	as *Sesarma moeschii*; new distribution records (Sedili River, Johor, Peninsular Malaysia), morphological and taxonomic notes	taxonomy	Malaysia (Peninsular Malaysia)

Table 3.62, continued.

McLaughlin et al. (1996)	physiological study on the branchial Na, KATPase new distribution record (Thailand); activity and osmotic and chloride ion regulation in *Pseudosesarma moeschi*	physiology	Thailand
Guerao et al. 2007	larval morphology of *Pseudosesarma bocourti* and *P. moeschi* (Indo-West Pacific)	ontogenesis	IWP
Guerao 2008	resistance to starvation and salinity tolerance in first zoeal stages of *P. bocourti* and *P. moeschi*	ontogenesis	IWP
Brösing 2014	description of the foregut structure from molted exuviae	anatomy/ morphology	IWP

Figure 3.38: *Pseudosesarma moeschi.* Male specimen (Temburong_151013, from the Brunei Bay collection, loc. Sungai Belayang, see Chapter 4). Dorsal (above), ventral (middle) and frontal view (below). Scales are in mm. Pictures by G. Polgar.

3.3.13 Genus *Sarmatium* Dana, 1851

The genus *Sarmatium* has been established by Dana (1851), to include a single species, *S. crassum*, from Samoa. The genus was later expanded by Tesch (1917), who added six other Indo-West Pacific species [*S. integrum*, *S. inermis*, *S. indicum*, *S. punctatum*, *S. biroi*, and *S. fryatti* (= *S. rotundifrons*)] and two Atlantic species (*S. curvatus* and *S. pectinatus*).

Subsequently, Serène and Soh (1970) transferred the two Atlantic species to the previously established genus *Metagrapsus* H. Milne Edwards, 1853, which had been considered a junior synonym of *Sarmatium* by Tesch (1917). In particular, Serène and Soh (1970) provided a series of diagnostic characters to separate the two genera. Moreover, these authors placed all the six IWP species in their newly established genus *Neosarmatium*, therefore leaving *Sarmatium* with one species only, *S. crassum*, with its synonym, *Sesarma germaini* (Serène & Soh, 1970). In particular, at that time the latter species was considered as a junior synonym of *S. crassum*, following a previous note by De Man (1891). However, a year later *Sarmatium germaini* was again re-considered a valid species by Serène and Soh (1971).

Davie (1992) revised the whole genus, providing diagnostic characters to separate the genus from the two closest genera, *Neosarmatium* and *Metagrapsus,* especially considering the ocular peduncle swollen basally, the cornea constricted and reduced, and the upper surface of palm of the male cheliped with a series of transverse grooves separating swollen ridges. This author provided also a taxonomic key and a detailed description of every species, including the previously known *S. crassum* and *S. germaini*, and three additional newly described species (*S. striaticarpus*, *S. hegerli* and *S. unidentatus*). The first of the new species included specimens collected by several authors from Singapore (Tweedie, 1936;

Serène & Soh, 1971), New Caledonia (Serène, 1973), Japan (Sakai, 1936, 1976), and Philippines (Davie, 1992), and previously considered as *S. crassum* (Davie, 1992). The latter two species were instead described on the base of new samples from northern Australia (Davie, 1992).

Sarmatium species have usually been found in mangrove forests of the whole IWP region, from South and East Africa (e.g. Barnard, 1955; Crosnier, 1965; Holthuis, 1977) to South East Asia (e.g. Tweedie, 1936; Serène & Soh, 1971; Diele et al., 2013), East Asia (Sakai, 1936, 1976; Soh, 1978), Australia (Davie, 1992), and Pacific islands (Serène, 1973; Davie, 1992).

Little is known about the ecology of these species. However, specimens have been collected from several mangrove forests (e.g. Crosnier, 1965; Serène, 1973; Sakai, 1976). Some authors provided a few details of the sampling sites, such as *Ceriops* or mixed mangrove zones along creeks (Hartnoll, 1975; Davie, 1992), a mudbank at low tide at the mouth of a river, on a muddy substrate in *Rhizophora* or *Avicennia* zones (Davie, 1992). Moreover, a few authors reported that their specimens were found "nearly always out of the water" (A. Milne Edwards, 1869), at low tide (Davie, 1992), at the "burrow entrance at night 10 m inland from creek bank" (Davie, 1992), in "burrows in riverbanks and banks of drainage channels, moist to very sloppy mud, not restricted to a particular mangrove zone" (Davie, 1992), "amongst debris on mud floor in *Rhizophora* mangrove forest" (Davie, 1992). Davie (1992) also observed that one of his specimens apparently built a burrow with a raised entrance, even though this structure does not look typical for these species.

Two species have been recorded until now from Peninsular Malaysia, Singapore, and/or northern Borneo:

- *S. germaini* (H. Milne-Edwards, 1869)
- *S. striaticarpus* Davie, 1992 (considered *S. crassum* until 1992)

Table 3.63: List of the main studies conducted on the genus *Sarmatium* (including taxonomic studies and reviews of the genus).

Author and Year	Subject of the study
Dana 1851	genus description, including one species (*S. crassum*), from Samoa
De Man 1891	*S. germaini* synonymised with *S. crassum*
Tesch 1917	additional 8 species are included in the genus; species included in checklist and in diagnostic key of sesarmid species
Serène & Soh 1970	2 species transferred to *Metagrapsus*, and 6 species transferred to *Neosarmatium*
Serène & Soh 1917	*S. germaini* re-considered a valid species
Davie 1992	revision of the genus; diagnostic key to the species, description of 3 new species (*S. striaticarpus*, *S. hegerli*, *S. unidentatus*)

3.3.13.1 *Sarmatium germaini* (H. Milne-Edwards, 1869)

This species was described by H. Milne-Edwards (1869) as *Sesarma germani*, from a single specimen collected in Poulo Condore Island (today Con Dao Islands, South China Sea). De Man (1887) examined the type specimen, and added a few morphological notes, suggesting a similarity with *Sesarma smithi* (today *Neosarmatium smithi*). A few years later, the same author re-examined the type specimen and concluded *S. germani* to be a junior synonym of *Sarmatium crassum* (De Man, 1891).

In the following years, this species was not recorded in the literature until the 1970s, although a few specimens were deposited in the National Museum of Singapore, usually as *S. crassum*, obtained from sampling field trips conducted in Peninsular Malaysia and Singapore (see Serène & Soh, 1971).

Serène and Soh (1970) briefly stated that the genus *Sarmatium* included two species, *S. crassum*, and *S. germaini*, therefore considering the latter as a distinct species. The same authors officially re-transferred *S. germaini* to a specific level, and provided taxonomic details and morphological differences to discriminate the two species (Serène & Soh, 1971). In particular, these authors examined the Malaysian specimens of *S. crassum*, which are today considered as *S. striaticarpus* (see also Subchapters 3.3.13 and 3.3.13.2).

Subsequently, *S. germaini* has been recorded from Hong Kong (Soh, 1978), Peninsular Malaysia (Davie, 1992), Thailand (Frith et al., 1976), Philippines (Davie, 1992; Masagca, 2009), Australia (Davie, 1992; Salgado Kent & McGuinness, 2006), Indonesia (Nordhaus et al., 2009), and Vietnam (Diele et al., 2013). In particular, Frith et al. (1976) reported this species from a mangrove forest on Phuket Island (southwestern Thailand), in the landward and middle part of a *Rhizophora apiculata* dominated forest, on muddy substrate and in saltwater conditions (Frith et al., 1976). Nordhaus et al. (2009) recorded this species from an estuarine lagoon in Java (Indonesia), where it was found in a mangrove site dominated by *Avicennia marina*, *Ceriops tagal*, and *Rhizophora mucronata*, with brackish to saltwater salinity conditions, on sandy substrate. The site was close to a city and an oil refinery. Diele et al. (2013) found this species in monocultured *Rhizophora apiculata* stands, both in intact patches (trees aging ~20 years), and in open gaps impacted by typhoons, with 100% tree mortality.

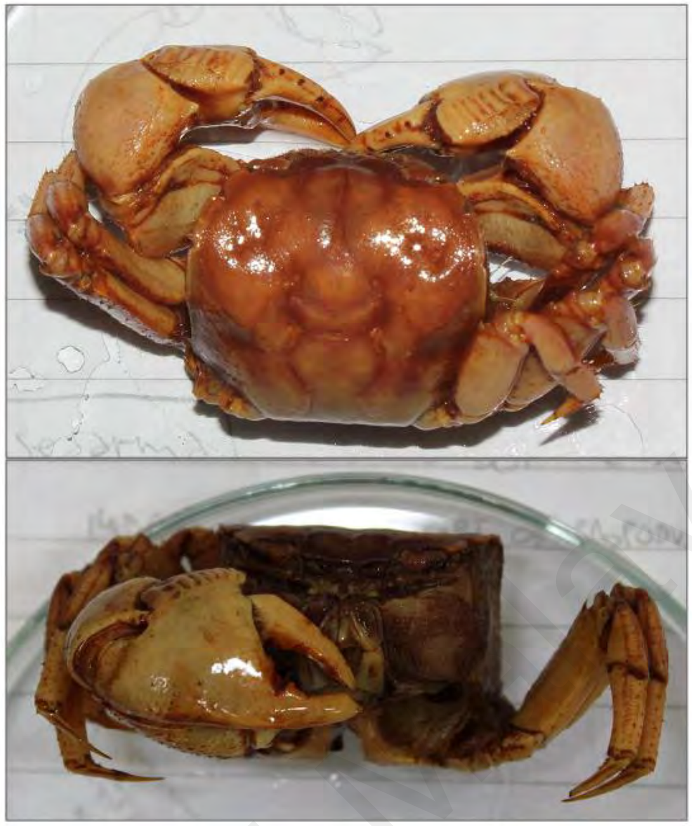

Figure 3.39: *Sarmatium germaini.* Male specimen. From the reference collection of the Raffles Museum of Biodiversity Research in Singapore (Lee Kong Chian Natural History Museum, National University of Singapore), visited by the author in 2011-2012. Specimen number: ZRC 1970.2.20.3. Dorsal (above) and frontal view (below).

Table 3.64: List of the studies conducted on *Sarmatium germaini.*

Author and Year	Subject of the study	Field	Country
H. Milne-Edwards 1869	species description as *Sesarma germani* (Poulo Condore Island = Con Dao Islands, South China Sea)	taxonomy	South China Sea
De Man 1887	as *Sesarma germani* (examined specimens from Pulo Condore = Con Dao Islands, South China Sea); morphological notes	taxonomy	South China Sea
De Man 1891	as *Sesarma germani* (pag. 51); examination of the type specimen; species synonymised with *S. crassum*	taxonomy	South China Sea
Tesch 1917	included in *Sarmatium crassum*; species included in checklist and in diagnostic key of sesarmid species	distribution record (only)	IWP

Table 3.64, continued.

Serène & Soh 1970	*S. germaini* considered as a valid species, within the genus *Sarmatium*	taxonomy	IWP
Serène & Soh 1971	*S. germaini* officially re-transferred to specific level; taxonomic distinction and morphological differences between *Sarmatium germaini* and *S. crassum* (today *S. striaticarpus*) (Singapore; Port Klang, Prai, Peninsular Malaysia)	taxonomy	Malaysia, Singapore
Frith et al. 1976	zonation and abundance of mangrove macrofauna on Phuket Island (Thailand)	spatial ecology	Thailand
Soh 1978	reference collection of sesarmid crabs from Hong Kong	distribution record (only)	Hong Kong
Davie 1992	revision of the genus; diagnostic key to the species	taxonomy	IWP
Kwok & Tang 2005	checklist of the sesarmid crabs of Hong Kong	distribution record (only)	Hong Kong
Salgado Kent & McGuinness 2006	comparison of methods for estimating relative abundance of grapsoid crabs (Australia)	sampling methodology	Australia
Masagca 2009	feeding ecology, burrowing and tree climbing skills of sesarmid crabs in Luzon (Philippines)	distribution record (only)	Philippines
Nordhaus et al. 2009	spatio-temporal variation of macrobenthic communities in an impacted mangrove-fringed lagoon (Segara Anakan lagoon, Indonesia)	spatial ecology	Indonesia
Diele et al. 2013	impact of typhoon on diversity of key ecosystem engineers (Vietnam)	spatial ecology	Vietnam

3.3.13.2 *Sarmatium striaticarpus* Davie, 1992

This species was described by Davie (1992), on the base of specimens previously considered as *Sarmatium crassum*, from East and South East Asia. In particular, this author pointed out that the records of *S. crassum* from this geographic area appeared to be taxonomically distinct from the classic description of this species, prompting him to describe a new species for these samples, i.e. *S. striaticarpus*.

Therefore, previous records of this species as *S. crassum* from Singapore and Peninsular Malaysia [as *Sesarma* (*Sarmatium*) *crassum*, Tweedie, 1936; Serène & Soh, 1971; Berry, 1972; Sasekumar, 1974], Thailand (Frith et al., 1976), New Caledonia (Serène, 1973), and Japan [as *S. crassum* or *Sarmatium* sp. (aff. *S. crassum*), Sakai, 1936, 1976)], are now considered as belonging to *S. striaticarpus*. Moreover, Davie (1992) provided additional distribution records from the Philippines.

Berry (1972) recorded this species from the West coast of Peninsular Malaysia, from the middle and upper parts of the investigated mangrove forests. Sasekumar (1974) reported this species from an estuarine mangrove forest in Selangor (Peninsular Malaysia), from the inner zone of the forest, dominated by *Bruguiera* spp. and *Rhizhophora mucronata* trees. In the investigated sites the substrate was predominantly composed of fine sand and silt, with salinity values ranging from ~3 to nearly 50, with extremes occurring during neap tides (Sasekumar, 1974). Frith et al. (1976) found this species in several stations of their investigated mangrove forest (Thailand), i.e. the whole intertidal extension of a *Rhizophora apiculata* dominated forest, including a landward edge with scattered clumps of nipah palms, the middle part of the forest, and a seaward zone, partially unvegetated and characterised by a sand flat. Sasekumar and Ooi (2005) reported this species as *Sarmatium crassum* from Langkawi (Peninsular Malaysia) from riverine mangrove stands dominated by *Rhizophora* spp. trees. Leh et al. (2010) recorded it as *S. crassum* as well, in a study based on 1980s specimens collected from a Selangor mangrove forest (Peninsular Malaysia). This species was found in both a undisturbed forested area and a cleared one, unvegetated and covered by fallen trunks and scattered branches (Leh et al., 2010). Diele et al. (2013) recorded *S. striaticarpus* from Vietnam, co-existing with the congeneric *S. germaini* (see also Subchapter 3.3.13.1).

Table 3.65: List of the studies conducted on *Sarmatium striaticarpus.*

Author and Year	Subject of the study	Field	Country
Tesch 1917	included in *Sarmatium crassum*; morphological notes; species included in checklist and in diagnostic key of sesarmid species	distribution record (only)	IWP
Sakai 1936	as *Sarmatium* sp. (aff. *S. crassum*), new distribution record (Japan)	distribution record (only)	Japan
Tweedie 1936	as *Sarmatium* sp. (aff. *S. crassum*); new distribution records (Singapore; Johor Strait; Port Swettenham = Port Klang, Peninsular Malaysia)	distribution record (only)	Singapore, Malaysia (Peninsular Malaysia)
Serène & Soh 1971	taxonomy, taxonomic distinction and morphological differences between *Sarmatium germaini* and *S. crassum* (today *S. striaticarpus*) (Singapore, Peninsular Malaysia)	distribution record (only)	Singapore, Malaysia (Peninsular Malaysia)
Serène 1973	as *Sarmatium crassum*; new distribution records (New Caledonia; morphological and taxonomic notes; morphometric measurements	taxonomy	New Caledonia
Sasekumar 1974	as *Sarmatium crassum*; distribution, abundance and zonation of mangrove macrofauna in Port Klang (Peninsular Malaysia)	spatial ecology	Malaysia (Peninsular Malaysia)
Frith et al. 1976	as *S. crassum*; zonation and abundance of mangrove macrofauna on Phuket Island (Thailand)	spatial ecology	Thailand
Sakai 1976	as *Sarmatium crassum*; distribution record (Japan)	distribution record (only)	Japan
Choy 1991	as *Sarmatium crassum* ; checklist of Crustacea of Brunei Darussalam	distribution record (only)	Brunei Darussalam
Davie 1992	species description as *Sarmatium striaticarpus,* from specimens previously attributed to *S. crassum*; new distribution record (Philippines)	taxonomy	Philippines
Sasekumar & Ooi 2005	as *Sarmatium crassum*; faunal diversity in Langkawi mangrove forests (Peninsular Malaysia)	spatial ecology	Malaysia (Peninsular Malaysia)
Leh et al. 2010	as *Sarmatium crassum*; biomass and abundance of sesarmid crabs in a natural and disturbed mangrove area in Selangor (Peninsular Malaysia)	spatial ecology	Malaysia (Peninsular Malaysia)
Diele et al. 2013	as *Sarmatium striaticarpus*; impact of typhoon on diversity of key ecosystem engineers (Vietnam)	spatial ecology	Vietnam

3.3.14 Genus *Selatium* Serène & Soh, 1970

The genus *Selatium* has been described as a subgenus within the genus *Neoepisesarma*, by Serène and Soh (1970), in their revision of the IWP sesarmid genera. In particular, these authors subdivided their newly established genus *Neoepisesarma* in three subgenera, namely *Neoepisesarma* (*Neoepisesarma*), *N.* (*Muradium*), and *N.* (*Selatium*) (Serène & Soh, 1970; see also Subchapter 3.3.3). The latter subgenus was established to include a single species, *N.* (*Selatium*) *brockii*, which was previously included in the broader genus *Sesarma* (Serène & Soh, 1970).

A few years later, several authors suggested and acknowledged *Selatium* as a distinct genus, without further explanations (Hartnoll, 1975; Holthuis, 1977; Sivasothi et al., 1993; Tan & Ng, 1994; Ng & Sivasothi, 1999). Moreover, the previously described *Sesarma elongatum* A. Milne-Edwards, 1869 was transferred to *Selatium* (see Hartnoll, 1975; Vannini et al., 1997; Ng et al., 2008), which therefore currently includes two species (Schubart et al., 2009). Two molecular studies recently conducted on several sesarmid species (Fratini et al., 2005; Schubart et al., 2006) further supported this new arrangement, showing that both the *Selatium* species are sister taxa, and are generically distinct from the closely related *Episesarma*, *Neosesarma*, and *Clistocoeloma*, on the basis of evidence from two mitochondrial genes. Schubart et al. (2009) revised the genus, providing morphological and molecular data that consolidated *Selatium* as a distinct genus from *Episesarma*, and discussed taxonomic differences between *S. brockii* and *S. elongatum*. Moreover, these authors established a new genus, allied to *Selatium* and *Clistocoeloma*, named *Lithoselatium*, whose species are found along intertidal rocky shores (Schubart et al., 2009).

Selatium species have been recorded from the whole Indo-West Pacific, from East Africa (Vannini & Valmori, 1981) to the Western Pacific (Schubart et al., 2009). Several studies have reported the tree-climbing behaviour of these species, which inhabit coastal mangrove forests, and are usually observed within crevices and inside hollow trees or other natural hides (Hartnoll, 1975; Sivasothi et al., 1993; Sivasothi, 2000). Cannicci et al. (1999) found that these crabs were generally active during high tide, when they were seen feeding on floating algae and mangrove leaves. Moreover, the same authors observed also that male individuals were defending their activity area from other large males, thus suggesting a kind of territoriality (Cannicci et al., 1999).

A few studies investigated the feeding behaviour and ecology of these species, which were found to be feeding at night, mainly on algae, in contrast with most of the other sesarmid species, which prefer instead mangrove leaves and litter (Cannicci et al., 1999; Dahdouh-Guebas et al., 1999; Sivasothi, 2000). The larval morphology was investigated for *S. brockii* (Vijayakumaran & Kunnupandi, 1987).

Only one of the two species of this genus, *S. brockii* (De Man, 1887), has been recorded from Peninsular Malaysia, Singapore, and/or northern Borneo. The other species, *S. elongatum* (A. Milne-Edwards, 1869), has been recorded from the Andaman Sea, which some authors consider as geographically part of the region of the Malay Peninsula. Therefore, this species has been included in the present synopsis.

Table 3.66: List of the main studies conducted on the genus *Selatium* (including taxonomic studies and reviews of the genus).

Author and Year	Subject of the study
Serène & Soh 1970	genus description
Schubart et al. 2009	genus revision, molecular analysis

3.3.14.1 *Selatium brockii* (De Man, 1887)

This species was described as *Sesarma brockii* from Ambon Island (Meluku Archipelago, Indonesia), by De Man (1887). However, this first description was a very brief diagnosis, and the following year the same author provided a further description, with figures and additional details (De Man, 1888).

In the following years, several authors reported it from other localities across South East Asia, including Indonesia (Thallwitz, 1891; De Man, 1902), Peninsular Malaysia and Singapore (Nobili, 1900; Tweedie, 1936), Borneo (De Man, 1895, 1901; Nobili, 1901, 1903a), Andaman Islands (Alcock, 1900), New Guinea and Pacific Ocean (Ortmann, 1894a; Tesch, 1917). More recently, *S. brockii* has been recorded from East Africa (Hartnoll, 1975; Vannini et al., 1997; Fratini et al., 2005; Schubart et al., 2006), and India (Vijayakumaran & Kunnupandi, 1987; Ravichandran et al., 2007; Varadharajan et al., 2013; Varadharajan & Soundarapandian, 2014; Kamalakkanan, 2015; Maharajan et al., 2015; Trivedi et al., 2015).

Most of these studies also provided additional morphological and taxonomic notes, while a few works reported notes on the ecological conditions where the specimens were collected (e.g. Tweedie, 1936; Vannini et al., 1997; Sivasothi, 2000). Tweedie (1936) found his specimens "associated with *Metopograpsus* spp., on the wooden piles of fishing stakes and bathing enclosures, not, like most of the other marine members of the genus, in mangrove swamp" (Tweedie, 1936, p. 51). Sivasothi et al. (1993) reported that this species perform tree-climbing behaviour and they considered it as a "non-burrowing habitual climber" species, which has been observed up to 4 m high on the tree trunks. Moreover, these authors reported *S. brockii* to be feeding at night, mainly on algae, lichens and fungi, and occasionally scavenging (Sivasothi et al., 1993).

Vannini et al. (1997) reviewed the tree climbing behaviour of this species (as *Sesarma brocki*) from Kenya, and considered this species as an exclusively arboreal species, living only on mangrove roots and trunks. These authors found this species to be associated mainly with *Avicennia* trees. Sivasothi (2000) investigated the niche preferences of the arboreal species of grapsoid crabs in the mangrove forests of Singapore (i.e. *Selatium brockii*, *Metopograpsus* spp., *Episesarma* spp.), in particular regarding their diet, distribution in the mangrove, and spatial strategies. *S. brockii* was found in the seaward zone of the investigated forest, consisting of a sandbar, hosting mainly *Sonneratia ovata* and *Avicennia alba*, and it was observed mainly on tree trunks, climbing up to 4 m, grazing on algae at night (Sivasothi, 2000).

Ravichandran et al. (2007) recorded this species as *Sesarma brockii* from each of their investigated stations, in an estuarine mangrove forest on the East coast of India. Varadharajan et al. (2013) reported it twice in their checklist, as *Selatium brockii*, belonging to the Grapsidae family, and also as *Sesarma brocki* (Sesarmidae family), possibly due to taxonomic confusion. Varadharajan and Soundarapandian (2014) found *S. brockii* in all the investigated study sites (southeastern coast of India), and observed that this species is commonly found "underneath the bark of dead trunks or inside hollow trees".

Vijayakumaran and Kunnupandi (1987) described the larval morphology of this species, including four zoeal and one megalopal stages. Fratini et al. (2005) conducted molecular analyses on the tree-climbing species of sesarmid and other grapsoid crabs (including also *S. brockii*), to investigate whether the tree-climbing behaviour has a monophyletic origin, or it is instead due to convergent evolution.

Figure 3.40: ***Selatium brockii.*** Female specimen (P-Bedukang_131013_7, from the Brunei Bay collection, loc. Pulau Bedukang, see Chapter 4). Dorsal (above), ventral (middle) and frontal view (below). CW = 2.54 cm.

Table 3.67: List of the studies conducted on *Selatium brockii.*

Author and Year	Subject of the study	Field	Country
De Man 1887	species description as *Sesarma brockii* (Amboina = Ambon Island, Indonesia)	taxonomy	Indonesia
De Man 1888	as *Sesarma brockii* (Ambon, Indonesia), additional description, with figures and details	taxonomy	Indonesia
Thallwitz 1891	as *Sesarma brockii* (Ternate, Indonesia)	distribution record (only)	Indonesia
Ortmann 1894a	as *Sesarma brockii* (Pacific Ocean)	distribution record (only)	Pacific Ocean

Table 3.67, continued.

De Man 1895	new distribution records as *Sesarma* (*Episesarma*) *brockii* (Pontianak, Kalimantan); morphological and taxonomic notes; morphometric measurements	taxonomy	Indonesia
Alcock 1900	as *Sesarma brockii*; morphological and taxonomic notes (Andaman Islands)	taxonomy	Andaman Islands
Nobili 1900	as *Sesarma* (*Sesarma*) *brockii*; morphological and taxonomic notes (Malaya = Peninsular Malaysia)	taxonomy	Malaysia (Peninsular Malaysia)
Nobili 1901	as *Sesarma* (*Episesarma*) *brockii*, new distribution records (Sarawak, East Malaysia)	distribution record (only)	Malaysia (East Malaysia)
De Man 1902	as *Sesarma* (S*esarma*) *brockii*, new distribution records (Halmahera, Indonesia); morphological and taxonomic notes; morphometric measurements	taxonomy	Indonesia
Nobili 1903a	as *Sesarma* (*Sesarma*) *brockii ,* new distribution records (Samarinda, Kalimantan, Borneo)	distribution record (only)	Indonesia
Tesch 1917	as *Sesarma* (*Sesarma* s.s.) *brockii,* examination of Leiden Museum specimens (New Guinea); morphological notes; species included in checklist and in diagnostic key of sesarmid species	taxonomy	Papua New Guinea
Tweedie 1936	as *Sesarma* (*Sesarma*) *brockii*; new distribution records (Singapore); ecological, morphological and taxonomic notes	taxonomy/spatial ecology	Singapore
Hartnoll 1975	as *Selatium brocki*, new distribution record (Tanzania)	distribution record (only)	Tanzania
Vijayakumaran & Kunnupandi 1987	zoeal and megalopal morphology of *S. brockii*	ontogenesis	India
Sivasothi et al. 1993	tree climbing and herbivory of mangrove crabs (Singapore)	feeding ecology/tree climbing	Singapore
Vannini et al. 1997	as *Sesarma brockii*; tree-climbing patterns in mangrove crabs (Kenya)	distribution record (only)	Kenya
Sivasothi 2000	diet, distribution and spatial strategy of the tree climbing grapsoid species of Singapore mangroves	spatial ecology / feeding ecology	Singapore
Fratini et al. 2005	phylogeny, evolutionary origin of tree-climbing behaviour in grapsoid crabs, convergence, 16S and 12S rRNA genes	phylogenesis / molecular ecology	IWP

Table 3.67, continued.

Ravichandran et al. 2007	diversity and habitat preference of crabs in Pichavaram mangrove system (India)	spatial ecology	India
Varadharajan et al. 2013	crab diversity of Puducherry (India)	distribution record (only)	India
Varadharajan & Soundarapandian 2014	crab diversity of the South East coast of India	spatial ecology	India
Kamalakkanan 2015	as *Sesarma brockii*; habitat distribution and diversity of mangrove crabs in Pondicherry (India)	distribution record (only)	India
Maharajan et al. 2015	as *Sesarma brooki*; brachyuran diversity Yuthu Pettai (Tamil Nadu, India)	distribution record (only)	India
Trivedi et al. 2015	checklist of crustacean fauna of Gujarat (India)	distribution record (only)	India

3.3.14.2 *Selatium elongatum* (A. Milne-Edwards, 1869)

This species was described as *Sesarma elongatum* by A. Milne Edwards (1869), from Madagascar. A few years later, De Man (1887) provided additional morphological notes, and Ortmann (1894a) reported it as *Sesarma elongata* from Tanzania, adding taxonomic remarks. Alcock (1900) described a new species, *Sesarma latifemur*, from the Andaman Islands, which was later considered to be a junior synonym of *S. elongatum* (Ng et al., 2008). Alcock and McArdle (1903) also reported this species as *S. latifemur* from the Andaman Islands.

As a consequence, Tesch (1917) included both the species (as *S. elongata* and *S. latifemur*) in his key on the IWP sesarmid species. However, this author suggested that the two species may be identical, since Alcock (1900) himself admitted that *S. latifemur* showed a striking similarity with *S. elongata*. Nonetheless, Tesch (1917) highlighted a few morphological and taxonomic differences between the two species (pectinated crest near the upper border of the palm of the cheliped, and shape of the carapace).

Tesch (1918) reported this species as *S.* (*Holometopus*) *elongata* from New Guinea and Ceram (Maluku Islands, Indonesia). Later, Fourmanoir (1954) and Crosnier (1965) included this species in their checklists of the brachyuran fauna of Madagascar, as *Sesarma* sp. and *S.* (*Holometopus*) *elongatum*, respectively. Serène (1968) cited this species in his list on the brachyuran species of South East Asia.

In the following years, several authors reported it, generally as *Selatium elongatum*, from along the East coast of Africa, from Tanzania (Hartnoll, 1975), to Somalia (Vannini & Valmori, 1981) and Kenya (Cannicci et al., 1999; Dahdouh-Guebas et al., 1999, 2002; Bosire et al., 2004; Fratini et al., 2005). More recently, Masagca (2009) provided an additional record from the Philippines, while in their review of the genus, Schubart et al. (2009) examined specimens from Kenya, Philippines, Indonesia (Sulawesi), and Papua New Guinea.

Figure 3.41: *Selatium elongatum.* Male specimen. From the reference collection of the Raffles Museum of Biodiversity Research in Singapore (Lee Kong Chian Natural History Museum, National University of Singapore), visited by the author in 2011-2012. Specimen number: ZRC 2009.0567. Dorsal (above), ventral (middle) and frontal view (below left), and detail of the cheliped (below right). Scales are in mm.

A few of the studies from East Africa investigated ecological aspects and the behaviour of *S. elongatum* (Cannicci et al., 1999; Dahdouh-Guebas et al., 1999, 2002; Bosire et al., 2004). Vannini et al. (1997) reviewed the tree climbing behaviour of this species (as *Sesarma elongatum*) from Kenya, and considered this species as an exclusively arboreal species, living only on mangrove roots and trunks, and occasionally found on the forest floor. These authors found this species mainly associated with *Rhizophora* and *Sonneratia* trees.

Dahdouh-Guebas et al. (1999) investigated the feeding habits of 11 species of grapsoid and other brachyuran families commonly found in a Kenyan mangrove forest. These authors examined the gut contents of the selected species, and found that *S. elongatum* was only partly eating mangrove leaves, but mainly feeding on macro-algae, such as *Bostrichia tenella*, a very common species on the aerial roots of *Rhizophora mucronata*, where the specimens were collected (Dahdouh-Guebas et al., 1999). Moreover, these authors reported *S. elongatum* from both the landward *Avicennia* belt, and from the seaward *Rhizophora* and *Sonneratia* zone, while it was absent in the middle zone of the forest, dominated by *Rhizophora* and *Ceriops* trees (Dahdouh-Guebas et al., 1999).

Cannicci et al. (1999) conducted a study on the use of time, space and trophic resources of *S. elongatum*, with observations in the field and gut content analyses. This species was found to be very adapted to tree climbing, and generally to the mangrove habitat. It was observed to be active at high tide, both during the day and at night, and it was found along the tree trunks, just above the water level, feeding on floating algae and mangrove leaves (Cannicci et al., 1999). Observations on the behaviour and activity patterns revealed that larger males were always seen "within activity areas into which they allow females and smaller males but exclude males of the same size, which probably compete for females" (Cannicci et al., 1999).

Dahdouh-Guebas et al. (2002) explored the link between the distribution of mangrove tree species and that of selected crab species, by describing and confronting the zonation of mangrove and crab species. This study revealed that *S. elongatum* appeared to be associated with the seaward *Avicennia marina* and *Sonneratia alba* zone of the investigated area (Dahdouh-Guebas et al., 2002).

Bosire et al. (2004) investigated the spatial variation in the "recolonisation by crab species and sediment-infauna taxa in artificially regenerated mangrove stands of *Avicennia marina*, *Rhizophora mucronata* and *Sonneratia alba* (5 year old)". These authors collected their samples in both unvegetated sites (open areas without mangroves or denuded), reforested sites (rehabilitated through tree planting), and natural sites (relatively undisturbed), utilised as controls. *S. elongatum* was found in a natural site, dominated by *Rhizophora mucronata* (Bosire et al., 2004).

Masagca (2009) conducted field observations in the Philippines, investigating the crab habitats, feeding habits, and tree-climbing skills. In particular, *S. elongatum* was found to be a climber of mangrove trees exclusively (EMTC, i.e. "exclusive mangrove tree climber"), observed on trunks, branches and canopies (mainly *Rhizhophora*), on aerial roots, or inside trunks crevices (Masagca, 2009).

In their molecular study on the tree-climbing species of sesarmid and other grapsoid crabs (see also Subchapters 3.3.14 and 3.3.14.1), Fratini et al. (2005) found that *S. elongatum* can be considered a sister-species of *S. brockii*, therefore consolidating the current systematic position of these species within the genus *Selatium*.

Table 3.68: List of the studies conducted on *Selatium elongatum*.

Author and Year	Subject of the study	Field	Country
A. Milne-Edwards 1869	species description as *Sesarma elongatum* (Madagascar)	taxonomy	Madagascar
De Man 1887	as *Sesarma elongata* (no new locality); morphological notes	taxonomy	Madagascar
Ortmann 1894a	as *Sesarma elongata*; new distribution record (Tanzania)	distribution record (only)	Tanzania
Alcock 1900	species description as *Sesarma latifemur* (Andaman Islands)	distribution record (only)	Andaman Islands
Alcock & McArdle 1903	as *Sesarma latifemur* (Andaman Islands)	distribution record (only)	Andaman Islands
Tesch 1917	as *Sesarma* (*Holometopus*) *elongata* and as *Sesarma* (*Holometopus*) *latifemur*; species included in checklist and in diagnostic key of sesarmid species	distribution record (only)	IWP
Tesch 1918	as *Sesarma* (*Holometopus*) *elongata*; new distribution records (New Guinea; Ceram, Maluku Islands, Indonesia); morphological and taxonomic notes	taxonomy	Papua New Guinea, Indonesia
Fourmanoir 1954	as *Sesarma* sp. (Madagascar)	distribution record (only)	Madagascar
Crosnier 1965	as *Sesarma* (*Holometopus*) *elongatum*; taxonomy, presentation of the sesarmid and grapsoid species of Madagascar	taxonomy	Madagascar
Serène 1968	checklist of the non-planctonic marine fauna of South East Asia; new distribution record (South East Asia)	distribution record (only)	South East Asia
Hartnoll 1975	new distribution record (Tanzania)	distribution record (only)	Tanzania
Vannini & Valmori 1981	checklist of grapsoid species from Somalia	distribution record (only)	Somalia
Vannini et al. 1997	tree-climbing patterns in mangrove crabs (Kenya)	tree climbing	Kenya
Cannicci et al. 1999	use of time, space and food resources in *S. elongatum* (Kenya)	spatial ecology / feeding ecology	Kenya
Dahdouh-Guebas et al. 1999	feeding ecology, gut contents and feeding habits of 11 species of mangrove crabs (Kenya)	feeding ecology	Kenya

Table 3.68, continued.

Dahdouh-Guebas et al. 2002	zonation of mangroves species and grapsoid crabs, and mutual relationships (Kenya)	spatial ecology	Kenya
Bosire et al. 2004	ecology, spatial variation in macrobenthos in a post-recolonisation mangrove forest (Kenya)	spatial ecology	Kenya
Fratini et al. 2005	phylogeny, evolutionary origin of tree-climbing behaviour in grapsoid crabs, convergence, 16S and 12S rRNA genes	phylogeny	IWP
Masagca 2009	feeding ecology, burrowing behaviour and arboreal climbing skills of sesarmid crabs in Luzon (Philippines)	feeding ecology/ spatial ecology/ tree climbing	Philippines

3.3.15 Genus *Sesarmoides* Serène & Soh, 1970

The genus *Sesarmoides* has been described by Serène and Soh (1970) to accommodate the group of species included by Tesch (1917) in the division 12 of his diagnostic key. In particular, these species have been characterised by a flattened carapace with lateral border strongly divergent backward, basal antennular segment swollen and globular, antennal peduncle nearly longitudinal, a strong transverse rim with a deep median notch on the epigastric region, pereopods 2-5 slender and elongated (Serène & Soh, 1970). Additionally, Serène & Soh (1970) added other species to the genus, which were described after Tesch (1917), increasing therefore the number of species to eight, namely *S. kraussi*, *S. kraussi borneensis*, *S. longipes*, *S. cerberus*, *S. jacksoni*, *S. jacobsoni*, *S. verleyi*, and *S. jarvisi*.

More recently, Ng (2002) revised the genus, recognising 14 species, including 5 newly described species. He also noticed that this genus could be subdivided in two groups of species. The first was composed of only three species (*S. borneensis*, *S. kraussi*, *S.*

longipes), associated with mangrove forests, estuarine ecosystems, and occasionally coastal caves, while the second group included the rest of the species, which are typically associated with limestone or karst cave systems (Ng, 2002).

A second revision by Davie and Ng (2007) recognised these two groups as distinct genera, and provided a key to the species. In particular, the first group remained as *Sesarmoides sensu stricto*, while the second group of cavernicolous species was included in a new genus, *Karstama* (Davie & Ng, 2007). The two genera are distinguished by a few morphological characters, especially a unique stridulatory mechanism in the genus *Sesarmoides sensu stricto*, consisting of a longitudinal crest on the cheliped merus, which is rubbed against a ridge of suborbital granules (Davie & Ng, 2007).

Specimens of *Sesarmoides* have been collected from the whole IWP, including East and South Africa (Emmerson, 1994a; Bosire et al., 2004), India (De Man, 1887), Myanmar (De Man, 1888), Thailand and Andaman Sea (Alcock, 1900; Lundoer, 1974; Frith, 1977; Macintosh et al., 2002), Peninsular Malaysia and Singapore (Tweedie, 1936; Sasekumar, 1974; Rodelli et al., 1984; Al-Shami et al., 2014), Borneo (Tweedie, 1950a; Ashton et al., 2003b), Indonesia (Davie & Ng, 2007), Australia (Frusher et al., 1994; Salgado Kent & McGuinness, 2006, 2010), and Japan (Komai et al., 2004).

Little is known about the ecology of these species. However, most of the collected specimens have been found in mangrove forests, usually in mixed assemblages, on muddy or silty soil, in different parts of the forest and on the adjacent tidal flat (e.g. Frusher et al., 1994; Ashton et al., 2003b).

Two species have been recorded until now from Peninsular Malaysia, Singapore, and/or northern Borneo:

- *S. borneensis* (Tweedie, 1950)
- *S. kraussi* (De Man, 1887)

Table 3.69: List of the main studies conducted on the genus *Sesarmoides* (including taxonomic studies and reviews of the genus).

Author and Year	Subject of the study
Serène & Soh 1970	genus description
Ng 2002	new species of cavernicolous *Sesarmoides* crabs; key to the genus, morphological and taxonomic notes
Davie & Ng 2007	morphological and taxonomic notes; key of the genus; 12 species previously included in *Sesarmoides* transferred to newly established genus *Karstama*

3.3.15.1 *Sesarmoides borneensis* (Tweedie, 1950)

This species was described as *Sesarma kraussi borneensis*, a subspecies of the already existing *S. kraussi*, by Tweedie (1950a), from Borneo and Singapore. While Serène and Soh (1970) still maintained this taxon as a subspecies, several other authors considered it as a valid species and named it as *Sesarmoides borneensis* (e.g. Robertson & Daniel, 1989; Frusher et al., 1994; Ashton et al., 2003b). This species has been reported from Borneo (Tweedie, 1950a; Ashton et al., 2003b), Singapore (Tweedie, 1950a), and Australia (Robertson and Daniel, 1989; Frusher et al., 1994; Salgado Kent & McGuinness, 2006, 2010).

S. borneensis has been found in mangrove forests, such as mixed stands dominated by *Avicennia* or *Ceriops* species (Robertson & Daniel, 1989), or estuarine mixed mangrove systems (Frusher et al., 1994; Ashton et al., 2003b). In particular, Frusher et al. (1994) found one specimen of *S. borneensis* on a silt-clay substrate, in a riverine forest experiencing a wide range of salinity values (0-21‰ upstream, 4-34‰ at the river mouth). These authors, however, did not specify in which part of the river this species was collected (Frusher et al., 1994).

Ashton et al. (2003b) collected this species in a riverine mixed mangrove forest in Sarawak (Borneo), in brackish salinity conditions. Although they called the species *S. borneensis* in their species checklist, they also stated in their discussion that the mean density of *S. kraussi* in their study was 1.3 individuals m^{-2} (Ashton et al., 2003b). These authors also compared this data with another study from Peninsular Malaysia (i.e. Sasekumar, 1974), where the densities were much higher (2.9 individuals m^{-2}; see also Subchapter 3.3.15.2). This apparent taxonomic confusion is probably resulting from the previous nomenclature of this species, initially known as *S. kraussi borneensis*.

Salgado Kent and McGuinness (2010) recorded *S. borneensis* from the mangrove system boarding the coast of Darwin Harbour (northern Australia). In particular, these authors collected their specimens mostly in upstream sites, during spring tide, from both the forest, a tidal creek, and the adjacent tidal flat (Salgado Kent & McGuinness, 2010).

Table 3.70: List of the studies conducted on *Sesarmoides borneensis.*

Author and Year	Subject of the study	Field	Country
Tweedie 1950a	species description as subspecies *Sesarma kraussi borneensis* (Labuan, East Malaysia; Singapore)	taxonomy	Malaysia (East Malaysia), Singapore
Robertson & Daniel 1989	feeding ecology, influence of crabs on mangrove litter processing (Australia)	feeding ecology	Australia
Frusher et al. 1994	distribution and abundance of sesarmid crabs in the Murray River estuary (Australia), role of sediment characteristics and salinity, test on salinity tolerance and osmoregulatory ability	spatial ecology	Australia
Ashton et al. 2003b	ecology and diversity of crab and mollusc macrofaunal community in the Sematan mangrove forest (Sarawak, East Malaysia)	spatial ecology	Malaysia (East Malaysia)
Salgado Kent & McGuinness 2006	comparison of methods for estimating relative abundance of grapsoid crabs (Australia)	sampling methodology	Australia
Salgado Kent & McGuinness 2010	spatial and temporal variation in relative abundance of grapsoid crabs (Australia)	spatial ecology	Australia

Figure 3.42: ***Sesarmoides borneensis.*** Male specimen. From the reference collection of the Raffles Museum of Biodiversity Research in Singapore (today Lee Kong Chian Natural History Museum, National University of Singapore), visited by the author in 2011-2012. Specimen number: ZRC 1970-1-23-12-13. Dorsal (above), ventral (middle) and frontal view (below). The abdomen has been artificially removed. Scales are in mm.

3.3.15.2 *Sesarmoides kraussi* (De Man, 1887)

This species was described by De Man (1887-1888), as *Sesarma krausii*, from the Bengal Bay (India). However, a few years before, a specimen of this species was collected in Singapore, and included in the checklist of the Crustacean specimens of the British Museum (London) as *Sesarma longipes*, by White (1847). In particular, this reference has been cited by other authors (e.g. De Man, 1887-1888; Tesch, 1917; Tweedie, 1936) as White *nec* Krauss (1847), because Krauss is the author of *S. longipes*, although this specimen has been later considered to be *S. kraussi*.

In the years following the description, De Man (1888) and Alcock (1900) reported this species as *Sesarma kraussi* from Myanmar and the Nicobars Islands, respectively. Tesch (1917) included this species as *Sesarma* (*Sesarma* s.s.) *kraussi* in his diagnostic key of the IWP sesarmid species, while Tweedie (1936) reported this species from the West coast of Peninsular Malaysia. Guinot and Crosnier (1964) provided additional taxonomic and morphological notes, and compared this species and the conspecific *S. longipes*.

Berry (1972) reported this species from the West coast of Peninsular Malaysia, where it was collected from the upper and middle part of the investigated mangrove forests. Lundoer (1974) included *S. kraussi* in the list of specimens in the reference collection of the Phuket Marine Biological Center (Thailand). Sasekumar (1974) recorded this species from the West coast of Peninsular Malaysia (Port Klang, Selangor). This study was conducted in the Kapar Mangrove Forest Reserve, in an estuarine mangrove forest, in brackish to saltwater salinity conditions. In particular, *S. kraussi* was collected from a few of the investigated stations, including a broad, thinly forested strip along the top of the eroding mud-bank, with sparse populations of *Avicennia marina*, *Bruguiera parviflora* and *Rhizophora mucronata*;

the inner part of the estuarine mangrove forest, 120 m wide landwards, bordered by a low river mud-bank, with *B. parviflora* and *R. mucronata* predominant trees, with three streams meandering through the area; a belt, 15 m wide, running along the mud-bank top of the river side, dominated by thick stands of *B. parviflora* interspersed with *R. mucronata* (Sasekumar, 1974).

Frith (1977) collected this species in the mangrove stands of Surin Island (West coast of Thailand), from the seaward area of the forest, 40 m wide, dominated by *Rhizophora mucronata* and a few *R. apiculata* trees. A few decades later, Zakaria and Sasekumar (1994) found *S. kraussi* in Kapar forest (Selangor, Peninsular Malaysia) again, both from the forest and from an adjoining area, which had been deforested and then abandoned.

Macintosh et al. (2002) reported this species from the rehabilitated mangrove forests in Ranong Biosphere Reserve (Thailand), including areas with different past management history, and a natural, mature, mixed mangrove forest. Ashton et al. (2003a) recorded *S. kraussi* from Klong Nao forest (Ranong, Thailand) and Merbok estuary (Kedah, Peninsular Malaysia), the former included in a natural reserve, the latter partially managed on a low scale (for charcoal and poles). Both these sites were dominated by *Rhizophora* spp., in brackish salinity conditions (Ashton et al., 2003a).

Komai et al. (2004) reported this species from the Ryukyu Islands (Japan), where it was found burrowing "in well drained areas of sandy mud near the seaward edge of mangrove swamps", and occasionally co-occurring with another sesarmid species, *Clistocoeloma villosum*. Leh et al. (2010) presented a study based on samples collected in 1980-1981 from an upper intertidal mangrove site in Selangor (Peninsular Malaysia), in particular including an undisturbed mixed forest and a cleared area, where trees had been cut three months before the sampling. *S. kraussi* was collected from the disturbed area, almost unvegetated and rich in fallen trunks and scattered debris (Leh et al., 2010).

Rodelli et al. (1984) included this species as *Sesarma kraussi* among their investigated species, in a study on the isotopic carbon ratio ($\delta^{13}C$) of several mangrove plants and animals from the West coast of Peninsular Malaysia. In particular, *S. kraussi* isotopic carbon ratios were relatively high (~24-25 ‰), similar to those of other sesarmid species, thus suggesting a diet based mainly on mangrove leaves or litter (Rodelli et al., 1984). Leh and Sasekumar (1985) investigated the stomach content of this species from Selangor (Peninsular Malaysia). These authors found that 93% of the volumetric gut composition was made of mangrove plant materials, while mineral particles, brachyuran debris and insects represented 2%, 3% and 2% of the diet composition, respectively (Leh & Sasekumar, 1985).

Figure 3.43: ***Sesarmoides kraussi.*** Male specimen. From the reference collection of the Raffles Museum of Biodiversity Research in Singapore (today Lee Kong Chian Natural History Museum, National University of Singapore), visited by the author in 2011-2012. Specimen number: ZRC 1970.1.20.5-6. Dorsal (above), ventral (middle) and frontal view (below). Scales are in mm.

Table 3.71: List of the studies conducted on *Sesarmoides kraussi*.

Author and Year	Subject of the study	Field	Country
White 1847	as *Sesarma longipes*; species distribution record (Singapore), in the checklist of the Crustacean specimens of the British Museum of London; later cited as White *nec* Krauss 1847	distribution record (only)	Singapore
De Man 1887-1888	species description as *Sesarma krausii* (from Bengal Bay, India)	taxonomy	India
De Man 1888	as *Sesarma kraussi*; new distribution record (Kisseraing Island, Mergui Archipelago, Myanmar)	distribution record (only)	Myanmar
Alcock 1900	as *Sesarma kraussi*; new distribution record (Nicobars Islands, eastern Indian Ocean)	distribution record (only)	Nicobars
Tesch 1917	as *Sesarma* (*Sesarma* s.s.) *kraussi*; species included in checklist and in diagnostic key of sesarmid species	distribution record (only)	IWP
Tweedie 1936	as *Sesarma* (*Sesarma*) *kraussi*; new distribution records (Port Klang, Selangor, Peninsular Malaysia)	distribution record (only)	Malaysia (Peninsular Malaysia)
Guinot & Crosnier 1964	taxonomic and morphological notes; comparison between *S. kraussi* and *S. longipes*	taxonomy	IWP
Berry 1972	mangrove macrofauna of the West coast of Peninsular Malaysia	spatial ecology	Malaysia (Peninsular Malaysia)
Lundoer 1974	checklist of brachyuran crabs in the reference collection at Phuket Marine Biology Center (Thailand)	distribution record (only)	Thailand
Sasekumar 1974	distribution, abundance and zonation of mangrove macrofauna (polychaetes, gastropods, crustaceans, sipunculids, fishes) in Port Klang (Peninsular Malaysia)	spatial ecology	Malaysia (Peninsular Malaysia)
Frith 1977	distribution of benthic macrofauna of a mangrove, mudflat and sandflat at Koh Surin Nua Island (Thailand)	spatial ecology	Thailand
Rodelli et al. 1984	stable isotope ratio as a carbon tracer in mangrove ecosystems (West coast Peninsular Malaysia)	feeding ecology	Malaysia (Peninsular Malaysia)
Leh & Sasekumar 1985	food composition in the gut contents of Malaysian sesarmid crabs (Selangor, Peninsular Malaysia)	feeding ecology	Malaysia (Peninsular Malaysia)
Zakaria & Sasekumar 1994	macroinvertebrate fauna in cleared and intact mangrove forests in Selangor (Peninsular Malaysia)	spatial ecology	Malaysia (Peninsular Malaysia)

Table 3.71, continued.

Macintosh et al. 2002	ecology-conservation, intertidal diversity and mangrove rehabilitation in the Ranong mangrove system (Thailand)	spatial ecology	Thailand
Ashton et al. 2003a	new distribution records (Klong Ngao, Thailand; Merbok, Peninsular Malaysia); brachyuran community structure in four mangrove sites under different management systems	spatial ecology	Thailand, Malaysia (Peninsular Malaysia)
Komai et al. 2004	new records from Ryukyu Islands (Japan), taxonomic and ecological notes	taxonomy / spatial ecology	Japan
Leh et al. 2010	biomass and abundance of sesarmid crabs in a natural and disturbed mangrove area in Selangor (Peninsular Malaysia)	spatial ecology	Malaysia (Peninsular Malaysia)

3.3.16 Genus *Tiomanum* Serène & Soh, 1970

The genus *Tiomanum* has been described by Serène and Soh (1970), to include one species, *Tiomanum indicum*, previously known as *Sesarma indica* H. Milne Edwards, 1837, or also *Sesarma* (*Sesarma*) *tiomanense* Rathbun, 1913.

In particular, as Yeo et al. (1999) pointed out, Serène and Soh (1970) used different spellings for the genus name throughout their paper. The genus was called "*Tiomanium*" in the key to genera, species list, and figures captions, while the authors spelt "*Tiomanum*" in the official diagnosis and discussion of the genus (Serène & Soh, 1970; see also Yeo et al., 1999). Yeo et al. (1999) suggested that *Tiomanum* represented a typographical mistake and *Tiomanium* should be considered as the correct name, and pointed out that already Sakai (1976), Davie (1994) and Tan and Ng (1994) adopted the name *Tiomanium* (see Yeo et al., 1999). However, Ng et al. (2008) reported the genus as *Tiomanum*, following the original designation of the genus name by Serène and Soh (1970), which is therefore currently adopted.

Sesarma tiomanense was synonymised with *S. indica* by Tweedie (1950a). This author suggested that the diagnostic characters proposed by Rathbun (1913) to separate her new species from the existing *S. indica* were not sufficient to consider this as a distinct species (Tweedie, 1950a). This suggestion was adopted by Serène (1968).

The genus has been reported from Indonesia (H. Milne Edwards, 1837), Borneo and South China Sea (Yeo et al., 1999), Peninsular Malaysia and Singapore (Rathbun, 1913; Tweedie, 1936; Yeo et al., 1999), and the Indian Ocean (H. Milne Edwards, 1853). Specimens have been collected from "sandy-muddy areas behind coastal mangroves", where they "dig relatively deep burrows and come out at night to forage" (Yeo et al., 1999).

The only species of this genus, *T. indicum* (H. Milne Edwards, 1837), has been recorded from Peninsular Malaysia, Singapore, and/or northern Borneo.

Table 3.72: List of the studies conducted on the genus *Tiomanum*.

Author and Year	Subject of the study
Tweedie 1950a	as *Sesarma indica*; taxonomic notes; *Sesarma tiomanense* Rathbun, 1913 synonymised with *S. indica*
Serène & Soh 1970	genus description
Yeo et al. 1999	as *Tiomanium;* morphological and taxonomic notes; distribution notes; historical review on the genus and species

3.3.16.1 *Tiomanum indicum* (H. Milne-Edwards, 1837)

This species was described as *Sesarma indica* from Java (Indonesia), by H. Milne Edwards (1837). This species must not be confused with *Metagrapsus indicus* A. Milne-Edwards, 1868, currently known as *Neosarmatium indicum* (see Davie, 1994; see also Subchapter 3.3.8.2). Rathbun (1913) described the same species as *Sesarma* (*Sesarma*) *tiomanense*, from samples collected in Pulau Tioman (island, East coast of Peninsular Malaysia). However, this species was then synonymised with *S. indica* by Tweedie (1950a), due to taxonomic reasons.

T. indicum has been reported from the Indian Ocean (H. Milne Edwards, 1853, as *Sesarma indica*), Borneo (Tweedie, 1950a, as *Sesarma tiomanensis*), Indonesia [De Man, 1883, as *Sesarma indica*; Nobili, 1900, as *Sesarma* (*Sesarma*) *indica*], and Papua New Guinea [Nobili, 1899, as *Sesarma* (*Episesarma*) *indica*]. Tesch (1917) included this species in his checklist, both as *Sesarma* (*Sesarma*) *indica*, and as *Sesarma* (*Sesarma*) *tiomanensis*. For the former species, he also provided taxonomic notes and morphometric measurements, and he re-examined the specimens collected from Nias by Nobili (1900). Tweedie (1936) recorded this species as *Sesarma* (*Sesarma*) *tiomanensis* from the South Natuna Islands (Indonesia), in the South China Sea. Serène (1968) included *Sesarma* (*Sesarma*) *tiomanensis* in his checklist of the non-planctonic marine fauna of South East Asia.

Yeo et al. (1999) provided a detailed history of the taxonomy of this species (and genus), and stated that these crabs have been collected in "sandy-muddy areas behind coastal mangroves", and that they can "dig relatively deep burrows and come out at night to forage" (Yeo et al., 1999). Otherwise, no other information is available on the biology and ecology of this species.

Figure 3.44: ***Tiomanum indicum.*** Male specimen. From the reference collection of the Raffles Museum of Biodiversity Research in Singapore (Lee Kong Chian Natural History Museum, National University of Singapore), visited by the author in 2011-2012. Specimen number: ZRC 1965.8.2.232. Dorsal (above) and frontal view (below). CW = ~4 cm.

Table 3.73: List of the studies conducted on *Tiomanum indicum.*

Author and Year	Subject of the study	Field	Country
H. Milne-Edwards 1837	species description as *Sesarma indica* (Java, Indonesia); morphological and taxonomic notes	taxonomy	Indonesia
H. Milne-Edwards 1853	as *Sesarma indica*; new distribution records (Indian Ocean); morphological and taxonomic notes	taxonomy	Indian Ocean
De Man 1883	as *Sesarma indica*; new distribution record (Sumatra, Indonesia)	distribution record (only)	Indonesia
De Man 1887	as *Sesarma indica*; morphological notes (Indonesia)	distribution record (only)	Indonesia
Nobili 1899	as *Sesarma* (*Episesarma*) *indica*; new distribution records (New Guinea); morphological and taxonomic notes	taxonomy	Papua New Guinea
Nobili 1900	as *Sesarma* (*Sesarma*) *indica*; new distribution records (Nias, Indonesia); morphometric measurements	distribution record (only)	Indonesia
Rathbun 1913	species description as *Sesarma tiomanense* (Tioman Island, Peninsular Malaysia), later synonymised	taxonomy	Malaysia (Peninsular Malaysia)
Tesch 1917	as *Sesarma* (*Sesarma*) *indica*, taxonomic notes, examination of the specimens from Nias (collected by Nobili 1900), morphometric measurements; and as *Sesarma* (*Sesarma*) *tiomanensis*; species included in diagnostic key of sesarmid species	taxonomy	IWP
Tweedie 1936	as *Sesarma* (*Sesarma*) *tiomanensis*; new distribution records (South Natuna Islands)	distribution record (only)	Indonesia
Tweedie 1950a	taxonomic notes; *Sesarma tiomanensis* Rathbun, 1913 synonymised with *S. indicum* (Labuan, East Malaysia)	taxonomy	Malaysia (East Malaysia)
Serène 1968	as *Sesarma* (*Sesarma*) *tiomanensis*, included in the checklist of non-plactonic marine fauna of South East Asia	distribution record (only)	South East Asia
Yeo et al. 1999	as *Tiomanium indicum;* morphological and taxonomic notes; distribution notes; historical review on genus and species; checklist of freshwater and terrestrial decapods of Tioman Island (Peninsular Malaysia)	taxonomy	Malaysia (Peninsular Malaysia)

3.3.17 Geographic distribution, time frame and investigated aspects of the Malaysian species

3.3.17.1 Geographic distribution

In Figure 3.45, all the studies published worldwide for each of the species presented above have been categorised according to their geographic area (see Subchapters 3.3.1 - 3.3.16 for details). Checklists reporting records already published in other publications (i.e. not adding any new information on the species) have not been included in this account.

In particular, the Indo-West Pacific region has been arbitrarily subdivided in the following areas: Malay Peninsula and northern Borneo (including Peninsular Malaysia, Singapore, East Malaysia and Brunei Darussalam), other South East Asian countries (Thailand, Myanmar, Cambodia, Laos, Vietnam, Philippines), Indonesia and Papua New Guinea, East Asia (China, Taiwan, Hong Kong, North Korea, South Korea, Japan), Indian subcontinent (India, Sri Lanka, Pakistan, Bangladesh), Africa and Madagascar, Persian Gulf, Australia and Oceania. Figure 3.46 shows the studies conducted in the Malay Peninsula and northern Borneo only, subdivided in three areas: Peninsular Malaysia, northern Borneo (East Malaysia and Brunei Darussalam) and Singapore.

Twenty-one of the considered species have been reported from a relatively small area, i.e. including one or two of the considered geographic areas only (Fig. 3.45). In particular, *Bresedium sedilense*, *Haberma nanum*, *Nanosesarma nunongi*, *Neosarmatium spinicarpus*, *Parasesarma lanchesteri* and *Pseudosesarma johorense* have been found only in the Malay Peninsula and/or northern Borneo (Fig. 3.45). These species can be considered as endemisms for this geographic area, unless further records are found in other countries. Within this area (Fig. 3.46), *H. nanum* has been found only in Singapore, while *N. nunongi* has been reported only from Peninsular Malaysia. *B. sedilense*, *N. spinicarpus, P.*

lanchesteri and *P. johorense* have been recorded from Borneo and from the Malay Peninsula (either Peninsular Malaysia or Singapore).

Episesarma chentongense, *Parasesarma batavianum*, *Parasesarma calypso*, *Parasesarma indiarum*, *Parasesarma raouli*, *Parasesarma rutilimanum*, *Pseudosesarma granosimanum* and *Pseudosesarma laevimanum* have been found both in the Malay Peninsula and/or Borneo, and in Indonesia and/or Papua New Guinea (Fig. 3.45). *Nanosesarma tweediei*, *Neosesarma gemmiferum*, and *Parasesarma melissa* were reported from the Malay Peninsula and/or Borneo, and from other South East Asian countries (Fig. 3.45). *Clistocoeloma suvaense* and *Sesarmoides borneensis* have been recorded from the Malay Peninsula and/or Borneo, and from Australia/Oceania (Fig. 3.45). *Clistocoeloma lanatum* has been found in the Malay Peninsula and/or Borneo, and in the Indian subcontinent (Fig. 3.45). *Haberma kamora* has been found only in Indonesia: this species was included in this account because it was found in northern Borneo (Brunei Bay) during this project (see Chapter 4).

In contrast, ten species have been reported from more than six of the considered geographic areas (Fig. 3.45), showing therefore a relatively wide distribution range. In particular, *Nanosesarma minutum*, *Neosarmatium smithi* and *Selatium brockii* have been found in six of the eight considered areas, while *Clistocoeloma merguiense*, *Episesarma mederi*, *Episesarma versicolor*, *Neosarmatium asiaticum*, *Neosarmatium indicum*, *Parasesarma lenzii* and *Parasesarma semperi* were reported from five areas (Fig. 3.45). The remaining species have been found in three or four geographic areas (Fig. 3.45). Among these species, *Episesarma palawanense*, *Episesarma singaporense*, *Labuanium politum*, *Nanosesarma pontianacense*, *Parasesarma eumolpe*, *Parasesarma peninsulare*, *Parasesarma onychophorum*, *Pseudosesarma bocourti* and *Pseudosesarma moeschi* were reported from

South East Asian countries only (i.e. from the following considered areas: Malay Peninsula and/or Borneo, other South East Asian countries, Indonesia and/or Papua New Guinea) (Fig. 3.45).

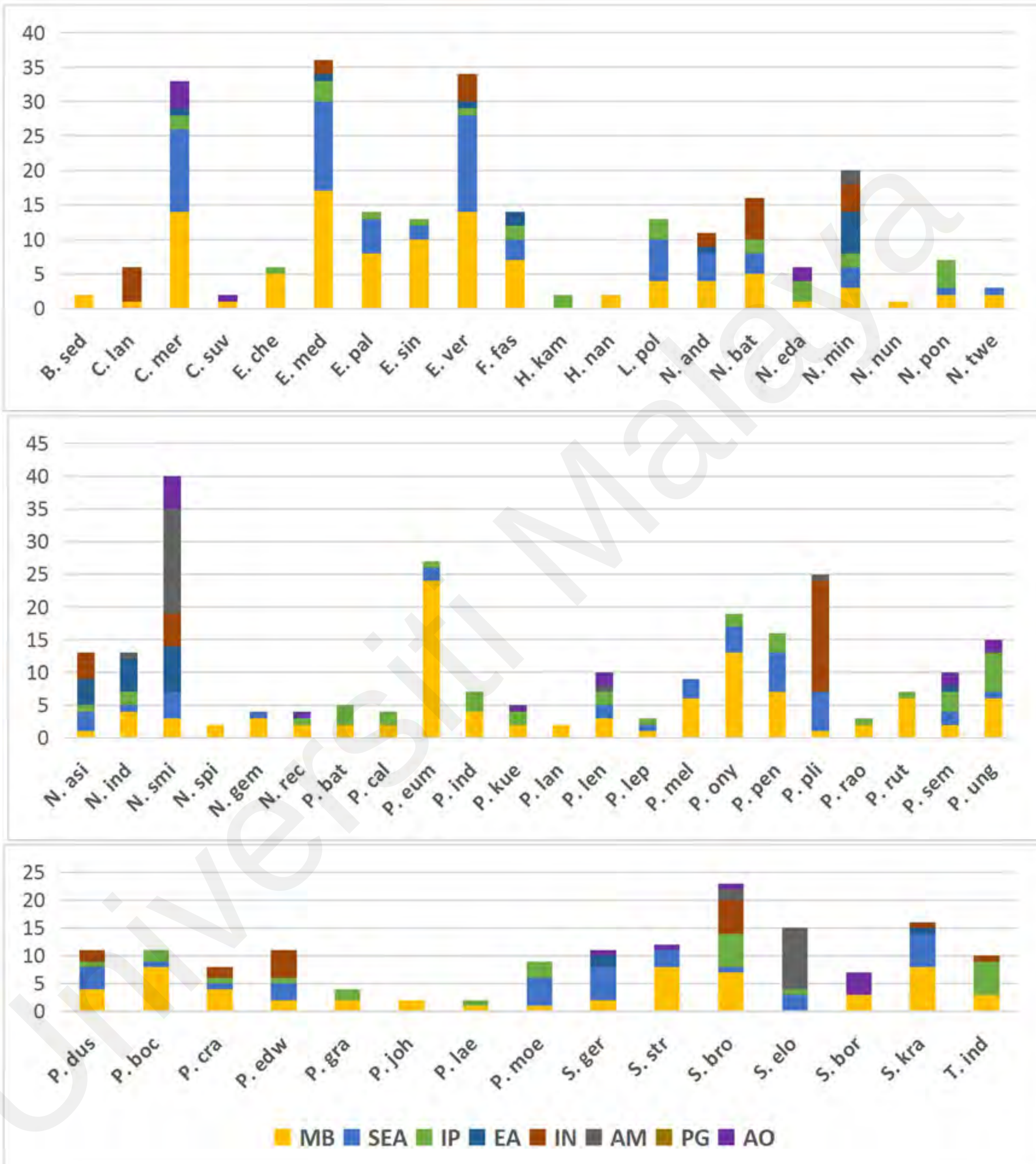

Figure 3.45: Papers published for each species per geographic area. Number of studies published worldwide for each of the species recorded in the Malay Peninsula and Borneo. Studies have been categorised according to their geographic area. MB = Malay Peninsula and/or Borneo, SEA = other South East Asian countries, IP = Indonesia and/or Papua New Guinea, EA = East Asia, IN = Indian subcontinent, AM = Africa and/or Madagascar, PG = Persian Gulf, AO = Australia and /or Oceania. Species abbreviations: the first letter refers to the genus and the following three letter to the species name (e.g. C. mer = *Clistocoeloma merguiense*, see Subchapter 3.3 for list of species).

When considering only the studies from the Malay Peninsula and Borneo (Fig. 3.46), fourteen species (*Clistocoeloma merguiense*, *Episesarma mederi*, *Episesarma palawanense*, *Episesarma versicolor*, *Fasciarma fasciatum*, *Labuanium politum*, *Nanosesarma batavicum*, *Neosesarma gemmiferum*, *Parasesarma eumolpe*, *Parasesarma onychophorum*, *Parasesarma rutilimanum*, *Parasesarma ungulatum*, *Sarmatium striaticarpus* and *Selatium brockii*) have been reported from both Peninsular Malaysia, Singapore and northern Borneo.

Four species (*Nanosesarma nunongi*, *Neosarmatium asiaticum*, *Parasesarma plicatum* and *Pseudosesarma moeschi*) have been found in Peninsular Malaysia, while they have not been reported from Singapore and northern Borneo (Fig. 3.46). Five species (*Nanosesarma edamense*, *Parasesarma indiarum*, *Parasesarma lepidum*, *Parasesarma semperi*, *Pseudosesarma laevimanum*) have been recorded from Borneo, while they have not been found in the Malay Peninsula (Fig. 3.46). *Clistocoeloma lanatum*, *Clistocoeloma suvaense* and *Haberma nanum* have been reported from Singapore, while it has not been found in Peninsular Malaysia and Borneo (Fig. 3.46).

Fourteen species have been recorded from the Malay Peninsula (i.e. Peninsular Malaysia and Singapore), while they have not been found in northern Borneo (*Episesarma chentongense*, *E. singaporense*, *Nanosesarma minutum*, *Nanosesarma pontianacense*, *Nanosesarma tweediei*, *Neosarmatium smithi*, *Parasesarma batavianum*, *Parasesarma melissa*, *Parasesarma peninsulare*, *Parasesarma raouli*, *Perisesarma dussumieri*, *Pseudosesarma edwardsii*, *Sarmatium germaini*, *Sesarmoides kraussi*; Fig. 3.46).

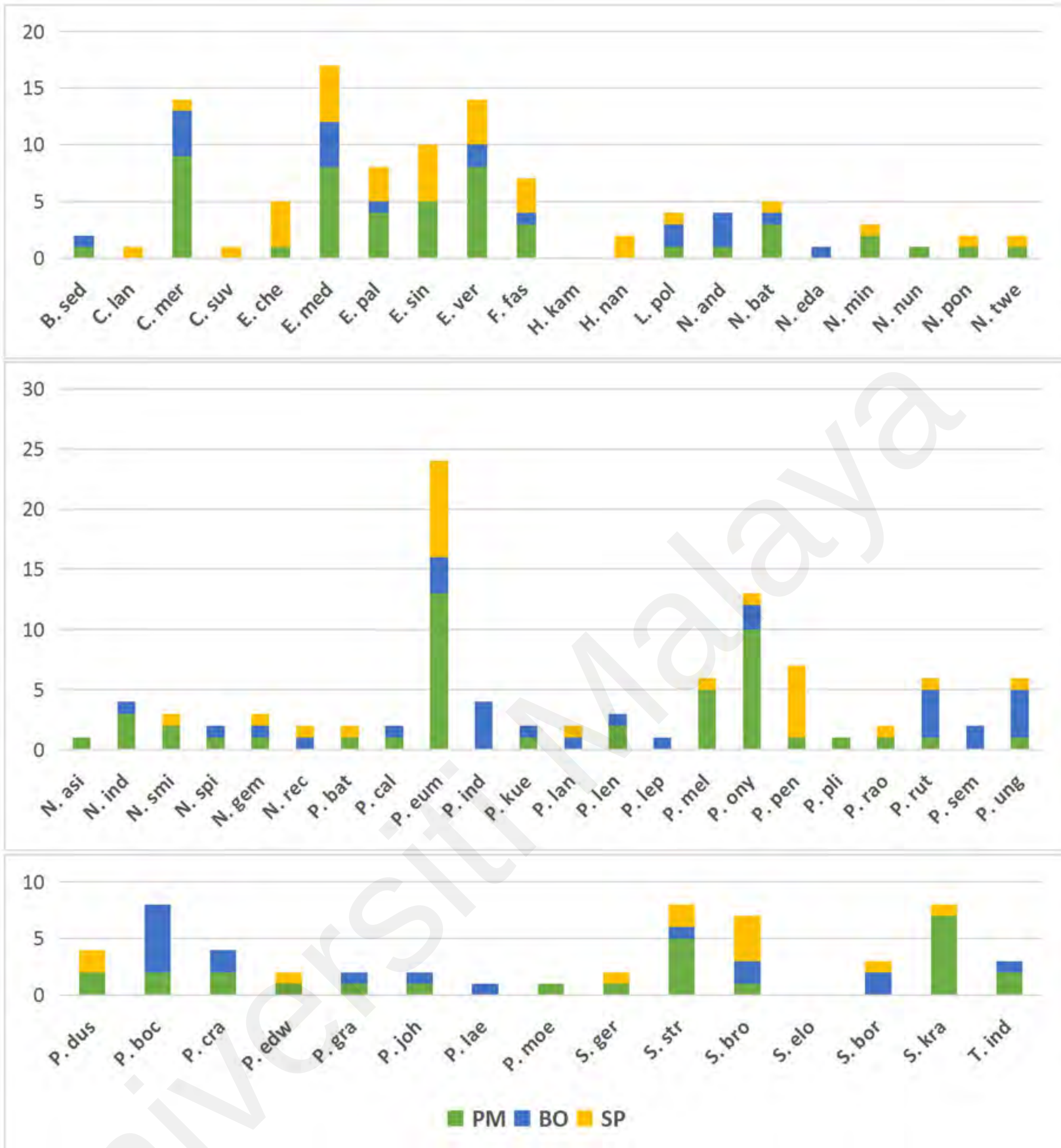

Figure 3.46: Number of studies published from the Malay Peninsula and Borneo, for each of the species recorded in this area. PM = Peninsular Malaysia, BO = northern Borneo, SP = Singapore. See Fig. 3.43 for species abbreviations.

3.3.17.2 Time-frame of the publications

A few species have not been mentioned in any recent publication, i.e. no records have been published after 1950. In particular, *Bresedium sedilense*, *Nanosesarma nunongi*, *Parasesarma lanchesteri*, *Pseudosesarma granosimanum*, and *Pseudosesarma johorense* have not been reported after 1950s. On the other hand, *Episesarma chentongense*, *Nanosesarma tweediei* and *Parasesarma raouli* have been described and recorded only after the 1960s-1970s, while *Haberma nanum* and *Haberma kamora* have been reported only after 2000.

Several species have been recorded only in a few studies. In particular, *Nanosesarma nunongi* has been recorded only in one study (and in the present project, see Chapter 4), while *Bresedium sedilense*, *Clistocoeloma suvaense*, *Haberma kamora*, *Haberma nanum*, *Nanosesarma tweediei*, *Neosarmatium spinicarpus*, *Neosesarma gemmiferum*, *Neosesarma rectipectinatum*, *Parasesarma lanchesteri*, *Parasesarma lepidum*, *Parasesarma raouli*, *Pseudosesarma johorense* and *Pseudosesarma laevimanum* have been reported from less than three studies (excluding general checklists, and the present project). *Nanosesarma edamense*, *Nanosesarma pontianacense*, *Parasesarma batavianum*, *Parasesarma kuekenthali*, and *Pseudosesarma granosimanum* have been recorded from less than five studies.

Only a few species have been extensively reported, such as *Clistocoeloma merguiense*, *Episesarma mederi*, *Episesarma versicolor*, *Neosarmatium smithi* (more than 30 studies), and *Nanosesarma minutum*, *Parasesarma eumolpe*, *Parasesarma plicatum* and *Selatium brockii* (more than 20 studies).

3.3.17.3 Investigated topics

Figure 3.47 shows the number of studies conducted worldwide for each species, categorised by the investigated biological aspect. In particular, studies have been subdivided according to the following topics:

- "taxonomy/systematic/distribution";
- "new records (only)", i.e. when the only info provided is the specimen(s) location;
- "spatial ecology", i.e. studies on zonation, spatial distribution within an investigated system, association with environmental parameters;
- "feeding ecology", i.e. studies on the foodweb, diet, food preferences;
- "burrowing ecology";
- "tree-climbing", i.e. studies investigating tree-climbing behaviour and habits;
- "behaviour/social", i.e. ethological studies, studies on the intra-specific and inter-specific social interactions and communication;
- "ontogenesis", i.e. studies on the larval development, larval ecology, larval distribution patterns;
- "physiology/anatomy/morphology";
- "phylogenesis";
- "population genetic".

Fifteen species (i.e. *Bresedium sedilense*, *Clistocoeloma suvaense*, *Nanosesarma edamense*, *Nanosesarma nunongi*, *Nanosesarma pontianacense*, *Nanosesarma tweediei*, *Neosesarma rectipectinatum*, *Parasesarma batavianum*, *Parasesarma calypso*, *Parasesarma lanchesteri*, *Parasesarma lepidum*, *Parasesarma raouli*, *Pseudosesarma granosimanum*, *Pseudosesarma johorense*, *Tiomanum indicum*) have been reported in taxonomic papers and as distribution records only, while their ecology and biology remain virtually unknown (Fig. 3.47).

Thirty-six species have been recorded in studies on the spatial ecology of brachyuran assemblages of IWP mangrove systems. In particular, *Clistocoeloma merguiense*, *Episesarma versicolor* and *Parasesarma eumolpe* have been found in more than 10 studies of this type (Tabs. 3.5, 3.12, 3.39; Fig. 3.47). Eighteen species have been investigated in studies on the feeeding ecology and, in particular, *Episesarma versicolor* has been reported from more than 10 studies on this topic (Fig. 3.47). The burrowing ecology has been investigated for *Episesarma chentongense*, *Episesarma versicolor*, *Neosarmatium smithi* and *Parasesarma eumolpe*, while the tree-climbing behaviour has been studied in *Episesarma chentongense*, *Episesarma singaporense*, *Episesarma versicolor*, *Selatium brockii* and *Selatium elongatum* (Fig. 3.47). Behavioural aspects and intra- and interspecific interactions have been investigated in *Clistocoeloma merguiense*, *Episesarma mederi*, *Episesarma versicolor*, *Haberma nanum*, *Parasesarma eumolpe* and *Parasesarma peninsulare* (Fig. 3.47).

Studies on the larval development have been conducted for eleven species (*Clistocoeloma lanatum*, *Episesarma singaporense*, *Fasciarma fasciatum*, *Nanosesarma andersonii*, *Nanosesarma batavicum*, *Neosarmatium indicum*, *Pseudosesarma bocourti*, *Pseudosesarma crassimanum*, *Pseudosesarma edwardsii*, *Pseudosesarma moeschi*, *Selatium brockii*), while physiological, morphological and anatomical aspects have been studied for seven species (*Episesarma versicolor*, *Fasciarma fasciatum*, *Neosarmatium smithi*, *Parasesarma eumolpe*, *Parasesarma peninsulare*, *Perisesarma dussumieri*, *Pseudosesarma moeschi*, Fig. 3.47). *Episesarma mederi*, *Nanosesarma minutum*, *Parasesarma semperi*, *Selatium brockii* and *Selatium elongatum* have been included in phylogenetic studies, while a study on population genetic have been conducted for *Episesarma versicolor* (Fig. 3.47).

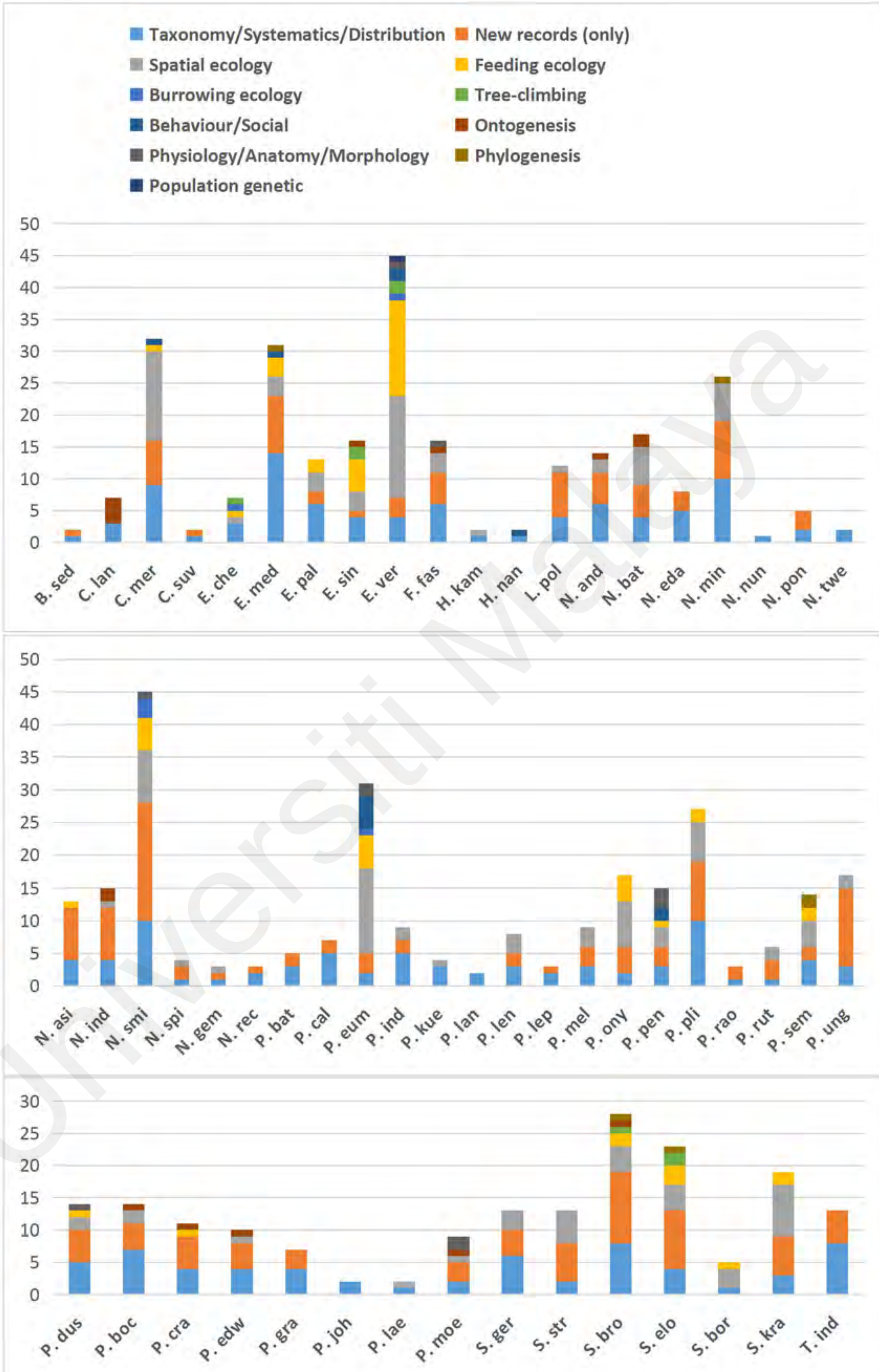

Figure 3.47: Number of studies published worldwide for each of the species recorded in Peninsular Malaysia and Borneo, according to the investigated subject.

Table 3.74 summarises the information on ecological and biological aspects available for each species, in term of ecosystem and habitat type, salinity, substrate, feeding habits, burrowing, tree-climbing behaviour, and larval development. The autoecological traits of several species are almost unknown (e.g. *Clistocoeloma lanatum*, *C. suvaense*, *Nanosesarma edamense*, *N. nunongi*, *N. pontianacense*, *N. tweediei*, *Parasesarma batavianum*, *P. calypso*, *P. kuekenthali*, *P lanchesteri*, *P. lepidum*, *P. raouli*, *Pseudosesarma crassimanum*, *P. edwardsii*, *P. granosimanum*, *P. johorense*).

Table 3.74: Information available for each of the species recorded in the Malay Peninsular and Borneo. See previous subchapters (3.3.1 - 3.3.16) for references.

Species	Ecosystem / Habitat / Microhabitat	Salinity	Substrate	Feeding habits	Burrowing	Tree-climbing	Larval development
Bresedium sedilense	nipah forest	freshwater / brackish, freshwater	muddy	-	-	-	-
Clistocoeloma lanatum	-	-	-	-	-	-	zoeal and megalopal stages described
Clistocoeloma merguiense	mangrove forests; widely distributed within investigated forests, found sometimes inside dead wood	brackish, saltwater	muddy, sandy/ muddy	gut content: mangrove plant material (97%), mineral and brachyuran debris (3%)	-	-	first zoeal stage described
Clistocoeloma suvaense	-	-	-	-	-	-	-
Episesarma chentongense	mangrove forests, bank slope of an estuarine lagoon, colonised by shrubs of *Derris trifoliata*	-	muddy	vascular plant material (leaf litter), occasionally scavenging	active burrower	facultative tree climber at nocturnal low tide or diurnal high tide	-
Episesarma mederi	mangrove forests; middle/upper intertidal zones	saltwater, freshwater	muddy	isotopic signature close to mangrove leaves and detritus	-	species can be found on tree trunks and roots	-
Episesarma palawanense	mangrove forests; upper intertidal zones, *Rhizophora* and *Bruguiera* forests, bank slopes colonised by *Derris trifoliata*	brackish / saltwater	muddy, silty/ muddy, sandy/ muddy	gut content: detritus, bark, leaf material	burrower	-	-

Table 3.74, continued.

Species	Ecosystem / Habitat / Microhabitat	Salinity	Substrate	Feeding habits	Burrowing	Tree-climbing	Larval development
Episesarma singaporense	mangrove forests; riverine mangroves, middle and upper intertidal zones, abundant in mud lobster mound systems, *Rhizophora* and *Bruguiera* forests, *Sonneratia* and *Avicennia* fringes, with *Acanthus* and *Derris trifoliata* shrubs)	brackish/ saltwater	fine sand/ silt	leaf litter, occasional scavenger; isotopic signature and gut content: mangrove leaves and detritus	burrower	facultative climber during nocturnal low tide or diurnal high tide	zoeal stages described
Episesarma versicolor	mangrove forests; lower, middle and upper intertidal zone, riverine mangroves, found in different vegetation types (*Rhizophora*, *Avicennia*, *Lumnitzera*, *Ceriops*, *Sonneratia* zones, *Acanthus* and *Derris trifoliata* shrubs, unvegetated areas	saltwater, brackish, species found to tolerate wide range of salinity	muddy	isotopic signature close to mangrove leaves and detritus, gut content: plant material (90%), brachyuran debris, inorganic sediment and insects (10%), occasional scavenger	burrower	facultative climber during nocturnal low tide or diurnal high tide	-
Fasciarma fasciatum	mangrove forests; middle and upper intertidal zones; higher, dryer, partially cleared sites; artificially altered area colonised by sedge *Fimbristylis schoenoides*, on mounds of mud lobster *Thalassina*	brackish, saltwater	sandy	-	-	-	zoeal, megalopal and first juvenile stages described
Haberma kamora	mangrove forests, river banks, upper intertidal zones	-	muddy, hard substrates	-	-	-	-
Haberma nanum	mangrove forests; open unvegetated habitats with dry substrate, disturbed areas	-	muddy	-	-	-	-
Labuanium politum	nipah forests/stands; living in the base of leaf stalks in the day, climbing on leaves at night	-	-	feeding at night on nipah leaves	-	obligate tree climber (on *Nypa* palms)	-

Table 3.74, continued.

Species	**Ecosystem / Habitat / Microhabitat**	**Salinity**	**Substrate**	**Feeding habits**	**Burrowing**	**Tree-climbing**	**Larval development**
Nanosesarma andersonii	mangrove forests; whole intertidal gradient, found along a river bank, in abandoned burrows of bivalve *Novaculina*, found on wood, and in wood cavities made by sphaeromatid isopods	freshwater, saltwater	-	-	-	-	zoeal and megalopal stages described
Nanosesarma batavicum	mangrove forests, middle and upper intertidal zones; found among clusters of shell of a oyster-bed or in natural cavities of laterite blocks, found on wood; found in a disturbed unvegetated area covered by wooden debris	freshwater, saltwater	muddy	-	-	-	zoeal and megalopal stages described
Nanosesarma edamense	mangrove forests	-	-	-	-	-	-
Nanosesarma minutum	mangrove forests and rocky shores; found among sessile mollusks on tree stems and on the ground, in rotten wood, in crevices of cobbles or oyster clusters; found in the middle and lower intertidal zones; found in *Rhizophora* forests	-	muddy, cobbles, rocky	-	-	-	-
Nanosesarma nunongi	-	-	-	-	-	-	-
Nanosesarma pontianacense	mangrove forests	-	muddy	-	-	-	-
Nanosesarma tweediei	-	-	-	-	-	-	-

Table 3.74, continued.

Species	**Ecosystem / Habitat / Microhabitat**	**Salinity**	**Substrate**	**Feeding habits**	**Burrowing**	**Tree-climbing**	**Larval development**
Neosarmatium asiaticum	mangrove forests; riverine and estuarine mangroves, *Bruguiera* zones, grassy river banks	-	-	leaf litter and mangrove propagules	not documented but probable (the sister species *N. africanum* is an active burrower)	-	-
Neosarmatium indicum	mangrove forests; different intertidal zones, stands of *Kandelia candel*	brackish, freshwater	muddy	-	burrower	-	embryo, zoeal and megalopal stages described
Neosarmatium smithi	mangrove forests; lower intertidal zone, *Rhizophora/ Bruguiera/ Avicennia/ Lumnitzera* zones, unvegetated cleared patches	saltwater, brackish/ saltwater	sandy	decaying mangrove leaves and litter; observed feeding on *Palaemonetes* shrimps at flood tide	burrower	-	-
Neosarmatium spinicarpus	nipah forests, freshwater ditch	freshwater	-	-	-	-	-
Neosesarma gemmiferum	mangrove forests; estuarine and riverine environments, *Rhizophora apiculata* forest, found associated with crevices in trees and fallen logs	freshwater	muddy	-	-	-	-
Neosesarma rectipectinatum	mangrove forests; lower-middle intertidal zones, associated with crevices in trees and fallen logs, found in burrows, on open substrate among *Avicennia* pneumatophores, found in steep eroding banks	-	muddy	-	burrower	-	-
Parasesarma batavianum	riverine and coastal environments	-	-	-	-	-	-

Table 3.74, continued.

Species	**Ecosystem / Habitat / Microhabitat**	**Salinity**	**Substrate**	**Feeding habits**	**Burrowing**	**Tree-climbing**	**Larval development**
Parasesarma calypso	-	-	-	-	-	-	-
Parasesarma eumolpe	mangrove forests; middle and upper intertidal zones, banks of tidal creeks and rivers, forests dominated by *Bruguiera*, *Rhizophora*, *Ceriops*, cleared areas, areas colonised by sparse *Nypa fruticans* and *Phoenix paludosa* palms, exploited and intact forests, coastal lagoon, found in area with mud lobsters mound system, from artificial lagoon with small stands of *Sonneratia* and *Avicennia* trees, from estuary closed by a sand bar dominated by *Nypa*, *Hibiscus*, *Intsia*, *Casuarina* species	saltwater, brackish	muddy	gut contents: mangrove plant materials (91%), mineral and brachyuran debris, insects (7%); vascular plants and sediments; mangrove leaves, roots, occasionally animal matter	burrower	-	-
Parasesarma indiarum	mangrove forests; mixed forest with numerous *Rhizophora* saplings and seedlings	saltwater	muddy, sandy	-	-	-	-
Parasesarma kuekenthali	mangrove forests; found in a *Rhizophora* forest	freshwater	-	-	-	-	-
Parasesarma lanchesteri	mangrove forests; riverine environment	-	-	-	-	-	-
Parasesarma lenzii	mangrove forests; upper intertidal zones, found in area with mud lobster mound system, found in mixed forests, monotypic *Rhizophora* plantation, estuarine and riverine forests	brackish	-	-	-	-	-

Table 3.74, continued.

Species	**Ecosystem / Habitat / Microhabitat**	**Salinity**	**Substrate**	**Feeding habits**	**Burrowing**	**Tree-climbing**	**Larval development**
Parasesarma lepidum	mangrove forests	-	-	-	-	-	-
Parasesarma melissa	mangrove forests; upper intertidal zones, found on the sides of streams crossing the forest, in a cleared unvegetated area , in mixed forest (*Bruguiera* spp., *Rhizophora* spp., *Xylocarpus granatum*)	brackish, saltwater	fine sand, silt/mud	-	-	-	-
Parasesarma onychophorum	mangrove forests; upper, middle and lower intertidal zones, seaward eroding banks, banks of rivers and creeks in the forest, *Bruguiera* spp., *Rhizophora* spp., *Avicennia*, *Xylocarpus* spp. forests, found in a rehabilitated forest, in both exploited and undisturbed forests, in cleared unvegetated areas, found in hollow tree trunks, fallen logs and debris	brackish, saltwater	sandy-muddy, muddy	mangrove leaves and litter; isotopic signature close to mangrove leaves and detritus; gut contents: mangrove plant material (83%), mineral and brachyuran debris, insects (17%)	-	-	-
Parasesarma peninsulare	mangrove forests; upper intertidal zones, areas previously cleared and then recolonised by *Nypa fruticans* and *Phoenix paludosa* palms, open areas with few *Bruguiera gymnorhiza* trees, dense forest of *Bruguiera gymnorhiza* and few *Rhizophora mucronata* trees	saltwater	muddy, sandy	mainly sediment grazers, also feeding on mangrove leaves, roots, occasionally animal matter; preferring *Avicennia alba* leaves to other species	-	-	-

Table 3.74, continued.

Species	**Ecosystem / Habitat / Microhabitat**	**Salinity**	**Substrate**	**Feeding habits**	**Burrowing**	**Tree-climbing**	**Larval development**
Parasesarma plicatum	mangrove forests; found on prop roots and tree trunks of *Rhizophora* spp., found associated with dead wood and rotting vegetation, found in a *Avicennia marina* forest, found in a coastal lagoon	saltwater	muddy, sandy/muddy	juveniles feeding on microphytobenthos	-	-	zoeal and megalopal stages described
Parasesarma raouli	mangrove forests; *Sonneratia alba* forest	-	sandy	-	-	-	-
Parasesarma rutilimanum	mangrove forests; riverine, estuarine and insular environments, mixed mangrove forests, found in areas colonised by mud lobster *Thalassina anomala*	brackish	sandy, muddy	-	-	-	-
Parasesarma semperi	mangrove forests; *Rhizophora* spp., *Bruguiera gymnorhiza*, *Xylocarpus granatum*, *Avicennia alba* forests	saltwater	muddy	mangrove leaves and propagules; detritus, mangrove litter and bark, roots, algae, animal matter	-	-	-
Parasesarma ungulatum	mangrove forests; upper intertidal zone, found in *Rhizophora stylosa* forest, in belts of grass *Sesuvium portulacastrum*, along saltwater ponds bordered by *Lumnitzera racemosa* and *Aegiceras* sp.	saltwater	sandy	-	-	-	-
Perisesarma dussumieri	mangrove forests; upper intertidal zones, found in disturbed area colonised by sparse *Nypa fruticans* and *Phoenix paludosa* palms	saltwater	muddy	-	-	-	-

Table 3.74, continued.

Species	**Ecosystem / Habitat / Microhabitat**	**Salinity**	**Substrate**	**Feeding habits**	**Burrowing**	**Tree-climbing**	**Larval development**
Pseudosesarma bocourti	mangrove forests, freshwater swamps, peat swamps	freshwater	peat, other	mangrove leaves and litter	burrower	-	zoeal and megalopal stages described
Pseudosesarma crassimanum	nipah forests along river sides, mangrove forests	freshwater	-	-	-	-	first zoeal stage described
Pseudosesarma edwardsii	mangrove forests	freshwater	-	-	-	-	zoeal and megalopal stages described
Pseudosesarma granosimanum	freshwater swamps; among nipah palms	freshwater	-	-	-	-	-
Pseudosesarma johorense	mangrove forests, riverine environments	-	-	-	-	-	-
Pseudosesarma laevimanum	mangrove forests; found in area with sparse *Sonneratia* and *Avicennia* trees, densely covered by shrubs *Acanthus* spp. and *Derris trifoliata*	freshwater, brackish	muddy	-	-	-	-
Pseudosesarma moeschi	nipah forests along river; lower tracts of estuaries	brackish; species found able to tolerate wide range of salinities	-	-	-	-	zoeal and megalopal stages described

Table 3.74, continued.

Species	Ecosystem / Habitat / Microhabitat	Salinity	Substrate	Feeding habits	Burrowing	Tree-climbing	Larval development
Sarmatium germaini	mangrove forests; upper and middle intertidal zones, found in *Rhizophora apiculata* stands, in a mixed forest (*Avicennia marina*, *Ceriops tagal*, *Rhizophora mucronata*), in intact and cleared areas	saltwater, brackish	muddy, sandy	-	-	-	-
Sarmatium spinicarpus	mangrove forests; upper, middle, lower intertidal zones, *Bruguiera* spp. and *Rhizophora* spp. forests, nipah stands, unvegetated areas, cleared areas covered by fallen trunks and branches	saltwater, brackish	fine sand, silt, sand	-	-	-	-
Selatium brockii	mangrove forests; lower intertidal zone, *Sonneratia ovata* and *Avicennia alba* stands; found on wooden piles of fishing stakes and bathing enclosures, found on tree trunks, underneath bark of dead trunks or inside hollow trees	saltwater	sandy, muddy	observed feeding at night on algae, lichen and fungi, occasionally scavenging	non-burrower	habitual tree climber	zoeal and megalopal stages described
Selatium elongatum	mangrove forests; upper and lower intertidal zones, *Avicennia*, *Rhizophora* and *Sonneratia* zones, observed on tree trunks, canopies, on aerial roots and inside trunks crevices			gut contents: mainly feeding on macroalgae growing on aerial *Rhizophora* roots, partly eating mangrove leaves; observed feeding on floating macroalgae at high tide		tree climber	

Table 3.74, continued.

Species	Ecosystem / Habitat / Microhabitat	Salinity	Substrate	Feeding habits	Burrowing	Tree-climbing	Larval development
Sesarmoides borneensis	mangrove forests; mixed stands dominated by *Avicennia* or *Ceriops*, estuarine and riverine mixed forests	brackish	muddy	-	-	-	-
Sesarmoides kraussi	mangrove forests; upper and middle and lower intertidal zones, found in a mixed mangrove fringe along the eroding mud-bank, a *Bruguiera parviflora* and *Rhizophora mucronata* estuarine forest and river mud-bank, a *Rhizophora* spp. fringe mangrove, cleared unvegetated areas, a rehabilitated mangrove forest, a partially managed forest	saltwater, brackish	muddy, sandy muddy	isotopic signature close to mangrove leaves and litter, gut contents: mangrove plant materials (93%), mineral and brachyuran debris, insects (7%)	-	-	-
Tiomanum indicum	sandy-muddy areas behind coastal mangroves	-	sandy-muddy	-	burrower	-	-

3.3.18 Studies on sesarmid crabs from mangrove ecosystems of Peninsular Malaysia, Singapore and northern Borneo

To date, 64 studies have been published on sesarmid crabs collected from mangroves and other coastal systems in Peninsular Malaysia, northern Borneo, and Singapore (Tab. 3.74). This account does not include studies on sesarmid species occurring exclusively in "non-mangrove" ecosystems (e.g. rainforests, limestone caves, and rocky shores). Moreover, general studies regarding the whole Indo-West Pacific region (e.g. Tesch, 1917; Ng et al., 2008) were not included, unless they provided new information on sesarmid diversity in this area.

In general, the first studies on sesarmid crabs in this geographic area consisted of annotated lists of species, which were based on specimens collected during early scientific expeditions in the nineteen and early twentieth centuries (e.g. Magenta expedition, Targioni-Tozzetti, 1877; Skeat expedition, Lanchester, 1901). In particular, the first account on sesarmid crabs from this area can be found in a study by White (1847), which listed the crustacean specimens in the collection of the British Museum of London, with notes on the localities and name of the collectors.

Several authors examined museum or private collections, providing a list of the specimens, and sometimes adding taxonomic notes or other remarks (Targioni-Tozzetti, 1877; De Man, 1880, 1892, 1895, 1896, 1902; Miers, 1880; Ortmann, 1894; Zehntner, 1894; Alcock, 1900; Lanchester, 1900a,b, 1901; Nobili, 1900, 1901; Rathbun, 1913). These early studies usually did not include notes on the environmental conditions or type of habitat where the samples were found, since usually the authors did not collect the samples, but examined samples already collected (e.g. De Man, 1880, 1892; Zehntner, 1894).

These authors also described new species from this geographic area, i.e. *Fasciarma fasciatum* [described as *Sesarma* (*Parasesarma*) *fasciata* from Singapore; Lanchester, 1900a], *Parasesarma eumolpe* [described as *Sesarma* (*Perisesarma*) *eumolpe* from Penang; De Man, 1895], *Parasesarma lenzii* [described as *Sesarma* (*Parasesarma*) *lenzii* from Penang and Indonesia; De Man, 1895], *Pseudosesarma laevimanum* [described as *Sesarma edwardsii* var. *laevimana* from Sarawak; Zehntner, 1894].

Few decades later (1930s-1950s), the sesarmid community of this geographic area was investigated by Prof. M. W. P. Tweedie, who was working at the National University of Singapore (Tweedie, 1936, 1940, 1950a, b, c, 1954).

Tweedie (1936) presented an annotated account of the grapsoid specimens in the collection of the Raffles Museum of Singapore, which consisted mainly of samples collected in the previous three years from mangroves sites in Singapore and Peninsular Malaysia (e.g. Selangor, Penang, Perak, Pahang, Johor, Tioman Island). In this paper, a few new species were described, namely *Episesarma singaporense* [described as *Sesarma* (*Sesarma*) *singaporensis*, from Singapore], *Neosesarma gemmiferum* [described as *Sesarma* (*Sesarma*) *gemmifera*, from the Johor Strait, Singapore, and Selangor], *Parasesarma lanchesteri* [described as *Sesarma* (*Parasesarma*) *calypso lanchesteri*, from Singapore], *Parasesarma rutilimanum* [described as *Sesarma* (*Parasesarma*) *rutilimana* from Singapore and Johor] (Tweedie 1936). Moreover, this author considered the previously described *Sesarma* (*Chiromantes*) *siamensis* as a synonym of *Sesarma fasciata* (today *Fasciarma fasciatum*), and provided few brief taxonomic notes for some of the species presented, and a diagnostic key for the species today included in the genus *Episesarma* (i.e. *Sesarma taeniolata*, *S. lafondi*, *S. singaporensis*, *S. palawanensis*; Tweedie, 1936).

Tweedie (1940) provided an account of sesarmid and varunid species collected from Singapore and the Malay Peninsula, Labuan (East Malaysia), Indonesia, and the Philippines. This paper provided also taxonomic remarks, and brief notes on the habitat where the specimens were collected. A few new species were also described, such as *Bresedium sedilense* (described as *Sesarma sediliensis* from Johor), *Episesarma versicolor* (described as *Sesarma versicolor* from Singapore, Penang and Pahang), *Pseudosesarma johorense* (described as *Sesarma johorensis* from Johor), and *Geosesarma penangense* (described as *Sesarma penangensisis* from Penang). Moreover, this author assigned a new name (*Sesarma bidens indiarum*) to the previously described *Sesarma bidens indica* (today *Parasesarma indiarum*), since the name was pre-occupied (see also Subchapter 3.3.10.4), provided the first description of male specimens of *Nanosesarma pontianacense* and *Episesarma palawanense*, and elevated the subspecies *Sesarma edwardsi crassimana* to species level (*Sesarma crassimana,* today *Pseudosesarma crassimanum*) (Tweedie, 1940).

Tweedie (1950a) examined a collection of samples from Labuan and Sarawak (East Malaysia), and provided for some species taxonomic notes and brief indications on the ecosystem. This paper also included considerations on the biogeographical distribution of sesarmid species, comparing the Bornean and Malayan assemblages. Moreover, a few species were described, i.e. *Neosesarma rectipectinatum* (described as *Sesarma rectipectinata*, from Labuan), *Parasesarma lepidum* (described as *Sesarma lepida*, from Labuan), and *Sesarmoides borneensis* (as *Sesarma kraussi borneensis*, from Labuan).

Tweedie (1950b) presented an account of species collected from Aor Island (South China Sea, off Johor coast) by the author during a two weeks survey in 1938. This paper included only one sesarmid species, *Sesarma punctata* (today *Neosarmatium punctatum*), although these specimens have been later re-examined by Davie (1994) and assigned to another species (*Neosarmatium indicum*, see Subchapter 3.3.8.2).

Tweedie (1950c) described the genus *Nanosesarma*, examining specimens from the whole Indo-West Pacific, including also the Malay Peninsula and Borneo, and providing a diagnostic key to the species. Moreover, a new species, *Nanosesarma nunongi*, was described, from Pahang and Penang (Peninsular Malaysia).

Tweedie (1954) discussed differences in assemblages of West and East coast of the Malay Peninsula, and northern Borneo, and provided a list of species with a restricted geographical distribution. In a second part of the paper, this author examined the use of auditory and visual signalling in ocypodid and grapsoid crabs (Tweedie, 1954).

In the 1960s and early 1970s, several studies on sesarmid crabs in this area were conducted by Prof. R. Serène and Prof. C. L. Soh, including mainly taxonomic works (Serène, 1967, 1968; Serène & Soh, 1967a,b, 1971). In particular, Serène (1967) described *Nanosesarma tweediei* from the East coast of Peninsular Malaysia, Singapore, and Vietnam, while Serène & Soh (1967b) described *Episesarma chentongense* [as *Sesarma* (*Sesarma*) *chentongensis*] from Singapore. Serène & Soh (1967a) provided taxonomic notes on "the 5 largest species of *Sesarma* in Malaysia and Singapore", i.e. the '*taeniolata* group' *sensu* Tweedie (1936) (today *Episesarma singaporense*, *E. mederi*, *E. chentongensis*, *E. versicolor*, *E. palawanensis*), together with different diagnostic keys based on the adult male cheliped, the colour of the cheliped, and the male first pleopod. Serène (1968) compiled a checklist of the non-planctonic brachyuran species of South East Asia. Serène and Soh (1971) provided a taxonomic account of *Sarmatium crassum* and *S. germaini*, with a comparisons between the two species.

In the 1970s, the first ecological studies were conducted in this geographic area (Berry, 1972; Sasekumar, 1974; Malley, 1978). In particular, Berry (1972) presented a review of the mangrove fauna of Peninsular Malaysia, which included a description of the general features of the local mangrove ecosystems, such as geological aspects, permanent and visitor fauna, zonation of the mangrove forest and fauna associated to each zone (seaward fore-shore, marine pioneer zone, eroded mangrove banks, true mangrove forest, rivers and streams, terrestrial margin, dead wood), and biological adaptations to this semi-terrestrial environment. This author highlighted the dominance of crabs and molluscs in the forests, and discussed the burrowing, breathing and feeding activities of mangrove crabs, including sesarmid species (Berry, 1972).

Sasekumar (1974) conducted an ecological study on the spatial distribution and zonation of the macrofaunal community of the Kapar Mangrove Forest Reserve (Selangor, Peninsular Malaysia). This author collected quantitative faunal samples (infauna, soil surface fauna, tree-dwelling fauna) from 8 stations representing different zones of the forest, and measured salinity, pH, and organic carbon of the soil in each station. A dendrogram of similarity among the different stations was also obtained, based on Jaccard's coefficient (Sasekumar, 1974).

Malley (1978) investigated the diet of *Parasesarma onychophorum* (as *Chiromantes onychophorum*), by examining the gut contents of specimens collected from Penang (Peninsular Malaysia). The study revealed that this species feeds mainly on mangrove leaf fragments, and the particle size decreases through the intestine, suggesting that this species has a role in degrading mangrove leaves to detrital-sized particles (Malley, 1978).

In the following decades, spatial and feeding ecology was investigated by several authors (Rodelli et al., 1984; Leh & Sasekumar, 1985; Sivasothi et al., 1993; Zakaria & Sasekumar, 1994; Sasekumar & Chong, 1998; Sivasothi, 2000; Ashton, 2002; Ashton et al., 2003a,b; Boon et al., 2008; Leh et al., 2010, 2012; Ng et al., 2015b; Zakaria & Rajpar, 2015; Le et al., 2017).

Rodelli et al. (1984) conducted a study on the ratio of stable carbon isotopes in several plants and animals from Malaysian mangrove swamps, coastal inlets, and offshore waters, in order to investigated how the carbon derived from different primary producers (mangroves, phytoplankton, and other algae) is utilised by macrofaunal consumers in mangals, coastal inlets, and nearshore waters. In particular, samples were obtained from the Sementa Besar coastal inlet and the Buloh River (Selangor, Peninsular Malaysia) (Rodelli et al., 1984).

Leh and Sasekumar (1985) examined the gut content of different sesarmid species (*Clistocoeloma merguiense*, *Episesarma versicolor*, *Parasesarma eumolpe*, *Parasesarma onychophorum*, *Sesarmoides kraussi*) from the Kapar Mangrove Forest Reserve (Selangor, Peninsular Malaysia). Moreover, these authors conducted experiments on leaf consumption (obtaining daily consumption rates) and faeces excretion for *P. eumolpe* and *P. onychophorum*.

Sivasothi et al. (1993) investigated the tree-climbing behaviour and the herbivory of grapsoid crabs (*Episesarma* spp., *Selatium brockii*, *Metopograpsus* spp.) in Singapore mangroves, and provided a general review on these two ecological aspects. These authors conducted field observations on the tree-climbing and feeding activity patterns and gut content analyses for these species, while laboratory experiments on the food preference were conducted for *Episesarma versicolor* (Sivasothi et al., 1993). A few years later, Sivasothi (2000) presented another study on the above mentioned tree-climbing species from Singapore, investigating their spatial niche preference (zonation within the forest), gut contents, burrowing habit and orientation. The results revealed that, despite spatial overlap of habitat, these species have different niche in terms of diet (herbivorous or algivorous diet), distribution in the mangrove (main forest, sandbank zone, mud-lobster mound system), spatial strategies (tree-dwelling, habitual tree-climbing, facultative tree-climbing), and temporal activity patterns (day/night, low/high tide) (Sivasothi, 2000).

Zakaria and Sasekumar (1994) investigated the macroinvertebrate community in Kapar Mangrove Forest Reserve (Selangor, Peninsular Malaysia), comparing an intact forest area and a cleared one, which had been recently deforested and then abandoned. Quantitative macrofaunal samples were collected, together with selected enviromental parameters (pH, temperature, relative humidity, salinity of sediment water, dissolved oxygen in sediment water), and a significant difference in macrofaunal composition and abundance was found between the two areas (Zakaria & Sasekumar, 1994).

Sasekumar and Chong (1998) conducted a study on the epifaunal and infaunal community of Matang mangrove forest (Perak, see also Subchapter 2.6), and compared diversity in sites at different stages of forest management cycle (i.e. mature forest not harvested, 15-year old forest, and 2-year old forest). Sesarmid crabs were identified at generic level.

Ashton (2002) conducted field and laboratory experiments on the food preference of sesarmid crabs from the Merbok estuary (Kedah), by providing the crabs with four different mangrove species (*Avicennia officinalis*, *Bruguiera gymnorrhiza*, *B. parviflora*, *Rhizophora apiculata*), in fresh and senescent conditions. In the field, experiments were conducted in both upstream and downstream sites on the whole sesarmid community, while in the laboratory, *Parasesarma eumolpe* and *P. onychophorum* were investigated only (Ashton, 2002).

Asthon et al. (2003a) investigated the structure of brachyuran communities in four mangrove sites under different management systems, i.e. the Klong Nao estuary (Thailand; biosphere reserve, previously a charcoal concession forest, a disused tin mine, and an abandoned shrimp pond along the estuary), the Merbok estuary (Kedah; partially managed forest, where trees are cut for charcoal and poles on a small scale and the forests are left to regenerate naturally), Matang (Perak; heavily exploited but well managed forest, see also chapter 2.6), and Kuala Selangor Nature Park (Selangor; nature reserve since 1987). The results suggested that the management history has a significant role in shaping the crab community structure, which is also related to the age of the mangrove forest stand (Ashton et al., 2003a).

Ashton et al. (2003b) conducted a baseline study on the crab and mollusc communities at Sematan mangrove estuary (Sarawak), investigating diversity, density, biomass and community structure in several stations along two transects at different intertidal positions along the estuary. Several environmental parameters were measured (salinity, redox potential, pH and temperature for water at the surface and at 50 cm depth, and air temperature) and the composition of the vegetation was also recorded.

Boon et al. (2008) conducted field observations and laboratory experiments to investigate the mangrove leaf species preferences, leaf age preferences, and feeding rates of *Parasesarma eumolpe* and *P. indiarum* from Singapore (see Subchapters 3.3.10.3, 3.3.10.4, and 3.3.10.11 for further details).

Leh et al. (2010) investigated the biomass and abundance of sesarmid crabs in the Kapar Mangrove Forest Reserve (Selangor), in the upper zone of the forest, in a undisturbed area and in a disturbed one. This study revealed differences in the structure and composition of the assemblages of the two areas, suggesting that forest structure, sediment water content and timber harvest have a significant impact on the sesarmid community (Leh et al., 2010).

Leh et al. (2012) investigated the feeding biology of the eel catfish *Plotosus canius* in two Malaysian mangrove sites [Sungai Sementa Kecil (estuarine mangrove site) and Sungai Buloh (mudflat), Selangor]. The results revealed that, in the estuarine site, sesarmid crabs were one of the most relevant food items in the diet of this fish (Leh et al., 2012).

Zakaria and Rajpar (2015) investigated the diversity of the Marudu Bay Forest (Sabah), although these author reported only *Aratus pisonii*, which is actually an American species.

Several papers addressed taxonomic aspects, and provided new information on the species distribution (Tan & Ng, 1988; Davie, 1994; Tan & Ng, 1994; Ng, 1995b; Yeo et al., 1999; Ng & Schubart, 2002; Sasekumar & Ooi, 2005; Rahayu & Ng, 2009; Sasekumar & Moh, 2010; Taufek, 2013; Lee et al., 2015; Ng et al., 2015b).

Tan and Ng (1994) provided a checklists for the mangrove brachyuran fauna of Malaysia (East and West Malaysia) and Singapore, with notes on unsolved taxonomic aspects. Ng (1995) investigated the diversity of the freshwater crabs and prawns of Bako National Park (Sarawak), and reported *Pseudosesarma bocourti* from this site, while Yeo et al. (1999) provided a checklist of the freshwater and terrestrial decapods of Pulau Tioman (East coast of Peninsular Malaysia), which included a few sesarmid species (*Geosesarma* spp., *Neosarmatium indicum*, *Pseudosesarma bocourti*, and *Tiomanum indicum*).

Davie (1994) described *Neosarmatium spinicarpus* from Sarawak (Borneo), in his review of the genus. Ng and Schubart (2002) described the new genus *Haberma*, and the species *H. nanum*, from Singapore, while Rahayu and Ng (2009) described *Parasesarma raouli* from Sungai Melayu, Johor (Peninsular Malaysia).

Sasekumar and Ooi (2005) investigated the macrofauna of Langkawi mangrove forests, in particular the north-eastern part (Sungai Kisap, Sungai Air Hangat, Sungai Kilim), reporting four sesarmid species from this site (*Parasesarma eumolpe*, *Episesarma versicolor*, *Sarmatium crassum*, and *Clistocoeloma merguiense*). Sasekumar and Moh (2010) surveyed the flora and fauna diversity of mangrove forests in Bachok (Kelantan, East coast of Peninsular Malaysia), where they found *Parasesarma eumolpe* and *Episesarma* sp. Taufek (2013) investigated the community structure of the brachyuran community of the Setiu coastal lagoon (Terengganu; unpublished thesis).

Ng et al. (2015b) provided ecological and taxonomic notes for *Labuanium politum* from Singapore, and recorded this species for the first time from this island. Lee et al. (2015) reviewed the taxonomy of the five species of *Episesarma* present in Singapore, providing updated taxonomic keys.

More recently, other aspects were also investigated, such as larval morphology (Guerao et al., 2004), anatomical, morphological and physiological aspects (Huang et al., 2008; Wang & Todd, 2012), behaviour and social interactions (Boon et al., 2009; Todd et al., 2011; Chen et al., 2014; Lee et al., 2014; Su & Lim, 2016).

Several authors investigated the facial bands of *Parasesarma eumolpe* and *P. indiarum* (today considered *P. peninsulare*, see Subchapter 3.3.10.11) from Singapore, and in particular, their intra- and inter-specific variability (Huang et al., 2008), their function in intraspecific communication (Todd et al., 2011) and the production of carotenoid pigments in these bands (Wang & Todd, 2012). Boon et al. (2009) conducted studies on the sound production and reception in these two species of *Parasesarma*, while Chen et al. (2014) investigated the role of post-contest acoustic stridulation as a victory display in *P. eumolpe*.

Lee et al. (2014) presented a study (from Singapore) on the role of the layer of setae covering the body of *C. merguiense*, suggesting that this layer may act as "masking camouflage" for this crab, allowing it to avoid predators. Su and Lim (2016) conducted a study on the anti-predatory response in *Haberma nanum* and *Paracleistostoma depressum* in mangrove forests from Singapore, and found that the former species chose a flight behaviour when exposed to predators, and showed strong predator recognition capabilities.

Finally, Guerao et al. (2004) described the complete larval and early juvenile development of *Fasciarma fasciatum* from specimens collected in Singapore mangroves, and compared it with other species of the same genus.

Table 3.75: List of the papers published on sesarmid crabs from mangrove systems from the Malay Peninsula (Peninsular Malaysia and Singapore) and northern Borneo (East Malaysia). *Location* = areas/localities within the Malay Peninsula and Borneo included in the publication (i.e. the column does not include localities cited in the publication which are from other geographic areas).

Author and Year	**Investigated subject**	**Location**
White (1847)	Taxonomy, distribution	Singapore, Borneo
Targioni-Tozzetti (1877)	Taxonomy, distribution	Singapore
Miers (1880)	Taxonomy, distribution	Borneo
De Man (1880)	Taxonomy, distribution	Borneo
De Man (1892)	Taxonomy, distribution	Penang (Peninsular Malaysia)
Ortmann (1894)	Taxonomy, distribution	Singapore
Zehntner (1894)	Taxonomy, distribution	Sarawak (Borneo)
De Man (1895)	Taxonomy, distribution	Penang (Peninsular Malaysia)
De Man (1896)	Taxonomy, distribution	Penang (Peninsular Malaysia)
Alcock (1900)	Taxonomy, distribution	Penang (Peninsular Malaysia)
Lanchester (1900a)	Taxonomy, distribution	Malacca (Peninsular Malaysia), Singapore
Lanchester (1900b)	Taxonomy, distribution	Sarawak (Borneo)
Nobili (1900)	Taxonomy, distribution	Singapore, Sarawak (Borneo)
Lanchester (1901)	Taxonomy, distribution	Terengganu (Peninsular Malaysia)
Nobili (1901)	Taxonomy, distribution	Sarawak (Borneo)
De Man (1902)	Taxonomy, distribution	Baram River (Sarawak, Borneo)
Rathbun (1913)	Taxonomy, distribution	Tioman Island (Peninsular Malaysia)
Tweedie (1936)	Taxonomy, distribution	Port Klang, Kuantan, Penang, Perak, Johor (Peninsular Malaysia), Singapore
Tweedie (1940)	Taxonomy, distribution, brief ecological notes	Muar, Sedili River, Aor Island, Kota Tinggi, Pendas River (Johor, Peninsular Malaysia), Prai (Penang, Peninsular Malaysia); Kuantan (Pahang, Peninsular Malaysia), Labuan (East Malaysia), Singapore
Tweedie (1950a)	Taxonomy, distribution, brief ecological notes	Labuan, Kuching, (East Malaysia)
Tweedie (1950b)	Taxonomy, distribution, brief ecological notes	Aor Island (Johor, Peninsular Malaysia)
Tweedie (1950c)	Taxonomy, distribution	Peninsular Malaysia, Borneo, Singapore
Tweedie (1954)	Distribution, behaviour	Peninsular Malaysia

Table 3.75, continued.

Author and Year	**Investigated subject**	**Location**
Serène (1967)	Taxonomy, distribution	Mersing (Peninsular Malaysia), Singapore
Serène and Soh (1967a)	Taxonomy, distribution	Peninsular Malaysia, Singapore
Serène and Soh (1967b)	Taxonomy, distribution	Johor Strait, Singapore
Serène (1968)	Taxonomy, distribution	Peninsular Malaysia, Singapore, Borneo
Serène and Soh (1971)	Taxonomy, distribution	Port Klang (Selangor, Peninsular Malaysia), Prai (Penang, Peninsular Malaysia), Singapore
Berry (1972)	Spatial ecology	West coast of Peninsular Malaysia
Sasekumar (1974)	Spatial ecology	Port Klang (Selangor, Peninsular Malaysia)
Malley (1978)	Feeding ecology	Penang (Peninsular Malaysia)
Rodelli et al. (1984)	Feeding ecology	West coast of Peninsular Malaysia
Leh and Sasekumar (1985)	Feeding ecology	Selangor (Peninsular Malaysia)
Sivasothi et al. (1993)	Feeding ecology, tree climbing behaviour	Singapore
Davie 1994	Taxonomy	Sarawak (Borneo)
Tan & Ng (1994)	Distribution	Peninsular Malaysia, Singapore, Borneo
Zakaria and Sasekumar (1994)	Spatial ecology	Kapar (Selangor, Peninsular Malaysia)
Ng (1995)	Taxonomy, distribution	Bako (Sarawak, Borneo)
Sasekumar & Chong (1998)	Spatial ecology	Matang (Perak, Peninsular Malaysia)
Yeo et al. (1999)	Taxonomy, distribution	Tioman Island (Peninsular Malaysia)
Sivasothi (2000)	Spatial ecology, feeding ecology	Singapore
Ashton (2002)	Feeding ecology	Kedah (Peninsular Malaysia)
Ng & Schubart (2002)	Taxonomy	Singapore
Ashton et al. (2003a)	Spatial ecology	Merbok, Matang, Kuala Selangor (Kedah, Perak, Selangor, Peninsular Malaysia)
Ashton et al. (2003b)	Spatial ecology	Sematan (Sarawak, Borneo)
Guerao et al. (2004)	Ontogenesis	Singapore
Sasekumar and Ooi (2005)	Distribution	Langkawi (Peninsular Malaysia)
Boon et al. (2008)	Feeding ecology	Singapore
Huang et al. (2008)	Anatomy/morphology	Singapore
Boon et al. (2009)	Behaviour/social interactions	Singapore

Table 3.75, continued.

Author and Year	Investigated subject	Location
Rahayu and Ng (2009)	Taxonomy	Johor (Peninsular Malaysia)
Leh et al. (2010)	Spatial ecology	Kapar, Selangor (Peninsular Malaysia)
Sasekumar and Moh (2010)	Distribution	Bachok, Kelantan (Peninsular Malaysia)
Todd et al. (2011)	Behaviour/social interactions	Singapore
Leh et al. (2012)	Feeding ecology	Selangor (Peninsular Malaysia)
Wang and Todd (2012)	Physiology/anatomy	Singapore
Taufek (2013)	Spatial ecology	Setiu Lagoon (Terengganu, Peninsular Malaysia)
Lee et al. (2014)	Behaviour	Singapore
Chen et al. (2014)	Behaviour/social interactions	Singapore
Lee et al. (2015)	Taxonomy	Singapore
Ng et al. (2015b)	Taxonomy / spatial ecology	Singapore
Zakaria and Rajpar (2015)	Spatial ecology/ Biodiversity	Marudu Bay (Sabah, Borneo)
Su and Lim (2016)	Behaviour	Singapore
Le et al. (2017)	Feeding ecology	Setiu Lagoon (Terengganu, Peninsular Malaysia)

3.4 Discussion and Conclusion

This area hosts a relatively high biodiversity for this taxon (see Jones, 1984; Lee, 1998). This is not surprising, considering that both Borneo and the Malay Peninsula (Peninsular Malaysia and Singapore) are included in the Sundaland ecoregion (Myers et al., 2000), and in the East Indies Triangle (Briggs, 1999), both considered as biodiversity hotspots for several terrestrial and marine taxa (Briggs, 1999; Myers et al., 2000).

A few species (*Bresedium sedilense*, *Haberma nanum*, *Nanosesarma nunongi*, *Neosarmatium spinicarpus*, *Parasesarma lanchesteri* and *Pseudosesarma johorense*) can be considered as endemic of the considered geographic area (Malay Peninsula and/or Borneo), even though further investigations may reveal different patterns of distribution. For instance, *Parasesarma raouli*, a species recorded only from Peninsular Malaysia until very recently, has been found in Indonesia a few years ago (Widyastuti & Rahayu, 2016), indicating that our knowledge on the distribution of these taxa is still fragmentary. In general, however, the restricted areal of these species prompts for particular attention in conservation plans, since local extinctions may compromise the survival of the whole species.

A few species have not been recorded since the 1950s (*Bresedium sedilense*, *Nanosesarma nunongi*, *Parasesarma lanchesteri*, *Pseudosesarma granosimanum*, and *Pseudosesarma johorense*). It would be interesting to investigate whether these species have not been recorded due to lack of further studies in their distribution area, or whether they have disappeared as a consequence of the rapid habitat loss occurring in this region. For instance, the present project reported *Nanosesarma nunongi* from Peninsular Malaysia (see Chapter 4), reconfirming the presence of this species in this area. Interestingly, these species (except for *Pseudosesarma edwardsii*) have also a restricted distribution range (see Subchapter 3.3.17.1), making them of particular conservation interest.

Other species (*Episesarma chentongense*, *Nanosesarma tweediei*, *Parasesarma raouli*, *Haberma nanum* and *Haberma kamora*) have been described and reported only more recently (after 1960s). This datum reflects a general trend for sesarmid crabs, which include several species that have been described only recently (see Subchapter 2.1), suggesting that the knowledge on the diversity of these crabs is still incomplete. This is most likely related to challenges in taxonomic determination and difficulties in the field identification, which have hampered research efforts (Hogarth, 2007; Lee et al., 2017). Moreover, logistical and safety issues posed by mangrove forests, such as soft substratum, disturbing (e.g. biting insects) or dangerous wildlife (e.g. snakes, crocodiles and tigers), make these systems relatively tough to investigate (Lee et al., 2017).

In general, information on ecology and biology of most of the species is still scarce, and the autecology of several species remains practically unknown (*Bresedium sedilense*, *Clistocoeloma suvaense*, *Nanosesarma edamense*, *Nanosesarma nunongi*, *Nanosesarma pontianacense*, *Nanosesarma tweediei*, *Neosesarma rectipectinatum*, *Parasesarma batavianum*, *Parasesarma calypso*, *Parasesarma lanchesteri*, *Parasesarma lepidum*, *Parasesarma raouli*, *Pseudosesarma granosimanum*, *Pseudosesarma johorense*, *Tiomanum indicum*). Further investigations on habitat types and autecological traits of these species would be useful, in order to help individuating and preserving their habitats.

Most of the studies were conducted in a few mangrove sites, such as the Port Klang area and Kuala Selangor estuary (Selangor, e.g. Sasekumar, 1974; Ashton et al., 2003a), the Singapore and Johor mangrove systems (e.g. Sivasothi et al., 1993; Boon et al., 2008), and the Merbok estuary (Kedah, Ashton, 2002; Ashton et al., 2003a). Several mangrove sites have not ever been investigated (e.g.several sites in the states of Perak, Negeri Sembilan, Malacca, Pahang, Kelantan, Terengganu, Sabah), suggesting that the knowledge on the diversity and distribution of the sesarmid communities in this region is still fragmentary.

CHAPTER 4: ARTICLE 2 - UPDATE OF THE DISTRIBUTION DATASET

4.1. Introduction and brief Literature Review

The Malay Peninsula (Peninsular Malaysia and Singapore) and Borneo are part of a biodiversity hotspot, both terrestrial (Sundaland ecoregion, Myers et al., 2000) and marine (East Indies Triangle, Briggs, 1999; or Indo Australian Archipelago, Renema et al., 2008).

The terrestrial ecosystems of the Sundaland region have been identified as one of the top 8 hottest terrestrial biodiversity hotspots amongst the 25 proposed by Myers et al. (2000), defined as "areas featuring exceptional concentrations of endemic species and experiencing exceptional loss of habitat" (Myers et al., 2000, p. 853). The marine counterpart is instead included in the East Indies Triangle (or Coral Triangle), and its dynamics have been widely debated (Briggs, 2003). Several ecological gradients have been observed in this area, such as the species richness and genetic diversity decreasing outwardly, and the generic age and plesiomorphy increasing outwardly (Briggs, 1999); moreover, several routes of dispersal and extinction patterns originate from here. For these reasons, this area has been proposed as a centre of origin (Briggs, 1999), a source of speciation from where a flow of successful new species originate and continuously colonise periferical sink areas. In order to explain the occurrence of this centre of origin, Renema et al. (2008) recently proposed the geological changes occurring during collision of tectonic plates, which created new shallow water environments and formed islands, as the main driving force.

Conservationists strongly recommended hotspots as priority zones for the conservation policy and action, both because of their cost/benefit advantages, and because they act as a source of new species in a geological time scale (Briggs, 1999; Myers et al., 2000). A rapid loss of diversity in a hotspot would create a gap in the evolutive scenario over millions of years (Briggs, 1999).

Despite this consideration and increasing ongoing efforts, knowledge on the faunal assemblages is often still fragmentary, and several works have prompted for a better investigation of the area. For example, a relatively low diversity of polychaete worms recorded in Malaysia compared to the other Southeast Asian countries was attributed to a lack of studies in this area (Paxton & Chou, 2000; Idris & Arshad, 2013).

In a recent review on the Indian Ocean region, including the Malay Peninsula, Wafar et al. (2011) noticed a geographically heterogeneous state of knowledge of many marine taxa, attributed to the unequal amount of resources allocated for biodiversity studies in different countries (see also Subchapter 3.1). In particular, databases are often biased towards larger and commercially important groups, or groups for which taxonomic experts are available in the country. Moreover, spatial coverage is often inadequate, and diversity data for whole countries are sometimes inferred from surveys of small areas. For instances, despite India being one of the best studied countries of this region, only few major estuaries of the >200 present there have been surveyed, and the knowledge on the coral diversity of the Andaman-Nicobar Sea relies on collections from the Wandoor National Park, which included only a few of the 500 islands forming this archipelago (Wafar et al., 2011).

For the Malay Peninsula and Borneo, the most recent checklist of the mangrove grapsoid species present in this area is by Tan and Ng (1994). However, these authors highlighted that information on the brachyuran assemblages in this area was still incomplete. In the following years, the discovery of new species and new distribution records (e.g. Ng & Schubart, 2002; Rahayu & Ng, 2009) has further supported this statement. In this area, most of the studies on sesarmid crabs have been conducted in a few states only (e.g. Selangor, Penang, Kedah), while other coastal tracts remain almost unexplored (e.g. Negeri Sembilan, Malacca, Johor, East coast of Peninsular Malaysia, Sabah; see Subchapter 3.3.18).

Considering the loss of mangrove habitat ongoing in this area (see Subchapter 2.6), it is important to keep updating biodiversity checklists, to monitor the state of ecosystems. Because many mangrove sites have not been investigated, or they have been surveyed only long time ago (see Chapter 3), the current status of the local diversity (including also the number of species that may be locally or totally extinct) is poorly known. Improving the spatial coverage of biodiversity datasets is therefore fundamental, in order to manage these natural resources in a sustainable way.

During this project, several field investigations were conducted on the West coast of the Peninsular Malaysia, and in northern Borneo (Brunei Bay), in order to obtain inventories of species for sites which were previously uninvestigated, and to update the existing checklists.

4.2 Methodology

Two sets of surveys were conducted. A first set was conducted in Peninsular Malaysia, in several sites along the West coast (Langkawi, Kuala Selangor, Tanjung Tuan, Pulau Besar, Pulau Kukup, Pulau Merambong). These sites were chosen to represent different kind of mangrove systems occurring in these area, including both large mangrove forests and small fringe mangroves, mainland and insular systems, and different kind of sediment types (mud, mud/sand, sand/rock).

A second series of field trips was conducted in northern Borneo (Brunei Bay, Brunei Darussalam). In this case, sites were instead chosen to represent the variety of intertidal and supratidal systems occurring in a relatively small area (i.e. the Brunei Bay), such as mangrove stands, monotypic nipah forests, peat swamps, coastal lagoons, and upstream unvegetated river banks.

4.2.1 Study sites

4.2.1.1. Peninsular Malaysia

The climate of this area is tropical, with an average annual temperature of ~27°C, and average annual rainfall of ~2300 mm, with two peaks in correspondence of the transition to the Southwest monsoon (March - April), and the Northeast monsoon (October) (Tangang et al., 2007; Suhaila & Jemain, 2009; Wong et al., 2009). Sediment dynamics and intertidal systems along coast are shaped by tidal and fluvial actions. Several large rivers with high suspended load [e.g. Klang-Langat system, Sungai Selangor, Sungai Merbok, Sungai Kedah, Sungai Rokan, Sungai Kampar] discharge into the small basin of the Straits of Malacca, that is a semidiurnal meso-macrotidal system, with tidal ranges of approximately 1-3 m during neap tides and 3-5 m during spring tides (Coleman et al., 1970).

Six study sites were surveyed from 2012 to 2014 (Fig. 4.1): Langkawi (6°24’39.81”N, 99°51’35.91”E), Kuala Selangor (3°20’12.22”N, 101°14’7.40”E), Tanjung Tuan (2°24’52.57”N, 101°51’28.24”E), Pulau Besar (2°6’44.39”N, 102°19’37.11”E), Pulau Kukup (1°19’18.69”N, 103°25’30.61”E), and Pulau Merambong (1°18’55.53”N, 103°36’35.71”E). Every site, except Pulau Merambong, was surveyed at least twice. In each site, 2-3 different areas were surveyed, in order to obtain a better estimate of the intra-site variability. In each area, different sampling sessions were conducted, in GPS-delimited plots of 30 m x 30 m, that were sampled for 1 hour.

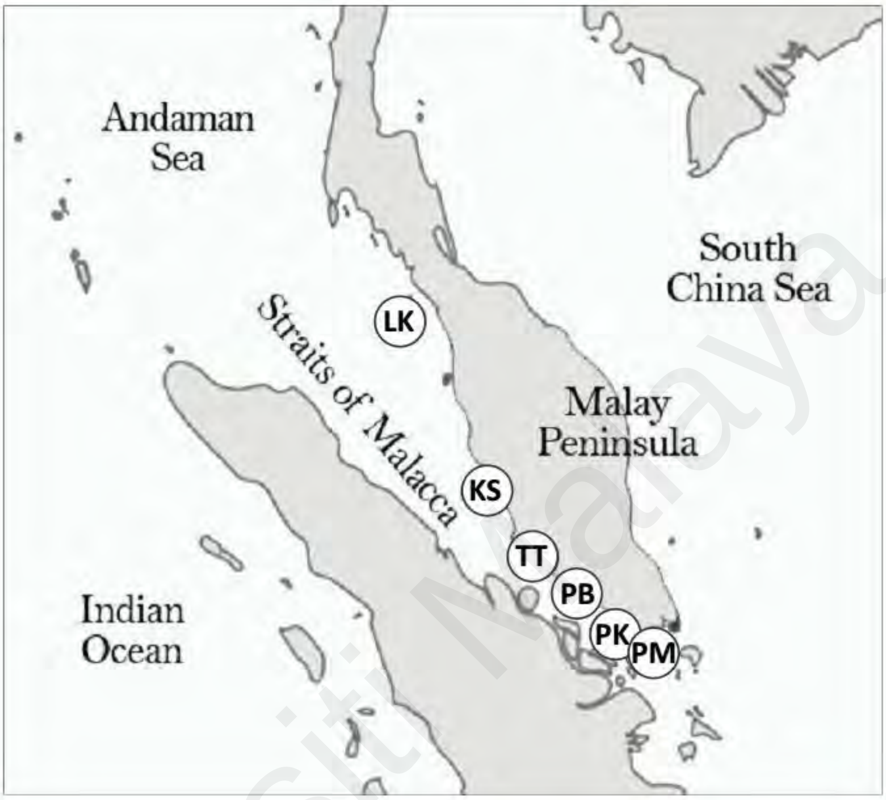

Figure 4.1: Sampling sites on the West coast of the Malay Peninsula. LK = Langkawi, KS = Kuala Selangor, TT = Tanjung Tuan, PB = Pulau Besar, PK = Pulau Kukup, PM = Pulau Merambong.

In particular, Langkawi was surveyed in November 2013 (3 surveys); Kuala Selangor in February, March, May, June and September 2012, and November 2013 (8 surveys); Tanjung Tuan in September and November 2012 (3 surveys); Pulau Besar in June and November 2012 (3 surveys); Pulau Kukup in December 2012 and March 2014 (3 surveys); and Pulau Merambong in November 2012 (1 survey). A description of the study sites is presented below (see also Fig. 4.2).

Langkawi. The Langkawi Archipelago is composed by 104 islands, mostly consisting of peaks of karstified sandstones and limestones, or granitic rocks, crossed by numerous streams and waterfalls. Unconsolidated recent sand and clay deposits have been deposited in narrow valleys and coastal plains, which have been partly colonised by mangroves. Three large mangrove systems are present, covering a total area of ~ 3000 ha: Kampong Kuala Kisap - Gua Cerita - Sungai Kilim; Sungai Ayer Hangat - Kubang Badak; and Pulau Dayang Bunting plus Pulau Tuba (Jusoff, 2008). The first two mangrove forests, located along the eastern coasts of the main island, are included in the Kilim Geoforest Park system (Langkawi UNESCO Geopark). Intertidal deposits range from muddy to sandy, and are mainly covered by *Rhizophora* and *Bruguiera* mangroves. Sampling surveys were conducted in two mangrove areas, along the banks of Sungai (= river) Ayer Hangat (06°26’46.43”N, 099°48’49.76”E, 3 sampling sessions) and Sungai Kilim (06°24’00.09”N, 099°51’31.17”E, 3 sampling sessions).

Kuala Selangor. The estuarine mangrove forest of Kuala Selangor is located at the mouth of the Sungai Selangor, ~ 360 km south of Langkawi, about half-way along the West coast of Peninsular Malaysia (Fig. 4.1). The forest fringe covers > 10 km along coast, and extends 100-2000 m from sea to land. On the southern side of the estuary, part of the mangrove forest (300 ha) is protected under the Kuala Selangor Nature Park, established in 1987. The substrate is consistently mud, and the forest is dominated by *Bruguiera parviflora*, with scattered trees of the genera *Avicennia, Sonneratia* and *Rhizophora*, the latter ones being more abundant along the forests’ marine fringe and on the banks of the creek network. Surveys were conducted in three different areas, one on the northern side of the estuary (03°20’38.15”N, 101°12’50.29”E, 2 sampling sessions), and two on the southern side (03°20’07.74”N, 101°14’04.30”E, 3 sampling sessions; 03°19’34.81”N, 101°14’16.68”E, 3 sampling sessions).

Tanjung Tuan. The coasts of the Tanjung Tuan promontory are colonised by dense mangrove forests. The northern coast is fringed by a ~ 150 m long and ~ 20 m wide mangrove forest, dominated by *Rhizophora apiculata* and *Sonneratia alba*, which grows on a sandy substrate. The forest grew at the foot of a steep rocky outcrop. In front of its marine edge, a sandy area and a reef flat are found. A larger forest, ~ 300 m long and ~ 100-200 m wide, colonises the southern coast, where a *Sonneratia* marine fringe is adjacent to a wider formation dominated by *Rhizophora* species and *Bruguiera gymnorrhyza*. In the back-forest, *Pandanus* palms and nibong palms (*Oncosperma tigillaria*) were observed. The substrate is either muddy or sandy; in the *Sonneratia* zone, the root system and the forest floor are colonised by dense algal mats. Surveys were conducted on both sides of the promontory (02°24’52.07”N, 101°51’13.49”E, 3 sampling sessions; 02°24’43.27”N, 101°51’32.99”E, 3 sampling sessions).

Pulau Besar. Pulau Besar is a ~ 1 km long mountainous island, located in the water off-shore Malacca. The island hosts small mangrove patches, 10-30 m wide from sea to land, on sandy or sand-muddy deposits. Most of these mangrove fringes are dominated by *Rhizophora* species. Artificial or natural eroding steps and sand berms separate the mangroves from the inland forests. Surveys were conducted in three mangrove areas, located on the northern (02°06’58.53”N, 102°19’38.44”E, 2 sampling sessions), north-western (02°06’49.64”N, 102°19’17.13”E, 2 sampling sessions), and south-eastern (02°06’18.07”N, 102°19’40.32”E, 2 sampling sessions) sides of the island.

Pulau Kukup. Pulau Kukup is a ~ 2 km long island, entirely covered by mangrove forests. Mangroves remained virtually undisturbed for the last 20 years, since this site has become a national park in 1997, and more recently, in 2003, it has been declared Ramsar site. The soil is muddy, and the forest is dominated by *Rhizophora* spp. and *Bruguiera* spp., with patches of *Sonneratia* species at the mouth of the Sungai Solok river. Several creeks and small inlets cross the island. Surveys were conducted along the eastern coast of the island, in the central part (01°19’34.87”N, 103°26’04.19”E, 3 sampling sessions) and in the north-eastern part (01°20’07.29”N, 103°25’26.19”E, 3 sampling sessions).

Pulau Merambong. Pulau Merambong is a small islet in the Johor Strait, ~200 m long. A narrow mangrove fringe, ~ 250 m long and 10-30 m wide, dominated by *Rhizophora stylosa* and *Bruguiera gymnorrhiza*, colonises the western part. Several scattered trees of *Ceriops* sp., *Sonneratia alba*, *Avicennia rumphiana* and *Xylocarpus granatum* are present. The substrate is either sandy or rocky. Surveys were conducted in three mangrove areas, in the north-western (01°18’57.55”N, 103°36’33.33”E, 1 sampling sessions), western (01°18’54.06”N, 103°36’35.08”E, 2 sampling sessions), and south-western (01°18’52.26”N, 103°36’38.18”E, 1 sampling session) sides of the island.

Figure 4.2: Habitat diversity of the investigated sites. Some of the different kind of habitat type encountered in the investigated area (Peninsular Malaysia). *Above left*: high intertidal *Rhizophora* zone (Tanjung Tuan), *above right*: fringe mangrove on sandy substrate (Pulau Besar), *middle left*: seaward *Sonneratia* pioneer shore (Tanjung Tuan), *middle right*: canal crossing the mangrove forest (Pulau Kukup), *below left*: *Bruguiera* zone heavily colonised by new saplings (Kuala Selangor), *below right*: eroding river mudbank (Kuala Selangor).

4.2.1.2 Brunei Bay

Brunei Darussalam is characterised by a tropical climate, with an average annual temperature of 27°C, and an average annual rainfall of 2,880 mm (average value from 1966 to 2006), with two peaks in correspondence of the southwest monsoon (May), and the northeast monsoon (December) (Brunei Meteorological Service, Department of Civil Aviation).

The Brunei Bay occupies an area of ~ 2,500 km^2. Several rivers flow into the bay, such as Sungai Brunei, Sungai Limbang, Sungai Temburong, Sungai Lawas, and Sungai Kilas (Yau, 1991). Several rivers also form wetlands and lagoons along the northern coast of Brunei, such as Sungai Tutong, Sungai Lumut, and Sungai Belait.

Nine sites were surveyed (Fig. 4.3) from May 2013 to March 2014: Pemburongunan Creek (5°2'36.46"N, 115°3'22.01"E), Pulau Bedukang (4°58.751'N, 115°3.603'E), Sungai Besar (4°55.674'N, 115°0.885'E), Sungai Bunga (4°54.949'N, 115°0.447'E), Sungai Labu (4°45.727'N, 115°10.084'E), Sungai Belayang (4°44.382'N, 115°2.969'E), Sungai Brunei (4°48.350'N, 114°49.930'E), Sungai Tutong (4°46.092'N, 114°36.402'E), Badas (4°34.200'N, 114°24.703'E). The study sites include several coastal wetlands in the Brunei Bay and along the northern coast of Brunei Darussalam on the South China Sea, influenced by both marine and fluvial action. These sites were characterised by different conditions of salinity, type of substrate, vegetation, and distance from the sea (Fig. 4.3, see Chapter 5, Tab. 5.3).

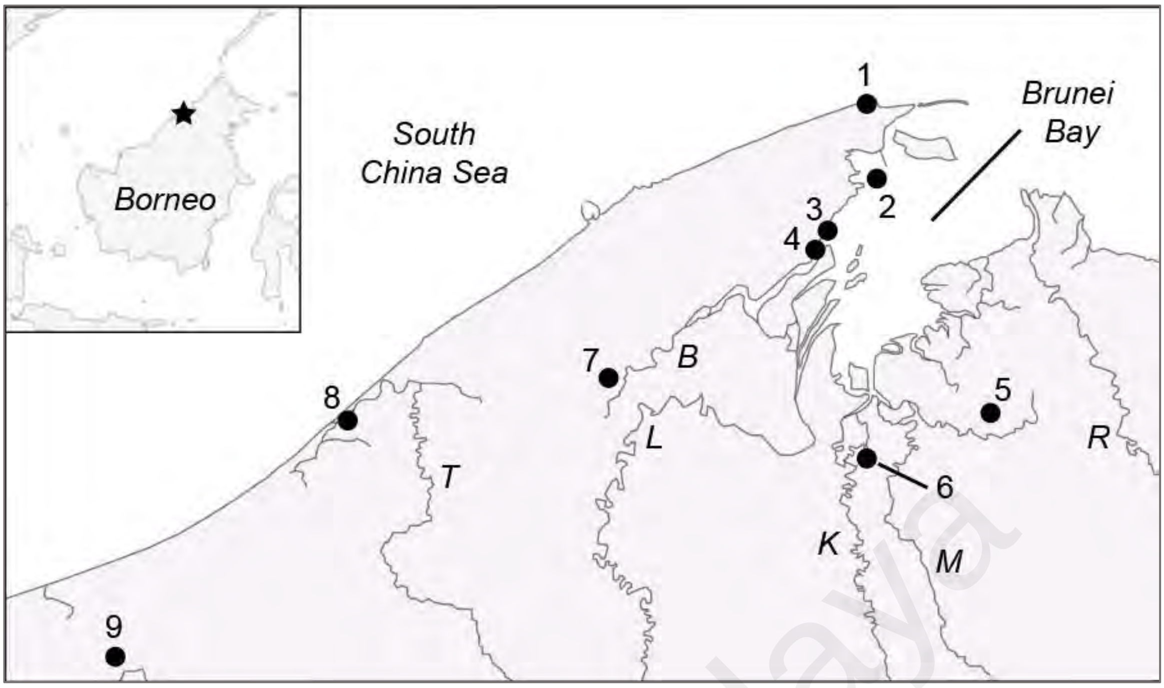

Figure 4.3: Map of the Brunei Bay (inset: *star*) and the study sites (*circles*). Study sites: 1 = Pemburongunan Creek; 2 = Pulau Bedukang; 3 = Sungai Besar; 4 = Sungai Bunga; 5 = Sungai Labu; 6 = Sungai Belayang; 7 = Sungai Brunei; 8 = Sungai Tutong; 9 = Badas. Rivers: *B* = Sungai Brunei; *K* = Sungai Kibi; *L* = Sungai Limbang; *M* = Sungai Temburong; *R* = Sungai Batang Tarusan; *T* = Sungai Tutong.

In particular, the sampled areas included mangrove forests dominated by *Rhizophora apiculata* (Sungai Brunei, Sungai Bunga, Pulau Bedukang), pioneer mangrove forests dominated by *Avicennia* and *Sonneratia* species (Sungai Besar, Pulau Bedukang, Pemburongunan Creek), dense monotypic stands of *Nypa fruticans* (Sungai Belayang, Sungai Bunga, Sungai Tutong), unvegetated mudbanks (Sungai Besar. Sungai Bunga), mudbanks colonised by grasses and sedges (Pemburongunan Creek), mixed peat swamp forests (Badas, Sungai Labu), and an artificial grass meadow near a river bank (Sungai Brunei). Mangrove systems were often adjacent to mangrove backforests, characterised by the presence of *Pandanus* palms, that formed ecotones with peat swamp or heath forests (kerangas) (Sungai Belayang, Sungai Brunei, Sungai Bunga, Sungai Labu, Sungai Tutong).

Thirty-one surveys were conducted in the 9 sampling sites, during day- or night-time; the surveyed areas were selected to represent the range of environmental and ecological conditions in each site. A description of the study sites is provided below, including also details on the area explored (A) and the time allocated to the sampling (T) for every survey.

Pemburongunan Creek (01 December 2013). Mangrove creek 10-20 m wide at its mouth, flowing into the South China Sea. The creek crosses the Meragang coastal lagoon, which is separated from the sea by a ~ 100 m-wide coastal ridge. Survey 1A (T: 60 min; A: 605 m^2): western bank of the lower tract of the Pemburongunan Creek, 140-320 m from its mouth; the lower, 1-2 m wide sloped bank was unvegetated, and separated by a steeper step (10-20 cm high) from the upper vegetated bank, dominated by halophytic grasses, where also stranded logs and scattered trees of *Nypa fruticans*, *Casuarina equisetifolia* and *Avicennia* sp. were found. Survey 1B (T: 50 min; A: 610 m^2): sparsely vegetated tidal flat above the lower tract of the creek, at 5-10 m from the bank and ~ 380 m from the creek mouth, crossed by few tidal inlets, with < 2 m tall *Avicennia* sp. trees, halophytic grasses, and numerous dead trees; substrate: prevalently muddy sand, sandy mud near the water. Survey 1C (T: 20 min; A: 160 m^2): upper portion of the tidal flat, at ~ 60-90 m from the creek bank, dominated by grasses and with scattered, large tidepools, few stunted trees and numerous dead trees.

Pulau Bedukang (A−C: 13 October 2013; D: 27 May 2013; E: 07 May 2013). Transect (~ 100 m) along the sea-to-land intertidal gradient, positioned on the west coast of the island, and pioneer *Rhizophora* fringe on the north coast. Survey 2A (T: 90 min; A: 680 m^2): *Sonneratia* pioneer shore with tidepools and fallen logs, adjacent to a 5-10 m mudbank covered by pneumatophores. Survey 2B (T: 60 min; A: 180 m^2): seaward margin of a *Rhizophora apiculata* forest, at the transition with the *Sonneratia* pioneer shore, with abundant tidepools and fallen logs. Survey 2C (T: 60 min; A: 450 m^2): inlet network inside the *Rhizophora* high-intertidal forest, with stands of *Bruguiera gymnorhiza*, *Avicennia officinalis*, mounds of *Thalassina* sp. and *Acrostichum* ferns. Survey 2D (T: 15 min; A: n/a): dense *Rhizophora* pioneer shore on the northern coast of the island, sampled at night. Survey 2E (T: 20 min; A: n/a): as in 2C, near inlets.

Sungai Besar (A, B: 10 October 2013; C: 24 May 2013). Tract of coast on the western bank of the Brunei Bay, colonised by a 100 m-long and ~ 15 m-wide mangrove fringe, located ~ 100 m north of the mouth of Sungai Besar. Survey 3A (T: 90 min; A: 250 m^2): *Avicennia* and *Sonneratia* spp. mangrove fringe and pneumatophore zone, adjacent to a tidally exposed bank. Survey 3B (T: 60 min; A: 390 m^2): 5-10 m wide backforest, with small and scattered plants of *Nypa fruticans*, *Hibiscus* sp. and *Rhizophora* sp., with abundant flotsam and fallen logs, and crossed by small tidal inlets. Survey 3C (T: 15 min; A: n/a): as in 3A, on the forest floor.

Sungai Bunga (A−C: 08 October 2013; D: 11 Oct 2013). Tract of coast on the western bank of the Brunei Bay, at the mouth of the Brunei river and in front of the northern tip of Berambang island. Survey 4A (T: 60 min; A: 634 m^2): *Rhizophora apiculata* pioneer shore, with patches of *Nypa fruticans*. Survey 4B (T: 60 min; A: 1054 m^2): mid-intertidal mangrove forest dominated by *R. apiculata*. Survey 4C (T: 60 min; A: 1660 m^2): high-intertidal mangrove forest with *Acrostichum* ferns, *Thalassina* mounds, *Acanthus* sp., adjacent to a transition to a freshwater backforest with *Pandanus* sp., *Hibiscus* sp., and thorny palms. Survey 4D (T: 60 min; A: 2500 m^2): mid- and high-intertidal forest as in 4B and 4C, sampled at night.

Sungai Labu (A: 29 November 2013; B: 30 March 2014; C, E: 28−30 March 2014; D: 26 February 2014). Forested swamp (Labu Forest Reserve) north of Sungai Labu, a tributary of Sungai Temburong, and at ~ 10−12 km from the coast. Survey 5A (T: 20 min; A: 1400 m^2): backmangrove swamp dominated by thorny palms and *Pandanus* species, behind a 5−10 m wide stand of *Nypa fruticans* fringing the northern bank of Sungai Labu. Survey 5B (T: 10 min; A: n/a): small area at the margin of a path carved through a thick and monotypic stand of *Pandanus* sp., at about 30 m from the southern bank of Sungai Labu. Survey 5C (T: n/a; A: n/a): baited pitfall trap to collect dung beetles, positioned on the floor of a mixed peat swamp forest, along the road under construction crossing the Labu Forest Reserve, at 1870 m from the closest northern bank of Sungai Labu (2100 m along the road in construction). Survey 5D (T: 15 min; A: n/a): mixed peat swamp forest, at 1620 m from the closest northern bank of Sungai Labu (1740 m along the road in construction), sampled at night. Survey 5E (T: n/a; A: n/a): baited pitfall trap (as in 5C), at 1840 m from the closest northern bank of Sungai Labu (2100 m along the road in construction).

Sungai Belayang (15 October 2013). Bank of a tributary of the Belayang river ~ 7 km from the river mouth; Sungai Belayang is a tributary of the Kibi river. The bank was fringed by a ~ 50 m wide monotypic stand of *Nypa fruticans*, and was positioned at ~ 8 km from the coastline of the Bay of Brunei. Survey 6A (T: 30 min; A: 630 m^2): along the river bank, at ~3 m from the water's edge, in a dense *Nypa* stand. Survey 6B (T: 30 min; A: 275 m^2): dense *N. fruticans* forest, at ~ 55 m from the river bank; Survey 6C (T: 20 min; A: 180 m^2): *N. fruticans* forest, at ~ 105 m from the river bank.

Sungai Brunei (10 October 2013). Riverine area at ~ 24 km from the river mouth. The riverine vegetation at the water's edge appeared to be freshly cut. Survey 7A (T: 60 min; A: 650 m^2): area in a recreational park 5−20 m from the northern bank of the Brunei River, covered by freshly-cut grass. The soil was water-saturated, and the area was covered by several pools < 10 cm deep. Under a stilt gazebo, an unvegetated patch of mud was highly bioturbated and contained numerous mud mounds. Survey 7B (T: 30 min; A: 685 m^2): small and dense mangrove stand on the southern bank of the river, dominated by *Rhizophora* sp., and *Bruguiera gymnorhiza*.

Sungai Tutong (A−C: 21 February 2014; D: 30 July 2014). Mangrove forest on the southern bank of the Tutong river estuary. Survey 8A (T: 15 min; A: 750 m^2): mangrove backforest and transition to heath forest (kerangas), 160 m from the bank of the Sungai river estuary; *Pandanus* species, rattans, *Oncosperma tigillarium* and other thorny palms dominated the vegetation, with few *Rhizophora* sp. trees. Several shallow pools filled with very dark water and a few cm deep covered the forest floor. Survey 8B (T: 15 min; A: 715 m^2): monotypic stand of *Rhizophora apiculata*, with abundant tide pools and inlets; area at 130 m from the bank of the Sungai river estuary. Survey 8C (T: 15 min; A: 1140 m^2): *Nypa fruticans* forest; the forest floor was flooded (< 50cm deep). Survey 8D (T: 30 min; A: 1020 m^2): same area of 8C, after sunset.

Badas (A: 18 May 2013; B: 23 March 2014). Peat swamp forest dominated by large trees of *Shorea albida*, at ~ 8.5 km from the coast and 1500 m from the bank of Sungai Belait, on the slope of the peat dome. Survey 9A (T: 60 min; A: n/a): Short survey made at night on the slope of the dome (several collectors); the forest floor was covered by thick litter, and pitcher plants (*Nepenthes ampullaria*, *N. bicalcarata*) were abundant on the forest floor and on lianas. Survey 9B (T: 55 min; A: 700 m^2): same area as 9A, but longer survey, including light hours. All sampled crabs were observed or collected after the sunset (ca. 5:45 pm), both on the peat substrate, and inside pitcher plants (several collectors).

4.2.2 Surveying and sampling methods

Surveys were conducted during the day (except than a few surveys in the Brunei Bay, see Subchapter 4.2.1.2), ± 2 hours around the predicted low tide.

Within each surveyed area, potential microhabitats of sesarmid crabs were sampled by hand or excavation, above or inside the substrate, including leaf litter, mangrove aerial root systems, flotsam and debris, burrows, tide pools, and dead wood (Smith et al., 1991; Frusher et al., 1994; Cannicci et al., 1996; Sivasothi, 2000; Lee & Kwok, 2002; Ashton et al., 2003b; Emmerson & Ndenze, 2007). Dead wood crab communities were sampled by crushing and sorting wooden debris, logs and branches. In the Labu forest reserve (Sungai Labu, Brunei Bay), crabs were also opportunistically sampled using baited pitfall traps meant to collect dung beetles.

The collected specimens were euthanized by chilling at 2-4 ºC until the animals were not moving, then freezing at −25 ºC for 1-2 hours, fixed in 70% ethanol or 5% formalin, and preserved in 70% ethanol. Some samples were fixed in 5% formalin and preserved in 70% ethanol. Subsamples (one limb) were preserved in 99% undenatured ethanol. Taxonomic collections were deposited in the Muzium Zoologi of the University of Malaya, and in the Lee Kong Chian Natural History Museum of Singapore.

Taxonomic discrimination was conducted to the genus or species level (Tesch, 1917; Tweedie, 1936, 1940, 1950a,c; Banerjee, 1960; Serène & Soh, 1967a,b, 1970; Davie, 1992, 1994, 2010; Ng & Schubart, 2002; Rahayu & Davie, 2002, 2006; Gillikin & Schubart, 2004; Ng, 2004; Rahayu & Ng, 2005, 2009, 2010; Ng, 2007; Schubart et al., 2009; Lee et al., 2013; Shahdadi & Schubart, 2017).

When specimens did not match existing described species, morphospecies units were used (e.g. sp. 1, sp. 2, etc.), as defined by Cronquist (1978), i.e., species are the smallest groups that are consistently and persistently distinct, and distinguishable by ordinary means. The proposed morphospecies are therefore hypotheses which are falsifiable when independent data, for example morphological synapomorphies and DNA sequences, become available.

Species from other families within Grapsoidea found during the surveys were also included (e.g. *Metopograpsus* spp. *Metaplax* spp.), in order to highlight pattern of diversity between Sesarmidae and other grapsoid families.

4.3 Results

In the surveys conducted along the West coast of Peninsular Malaysia, 28 species and one morphospecies (i.e. specimens morphologically distinct from described species; *Episesarma* sp.1), belonging to 11 genera of grapsoid crabs were found (Tab. 4.1). In particular, most of the species (n=21) belong to the family Sesarmidae, while 4 species of Grapsidae and 3 species of Varunidae were found.

In the Brunei Bay, 25 species and two morphospecies (*Episesarma* sp.1 and *Parasesarma* sp.1) were found. Moreover, 25 juvenile specimens were also collected, which could only be discriminated to the genus level; in total, 13 grapsoid genera were identified (Tab. 4.2).

In total, 41 species were found in this area (Peninsular Malaysia and/or Brunei Bay), belonging to 15 genera. Twelve species were found both in Peninsular Malaysia and Brunei Bay (Tabs. 4.1, 4.2).

Several species have been reported for the first time from the investigated areas (Peninsular Malaysia or Borneo) (Tabs. 4.1, 4.2, Fig. 4.4). In particular, *Nanosesarma edamense*, and *Metaplax distincta* are new records for the Malay Peninsula (i.e. Peninsular Malaysia and Singapore, see Chapter 3; Tan & Ng, 1994; Ng, 2007).

Fourteen of the species reported from the Brunei Bay are new records for Brunei Darussalam, and five of these species (*Episesarma singaporense*, *Haberma kamora*, *Neosarmatium inerme*, *Pseudosesarma moeschii*, *Varuna yui*) are also new records for Borneo (Choy, 1991; Choy & Booth, 1994; Tan & Ng, 1994; Ashton et al., 2003b; Tab. 4.2, Fig. 4.4).

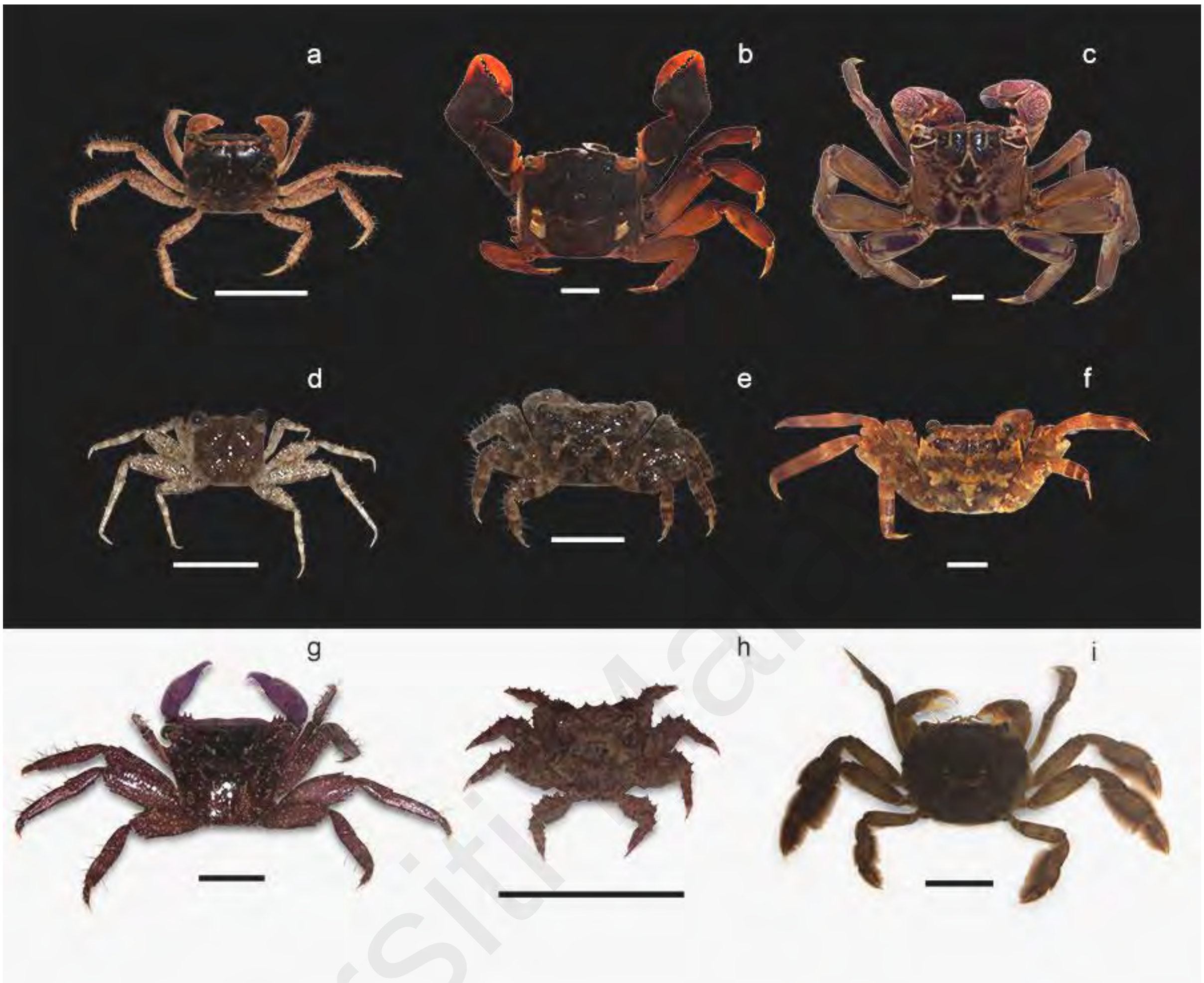

Figure 4.4. Some of the new records found in this study. a: *Fasciarma fasciatum* (ZRC 2018.0848); b: *Pseudosesarma bocourti* (ZRC 2018.0879); c: *Episesarma singaporense* (ZRC 2018.0918); d: *Haberma kamora* (ZRC 2018.0878); e: *Nanosesarma edamense* (ZRC 2016.0391); f: *Selatium brockii* (ZRC 2018.0847); g: *Metopograpsus latifrons* (ZRC 2018.0869); h: *Nanosesarma pontianacense* (ZRC 2018.0877); i: *Varuna yui* (ZRC 2018.0851).

Table 4.1: Presence-absence matrix (1 = present) of the grapsoid crabs recorded in the sampling sites of the Peninsular Malaysia. Site abbreviations: LK = Langkawi, KS = Kuala Selangor, TT = Tanjung Tuan, PB = Pulau Besar, PK = Pulau Kukup, PM = Pulau Merambong; * = first record for the Malay Peninsula (see Chapter 3, Tan & Ng, 1994; Ng, 2007), *Abb* = abbreviations utilised for the species (see Chapter 5).

		Sites					
SESARMIDAE	**Abb.**	**LK**	**KS**	**TT**	**PB**	**PK**	**PM**
Clistocoeloma merguiense De Man, 1888	mer	1	1	1		1	
Episesarma sp.1	e.sp1	1	1				
E. palawanense (Rathbun, 1914)	pal					1	
E. versicolor (Tweedie, 1936)	ver	1	1			1	
Fasciarm fasciatum (Lanchester, 1900)	fas	1	1				
Nanosesarma andersonii (De Man, 1895)	and		1				
N. batavicum (Moreira, 1903)	N.bat	1				1	
N. edamense (De Man, 1887)*	eda				1		1
N. minutum (De Man, 1887)	min		1		1		1
N. nunongi Tweedie, 1950	nun		1			1	
N. pontianacense (De Man, 1895)	pon		1		1		
Neosarmatium smithi (H. Milne Edwards, 1853)	smi		1				
Parasesarma batavianum (De Man, 1890)	P.bat			1	1	1	
P. eumolpe (De Man, 1895)	eum	1	1	1	1	1	
P. indiarum (Tweedie, 1940)[1]	ind	1					
P. lanchesteri (Tweedie, 1936)	lan		1				
P. melissa (De Man, 1887)	mel	1					
P. onychophorum (De Man, 1895)	ony	1	1			1	
P. plicatum (Latreille, 1806)	pli		1	1		1	
Sarmatium germaini (A. Milne-Edwards, 1869)	ger		1	1			
Selatium brockii (De Man, 1887)	bro		1		1		1
Sesarmoides kraussi (De Man, 1887)	kra		1				
GRAPSIDAE							
Metopograpsus frontalis Miers, 1880	fro			1			
M. latifrons (White, 1847)	lat	1	1		1		
M. oceanicus (Hombron & Jacquinot, 1846)	oce				1		1
M. quadridentatus Stimpson, 1858	qua			1	1		
VARUNIDAE							
Metaplax crenulata (Gerstaecker, 1856)	cre	1	1				
M. cf. *distincta* H. Milne Edwards, 1852*	dis			1			
M. elegans De Man, 1888	ele	1	1		1	1	

[1]this species may be also *P. peninsulare*, recently described from samples from this geographic area, previously considered as *P. indiarum* (see Shahdadi et al., 2018). However, since a re-examination of the samples has not been possible, I chose to maintain the previous name.

Table 4.2: Presence-absence matrix (1 = present) of the grapsoid crabs recorded in the sampling sites of the Brunei Bay. Site abbreviations: 1 = Pemburongunan Creek, 2 = Pulau Bedukang, 3 = Sungai Besar, 4 = Sungai Bunga, 5 = Sungai Labu, 6 = Sungai Belayang, 7 = Sungai Brunei, 8 = Sungai Tutong, 9 = Badas. * = first record for Brunei Darussalam (Choy, 1991; Choy & Booth, 1994); ** = first record for Borneo (Choy, 1991; Choy & Booth, 1994; Tan & Ng, 1994; Ashton et al., 2003b, see also Chapter 3); *Abb* = abbreviations utilised for the species (see Chapter 5).

	Abb	**Sites**								
SESARMIDAE		**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**
Clistocoeloma merguiense De Man, 1888	mer	1	1		1					
Clistocoeloma sp. (juv.)	c.sp jv						1			
Episesarma chentongense (Serène & Soh 1967)*	che		1		1					
E. mederi (A. Milne-Edwards, 1853)*	med				1				1	
E. singaporense (Tweedie, 1936)**	sin						1			
Episesarma sp. 1	e.sp1				1					
Episesarma sp. (juv.)	e.sp jv			1	1					
Fasciarma fasciatum (Lanchester, 1900)*	fas				1					
Geosesarma gracillimum (De Man, 1902)	gra					1				1
Haberma kamora Rahayu & Ng, 2005**	kam				1		1	1		
Nanosesarma batavicum (Moreira, 1903)*	bat		1	1	1					
N. edamense (De Man, 1887)*	eda	1	1							
N. pontianacense (De Man, 1895)*	pon		1	1						
Neosarmatium inerme (De Man, 1887)**	ine						1			
N. spinicarpus Davie, 1994	spi							1		
Parasesarma eumolpe (De Man, 1895)	eum	1			1					
P. indiarum (Tweedie, 1940)	ind	1	1	1	1		1			
P. plicatum (Latreille, 1806)	pli	1								
P. cf. *semperi* (Bürger, 1893)	sem		1							
P. cf. *ungulatum* (H. Milne Edwards, 1853)	ung	1							1	
Parasesarma sp. 1	p.sp1	1					1		1	
Parasesarma sp. (juv.)	p.sp jv	1	1	1	1		1			
Pseudosesarma bocourti (A.Milne Edwards,1869)*	boc					1				
P. moeschii (De Man, 1888)**	moe						1			
Selatium brockii (De Man, 1887)*	bro		1							
GRAPSIDAE										
Metopograpsus frontalis Miers, 1880	fro	1	1	1	1					
M. latifrons (White, 1847)*	lat		1	1	1					
Metopograpsus sp. (juv.)	m.sp			1						
VARUNIDAE										
Metaplax elegans De Man, 1888	ele	1								
M. tredecim Tweedie, 1950	tre	1	1	1	1					
Varuna yui Hwang & Takeda, 1986**	yui	1								

[1]this species may be also *P. peninsulare*, recently described from samples from this geographic area, previously considered as *P. indiarum* (see Shahdadi et al., 2018). However, since a re-examination of the samples has not been possible, I chose to maintain the previous name.

4.4 Discussion and Conclusion

The surveys conducted in Peninsular Malaysia and in the Brunei Bay provided a first inventory of grapsoid crabs for most of the study sites, which were previously uninvestigated.. However, the surveys were conducted in different months for each site, thus potential differences in the species richness and composition could be related to seasonal differences. In fact, little is known about seasonal dynamics of sesarmid crabs (Salgado Kent & McGuinness, 2010), and it is possible that changes in the environmental conditions related to seasonal variation (e.g. salinity changes linked to the rainy season) may affect the population dynamics of these crabs.

Several new records were found, especially for Brunei Darussalam and Borneo. The lack of previous distribution records for Borneo is possibly due to lack of investigations in this area (see Tan & Ng, 1994), further suggesting that the actual diversity of the Bornean assemblages is still underestimated.

Nanosesarma edamense was reported for the first time from the Malay Peninsula (Peninsular Malaysia and Singapore), since this species was previously known only from Borneo, Indonesia and New Caledonia (De Man, 1887, 1888; Tweedie, 1950a; Ng & Richer de Forges, 2007). Other interesting records included *Metopograpsus quadridentatus*, which according to Tan and Ng (1994) has not been previously recorded from the Malay Peninsula, and *Metopograpsus oceanicus* and *Metaplax* cf. *distincta*, which were not included in Tan and Ng (1994) checklist of mangrove brachyuran species of this area (i.e. Malay Peninsula and Borneo), although they may be present in other coastal ecosystems (P. K. L. Ng, pers. comm.). In particular, *M. distincta* has been previously reported only from India and Thailand (Ng, 2007). *Selatium brockii* has not been found by Tan and Ng (1994) in Borneo. However, Nobili

(1901) recorded this species in northern Borneo (Malaysia, Sarawak). The present study reconfirms therefore the presence of this species in this island.

Neosarmatium inerme has been previously recorded only from Vietnam (see Davie, 1994). Although Tweedie (1940, 1950a) reported specimens identified as *Sesarma* (*Sarmatium*) *inermis* from both Peninsular Malaysia and Borneo, Davie (1994) considered these specimens as belonging to the congeneric species *N. spinicarpus* (see also Subchapter 3.3.8.4). The records of *Pseudosesarma moeschii* and *Varuna yui* in Borneo is not too surprising, considering that these species have been reported from a wide range of localities across South East Asia (*P. moeschii*: Myanmar, Thailand, Peninsular Malaysia, Indonesia; *V. yui*: Taiwan, Southern China, Vietnam, Indonesia, Philippines, Singapore, West Malaysia, and Thailand; see Subchapter 3.3.12.7, and Ng, 2007, respectively). *Nanosesarma nunongi* has been been previously reported only by Tweedie (1950c), from Peninsular Malaysia only. The present record reconfirmed the presence of this species in this area, after 70 years from its only published record (see also Subchapter 3.3.7.5).

The inclusion of other families of Grapsoidea in this study intended to provide data on the relative proportion of sesarmid crabs in these ecosystems, compared to other closely related families. The small amount of species reported for non-sesarmid families confirmed that sesarmid crabs are the dominating family in grapsoid assemblages of mangrove forest. It is likely that sesarmid crabs have evolved to occupy the mangrove spatial and trophic niches, while other families are better adapted to other spatial niches (e.g. rocky shores, Grapsidae).

Only 12 out of 41 species were found both in Peninsular Malaysia and in the Brunei Bay. In fact, Tweedie (1954) has pointed out a differentiation between assemblages of Malay Peninsula and Borneo, and also between West and East coast of the Malay

Peninsula. This author listed species with a restricted distribution, such as *Metaplax crenulata*, *Parasesarma onychophorum* for the West coast of the Malay Peninsula, and *Metaplax tredecim*, *Parasesarma lepidum*, *P. semperi*, *Neosesarma rectipectinatum*, and *Pseudosesarma johorensis* for the Bornean assemblages.

Species richness of the investigated community (25 species and 2 morphospecies) is relatively high compared to previous studies from other South East Asian mangrove sites (e.g. Sasekumar et al., 1974; Frith et al., 1976; Ashton et al., 2003a,b; Diele et al., 2013, 12-17 species reported), although it is comparable to the values reported by Nordhaus et al. (2009) from an Indonesia lagoon system (21 species of grapsoid crabs reported). However, most of these studies investigated single mangrove forest sites, or different mangrove forests, but not other intertidal ecosystems (e.g. freshwater systems, nipah and peat swamp forests), making the comparison difficult to interpret. In general, however, the data obtained from this study confirmed this biogeographic region as a biodiversity hotspot (Briggs, 1999; Myers et al., 2001), hosting high levels of species richness for mangrove grapsoid crabs compared to other geographic areas, such as East and West Africa (e.g. Vannini & Valmori, 1981; Manning & Holthuis, 1981). Regionally high biodiversity levels are expected, since the investigated area is included in both the Sundaland ecoregion (Myers et al., 2000), and in the East Indies Triangle (Briggs, 1999).

Within Borneo, the only other quantitative paper on mangrove grapsoid crabs (Ashton et al., 2003b) reported 17 grapsoid species. Only 9 of these species have been found also in the sites investigated in the present study, suggesting that most of these crabs have a stenotypic geographic distribution, and the regional biodiversity is made of an heterogeneous patchwork of species. Choy (1991) reported 13 species (and 3 genera which were not identified at specific level) from the Brunei Bay, 9 of which have been reported also from the present study. Choy and Booth (1994) investigated the

Pemburongunan Creek, which corresponds to Site 1 (Brunei Bay, Fig. 4.3), where they recorded 9 species (and 1 genus). The present study found 7 of these species in the same site, while adding 4 species previously not reported.

The occurrence of new records in this area may also be related to the fact that night surveys were conducted in some of the study sites. Previous studies in this area have been usually conducted in daytime, thus possibly not detecting species which are active at night (e.g. Choy & Booth, 1994; Ashton et al., 2003b). For instance, some *Episesarma* species (*E. mederi*, *Episesarma* sp.1) have been recorded only during a night survey (see Chapter 5, Tab. 5.4). Possibly, *Episesarma* species tend to be more visible at night, when they climb on the tree trunks, while during daytime they tend to stay inside or nearby their burrows (Sivasothi et al., 1993), and are therefore less probable to be detected.

The occurrence of several new records found in a relatively small number of surveys suggests that only a small proportion of the species present in this area has been recorded up to date. Agricultural activities and urban coastal development are rapidly growing in Borneo (Struebig et al., 2015), and the knowledge of local assemblages is strategic to design conservation and management plans for coastal wetlands in this area. In particular, this region has been considered as a biodiversity hotspot in urgent need of taxonomic and ecological investigation, for both terrestrial and marine faunal assemblages (e.g. Briggs, 1999; Myers et al., 2000).

CHAPTER 5: ARTICLE 3 - DIVERSITY AND STRUCTURE OF SELECTED ASSEMBLAGES AND SPECIES ECOLOGICAL TRAITS

5.1. Introduction and brief Literature Review

The information on the structure and patterns of diversity of sesarmid communities is still relatively scarce, and autecological traits of the species are in many cases poorly investigated (e.g. Salgado Kent & McGuinness, 2010; Lee et al., 2017; see also Chapter 3).

In particular, the autecology of these crabs has been studied only in a few species, mainly in Neotropical and African systems (e.g. Cannicci et al., 1999; Emmerson & Ndenze, 2007; Erickson et al., 2008). In fact, autecological traits of most species are unknown, or based on fragmentary and anecdotal information contained in original descriptions (e.g. Tweedie, 1940; Tweedie, 1950c; Rahayu & Ng, 2009). Moreover, studies on distribution and abundance of grapsoid crabs in mangrove and coastal communities are limited, both at local and geographic scale (Salgado Kent & McGuinness, 2010). This lack of ecological information has been attributed to taxonomic uncertainty and complexity, practical field work limitations, and the challenges posed by density measurements (e.g. Salgado Kent & McGuinness, 2006; Hogarth, 2007; Lee et al., 2017).

In the Malay Peninsula and Borneo, although several studies have investigated the diversity and community structure of grapsoid crabs (e.g. Berry, 1972; Sasekumar, 1974; Asthon et al., 2003b), assemblages of several mangrove sites remain unknown.

In general, local assemblages are a subset of the regional pool of species, which is related to processes acting at a macroecological scale, such as geomorphic and topographic structures, climatic regimes and available habitat area (Ellison, 2002). Within mangrove sites, the structure of macrofaunal assemblages is influenced by several environmental parameters acting at the habitat level, such as water availability, edaphic conditions, mangrove stand age and species composition, and substrate elevation (e.g., Frusher et al., 1994; Lui et al., 2002; Ashton et al., 2003a,b; Morrisey et al., 2003). Therefore, environmental factors appear to influence the composition of communities at different spatial scales (Ellison, 2002).

In this chapter, the datasets obtained from the sampling surveys conducted along the West coast of Peninsular Malaysia and in the Brunei Bay were utilised to investigate (i) the structure and diversity of the assemblages across the different sites and within them, (ii) the spatial distribution of the species and their association with selected environmental parameters, and (iii) the co-occurrence and clustering of the species in the assemblages.

5.2 Methodology

5.2.1 Peninsular Malaysia

A dataset of presence-absence of the grapsoid species was obtained from the sampling surveys conducted along the West coast of Peninsular Malaysia (six study sites, see Chapter 4), which provided species richness and composition for each site, and the frequence of occurrence for each species.

In order to visualise differences in the taxonomic composition of the different sites, the presence-absence dataset was reorganised through a seriation method, using the algorithm described by Brower and Kile (1988; Past 2.09; Hammer et al., 2001; Hammer & Harper, 2005). Seriation is a exploratory technique that reorganises a data matrix such that the presences are concentrated along the diagonal, which represent a one-dimensional continuum (Liiv, 2010).

To explore how the sites differ in taxonomic composition (beta diversity), we used the Jaccard similarity index (*J*; Jaccard 1901, Schroeder & Jenkins 2018). In order to observe whether differences in taxonomic composition among sites follow geographic patterns, *J* values obtained for each couple of sites were plotted against the geographic distance (km) between them. A linear regression analysis was conducted to test whether *J* values are correlated with the geographic distance between sites (Past 2.09; Hammer et al., 2001; Hammer & Harper, 2005).

To investigate association among species and between species and study sites, the matrix of occurrence of the species in the different sites was analysed with a cluster analysis (Past 2.09; Hammer et al., 2001; Hammer & Harper, 2005), utilising the Jaccard similarity index and the strong linkage aggregation method (Johnson & Wichern, 1992).

Four ordinal variables were utilised to describe the environmental conditions in each study site: i) substrate type (ST), ii) insularity (IN), iii) areal extension of the forest (AF), iv) linear extension of the forest along the intertidal gradient (IG) (Tab. 5.1). In particular, several authors suggested that sediment size can affect the structure of mangrove macrofaunal assemblages (e.g. Frusher et al., 1994; Ashton et al., 2003b). Moreover, species area relationships (SARs) are common in several communities, including mangrove systems (Ellison, 2002; Polgar, 2009), thus suggesting that the extension of the forest can affect the diversity and distribution patterns of macrofaunal groups. In this study, we chose to consider both AF and IG, although these two variables may look apparently correlated. In fact, in this area the higher intertidal zone of several mangrove forests has been cleared for agricultural purposes, so that in some cases large forests spread quite extensively along the coast, but their intertidal extension has been drastically shortened (pers. obs.).

Table 5.1: Environmental parameters in the investigated sites (Peninsular Malaysia). Substrate type (ST): 1 = mud; 2 = mud and sand; 3 = sand, gravel and boulders (rocky shores). Insularity (IN): 1 = mainland; 2 = island. Areal extension of the forest (AF): 1 = 0-1 km^2; 2 = 1-25 km^2; 3 = 25-100 km^2. Linear extension of the forest along the intertidal gradient (IG): 1 = 0-100 m; 2 = 100-1,000 m; 3 = 1,000-10,000 m. All sub-sites exhibited the same conditions, within each site.

	ST	**IN**	**AF**	**IG**
Langkawi	2	2	3	3
Kuala Selangor	1	1	2	3
Tanjung Tuan	2	1	1	2
Pulau Besar	3	2	1	1
Pulau Kukup	1	2	2	3
Pulau Merambong	3	2	1	1

The multivariate correspondence between the environmental variables and the presence of the studied species in each site was assessed with Canonical Correspondence Analysis (CCA) (ter Braak, 1986; Legendre & Legendre, 1998; Past v.3.2, Hammer et al., 2001; Hammer & Harper, 2005). The CCA ordination method is a direct gradient analysis that elucidates the relationships between the species dataset and selected environmental variables (ter Braak, 1986).

5.2.2 Brunei Bay

In the field surveys conducted in the Brunei Bay (nine study sites, see Chapter 4), a quantitative sampling approach was adopted, in order to obtain measures of density of the species in each surveyed area.

During each survey, crabs were sampled by the author for 30-90 min (mean 40.9 ±23.9 min) in areas of 150-2,500 m^2 (mean 753.0 m^2 ± SD 540 m^2) (see also Subchapter 4.2.1.2). Sampling areas were measured using a GIS (Base Camp v. 4.7 ©Garmin Ltd) drawing polygons around GPS tracks from field surveys. For each survey, crab density (DsAT) was measured as the number of collected individuals per unit area (100 m^2) and time (60 min). Therefore, density was standardised using a time-based sampling method (modified from Ashton, 1999; Ashton et al., 2003b), using variable sampling areas and times.

Four variables were used to describe the environmental conditions in each surveyed area: i) salinity (SA); ii) type of sediment (SD); iii) type and density of vegetation coverage (DV); and iv) mean distance from the mangrove seaward fringe (DM) (see Tabs. 5.2, 5.3, Fig. 5.1). Several authors suggested that salinity and type of sediment (grain size) influence the structure of mangrove crab assemblages (e.g. Lee, 1998; Levin et al., 2001;

Ashton et al., 2003b). Salinity was measured during sampling surveys, with a hand-held refractometer; six to twelve salinity measurements were made in each sampling site (three measurements per survey), using substrate interstitial water at a depth of ~10 cm (English et al., 1999), or water bodies present in the sampling area, if the substrate was too dry. Six SA categories were defined (Tab. 5.2). The type of sediment was categorised by visually estimating the percentage of sand particles (grains visible to the naked eye), relative to the amount of silt and mud (grains not visible to the naked eye) (Fetter, 1988), and the relative amount of partly decomposed plant debris and organic matter: four SD levels were defined (Tab. 5.2). Vascular plant community composition and density of the vegetation coverage increased along the sea-to-land gradient (Polgar & Crosa, 2009; Polgar et al., 2010, 2017): nine plant communities with increasing DV levels were defined (Tab. 5.2). The minimum horizontal distance (m) was measured between the geometric centre of the georeferenced surveyed areas and the edge of the vegetation facing the closest water body using GPS data (e.g., perpendicular to the coastline, river or creek bank; Google Earth; www.google.com/earth); negative distance values were assigned to waypoints positioned between the vegetation margin and the water body: six DM intervals were defined (Tab. 5.2).

Grapsoid crab assemblages were described using univariate measures, i.e. number of species (S), crab density [DsAT, i.e. number of collected individuals per unit area (100 m^2) and time (60 min)], Simpson index (1-D), or evenness, and effective number of species (S_{eff}). S_{eff} is the exponential of the Shannon-Wiener index H′ (Jost, 2006), i.e. $\exp\left(-\sum_{i=1}^{S} p_i \ln p_i\right)$ where p_i is the proportion of the i^{th} species, and S is the species richness. S_{eff} is defined as the number of equally common species in a hypothetical community corresponding to the said H′ value, and has been considered a measure of 'true diversity' (Jost, 2006).

A Distribution-Abundance Plot was obtained, where log transformed average densities (DsAT) of each species were plotted against their distribution (i.e. number of surveys where the species occurred, logit transformed) (Verberk, 2011).

To explore the degree of association between crab species (and morphospecies) relative to sampling sites and surveys, agglomerative hierarchical clustering was performed with an unweighted pair-group average algorithm (UPGMA) and a Bray-Curtis similarity index, using the square-root transformed species abundance matrix (Johnson & Wichern, 1992; Past v. 3.2, Hammer et al., 2001; Hammer & Harper, 2005). Similarity patterns at both the system level (similarity among sites), and habitat level (among surveys) were explored. Groups of taxa were defined using an arbitrary 0.5 similarity cut-off value (Hammer & Harper, 2005).

The multivariate correspondence between the environmental variables and the abundance of the studied species in each survey was assessed with Canonical Correspondence Analysis (CCA) (ter Braak, 1986; Legendre & Legendre, 1998; Past v.3.2, Hammer et al., 2001; Hammer & Harper, 2005). The CCA ordination method is a direct gradient analysis correlating the abundance of species to a gradient of environmental variables which is known a priori.

Ten surveys were not included in the statistical analyses: five surveys (2D, 2E, 3C, 5B, 5D) lacked GPS data to calculate DsAT; three surveys were made by more than one researcher or by different researchers (5A, 9A, 9B); and two surveys were made using pitfall traps (5C, 5E).

Table 5.2: Environmental variables: definitions. Higher categorical values indicate more terrestrial conditions associated with grapsoid crabs.

Salinity (SA)	
1	>30
2	25 to 30
3	19 to 24
4	13 to 18
5	7 to 12
6	0 to 6
Type of sediment (SD)	
1	Muddy sand: sand visible and prevalent
2	Sandy mud: sand visible, mud prevalent
3	Mud: no sand visible
4	Peat and organic soil
Type and density of vegetation coverage (DV)	
1	Herbaceous vegetation
2	Lower-intertidal (pioneer) *Avicennia* and *Sonneratia* forests
3	Vegetated creek and river banks
4	Lower-intertidal *Rhizophora* forests
5	Mid-intertidal mangrove associations (*Rhizophora* and *Bruguiera* forests)
6	*Nypa fruticans* forests
7	High-intertidal mangrove associations (e.g. *Acrostichum* ferns, *Acanthus* species)
8	Mangrove backforests (e.g. *Pandanus* palms, transition to forested peat swamps or heath forests)
9	Supratidal forests (e.g. *Shorea albida* peat swamp)
Horizontal distance from the vegetation margin (DM)	
1	−25 m to 25 m*
2	26 m to 75 m
3	76 m to 125 m
4	126 m to 175 m
5	176 m to 225 m
6	> 225 m

* negative values refer to areas extending from the vegetation margin towards the sea (or river), i.e. usually unvegetated mudbanks

Table 5.3: Environmental variables measured in the investigated sites (Brunei Bay). For abbreviations of the variables see Tab. 5.2. Surveys: surveyed areas (see Fig. 4.3); n/a: missing value.

Surveys	1A	1B	1C	2A	2B	2C	2D	2E	3A	3B	3C	4A	4B	4C	4D	5A	5B	5C	5D	5E	6A	6B	6C	7A	7B	8A	8B	8C	8D	9A	9B
SA	n/a	n/a	n/a	1	n/a	1	n/a	n/a	3	5	n/a	3	3	5	n/a	6	6	6	6	6	4	5	5	6	6	6	6	4	2	6	6
SD	2	1	1	3	3	3	3	3	2	2	2	3	3	3	3	4	4	4	4	4	3	3	3	4	4	1	2	3	3	4	4
DV	1	2	1	2	4	7	4	7	2	3	2	4	5	7	5	8	8	9	9	9	6	6	6	1	5	8	7	6	6	9	9
DM	1	2	3	1	2	3	1	n/a	1	1	1	1	2	3	3	1	2	6	6	6	1	2	3	1	1	4	3	2	2	6	6

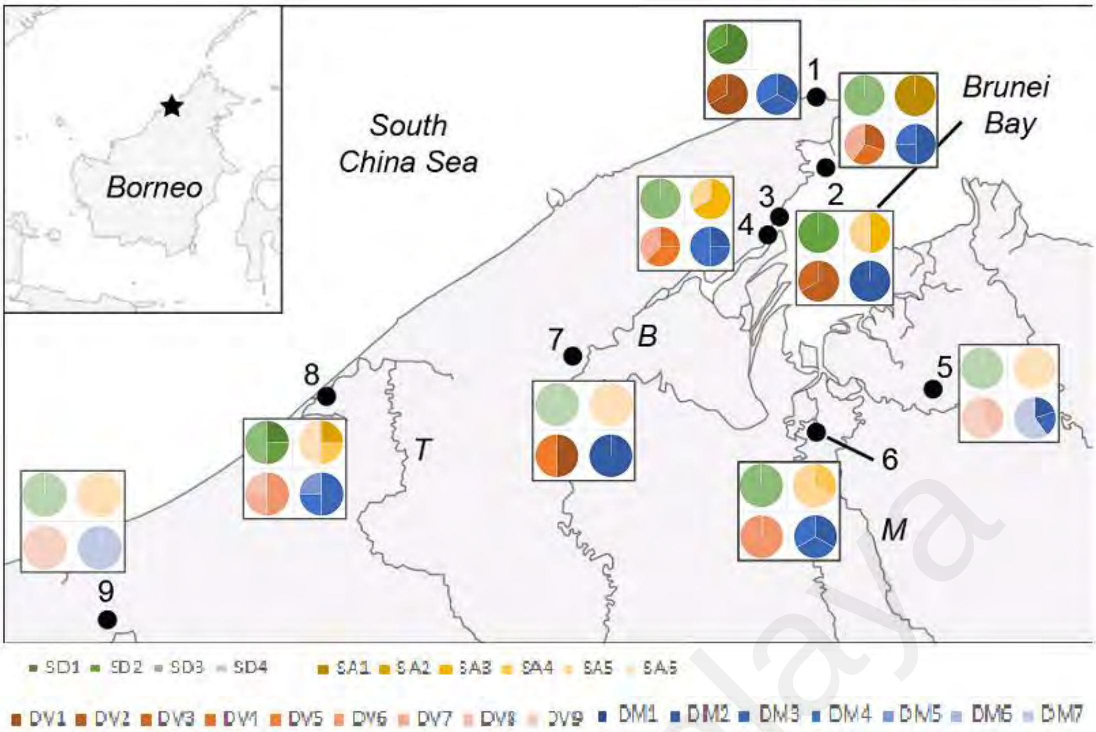

Figure 5.1: Environmental variables in the investigated sites of the Brunei Bay. Abbreviations as in Fig. 4.3 and Tab. 5.2.

5.3 Results

5.3.1 Peninsular Malaysia

For the total number of species found in this area, see Subchapter 4.3, and Tab. 4.1 (Chapter 4).

Four out of six of the investigated sites hosted a comparable number (8-12) of species, except Kuala Selangor (n = 19) and P. Merambong (n = 4).

Most of the species were recorded in 1-3 sites, and only 3 species occurred in ≥ 4 sites (Fig. 5.2, Tab. 4.1). In particular, the most common species were *Parasesarma eumolpe* (collected in 5/6 of the surveyed sites), *Clistocoeloma merguiense* and *Metaplax elegans* (each collected in 4/6 of the surveyed sites) (Tab. 4.1).

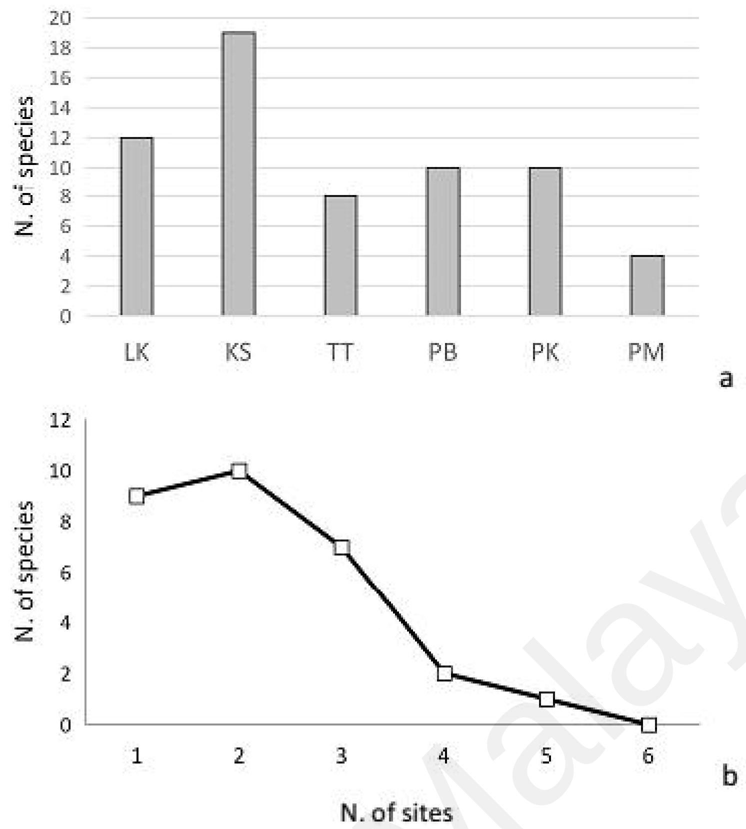

Figure 5.2: Species richness and frequency of occurrence (Peninsular Malaysia). (a): relative species richness per site. Sampling sites have been ordered along the latitudinal gradient (see Fig. 4.1 for abbreviations); (b): Frequence of occurrence of crab species; *N. of sites* = number of sites in which a certain species occurs.

The species spatial distribution is summarised by the seriation diagram and by the dendrogram of the cluster analysis (Figs. 5.3, 5.4).

In the seriation diagram a continuum of species can be visualised, with species with a similar distribution being located closest together, although no clear separation between sites assemblages has been detected (Fig. 5.3). In particular, this graph highlighted similarities between the assemblages of large insular systems (Langkawi and Pulau Kukup, species clumped on the left side of the graph), and also between sites with small mangrove fringes on coarse substrate (Pulau Besar and Pulau Merambong, species clumped on the right side of the graph). Kuala Selangor shared several species with all the other sites. A continuum of species can be visualised, with species with a similar distribution being located closest together, although no clear separation between sites assemblages has been detected (Fig. 5.3).

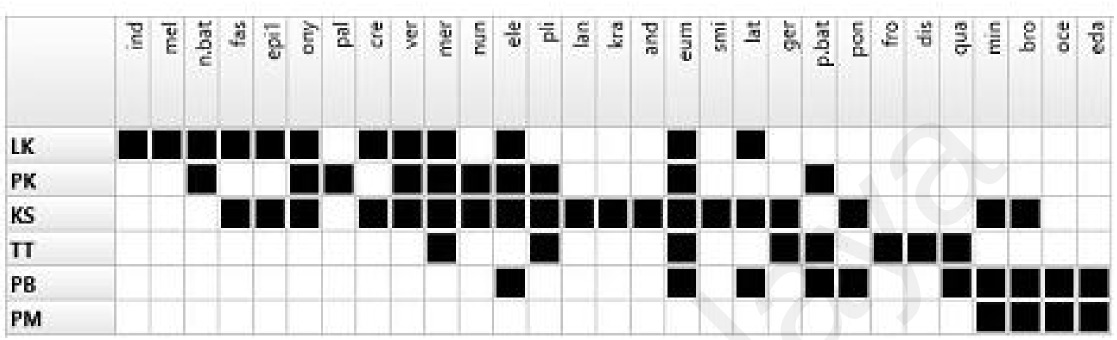

Figure 5.3: Seriation diagram. The diagram shows the distribution of species in the different study sites of Peninsular Malaysia, arranged according to similarities in species distribution patterns among sites. See Fig. 4.1 and Tab. 4.1 for abbreviations.

The values of Jaccard index between couples of sites (Fig. 5.4) showed that similarity in composition between assemblages is not related to the geographic distance between sites. The linear regression analysis obtained a value of *squared r* = 0.00027, rejecting the hypothesis that *J* values are correlated to the geographic distance between sites. Therefore, the assemblages are apparently not influenced by geographic patterns, at the scale of the investigated area.

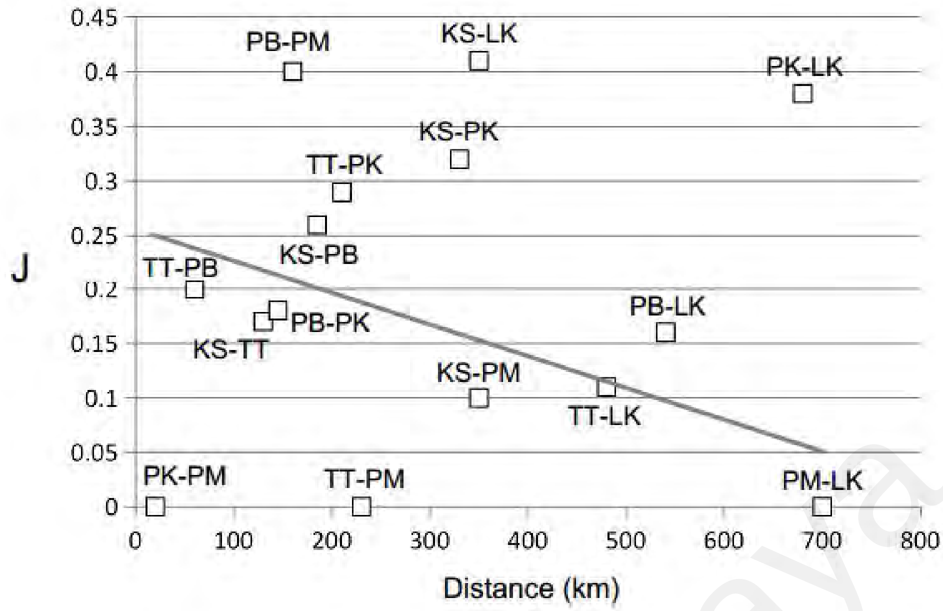

Figure 5.4. Jaccard similarity indexes (*J*) plotted against the geographic distance between couples of sites (in km). See Fig. 4.1 for sites abbreviations.

The cluster analysis identified eight groups of species (CS1–CS8) associated with different sites (Fig. 5.5). Group CS1 includes 2 species found in Tanjung Tuan and Pulau Besar, i.e. *Parasesarma batavianum* and *Metopograpsus quadridentatus*. *P. batavianum* was also found in Pulau Kukup. Groups CS2, CS6 and CS7 include species found in one study site only. In particular, group CS2 includes species that were found in Tanjung Tuan only (*Metopograpsus frontalis* and *Metaplax* cf. *distincta*). Groups CS6 and CS7 include species found only in Kuala Selangor (*Nanosesarma andersonii*, *Neosarmatium smithi*, *Parasesarma lanchesteri*, *Sesarmoides kraussi*) and Langkawi (*Parasesarma indiarum*, *Parasesarma melissa*), respectively. Groups CS3 and CS5 include species found in Kuala Selangor and either Langkawi (*Episesarma* sp.1, *Fasciarma fasciatum*, *Metopograpsus latifrons*, *Metaplax crenulata*) or Pulau Kukup (*Nanosesarma nunongi*, *Parasesarma plicatum*), respectively. *M. latifrons* occurred also in Pulau Besar (group CS3), while *P. plicatum* was collected also from Tanjung

Tuan (group CS5). Group CS4 includes species reported from several sites (*Clistocoeloma merguiense*, *Episesarma versicolor*, *Parasesarma eumolpe*, *Parasesarma onychophorum*, *Metaplax elegans*). All the species of this group were found in Langkawi, Kuala Selangor and Pulau Kukup, while some of them were collected also in Tanjung Tuan (*C. merguiense*, *P. eumolpe*) or Pulau Besar (*P. eumolpe*, *M. elegans*). Group CS8 includes species collected in small islands (Pulau Besar and Pulau Merambong; *Nanosesarma edamense*, *N. minutum*, *Selatium brockii*, *Metopograpsus oceanicus*). *Selatium brockii* and *Nanosesarma minutum* were also collected in Kuala Selangor. *Episesarma palawanense*, *Nanosesarma batavicum*, *N. pontianacense* and *Sarmatium germaini* were not included in any group, indicating that these species follow distinct distribution patterns (see Fig. 5.5).

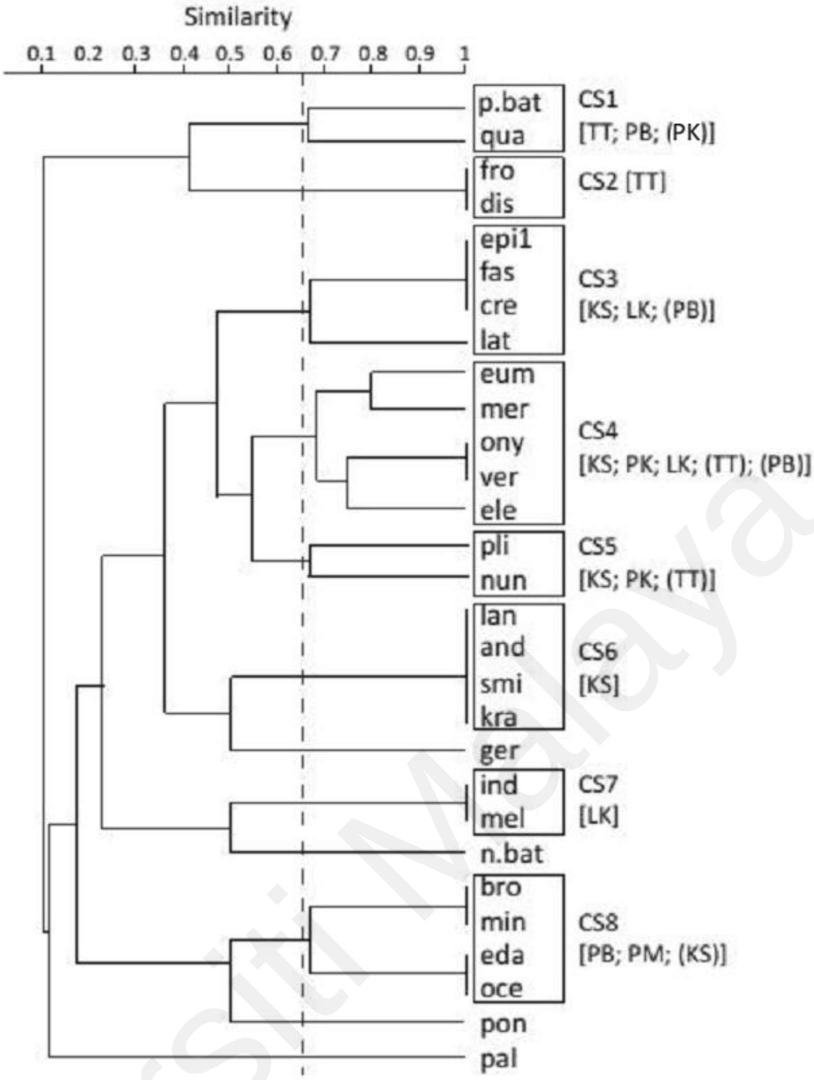

Figure 5.5: Hierarchical cluster analyses of the presence-absence dataset of grapsoid species relative to sampling sites. Eight groups of species (CS1–CS8) are associated with different sites (abbreviations in Fig. 4.1 and Tab. 4.1); *in square parentheses*: sampling sites in which the group's components were found; *in round parenthesis*: sites where only some of the species of the group were found; ger (found at sites KS and TT), n.bat (found at sites PK and LK), pon (found at sites KS and PB), pal (found at site PK) were not included in any group. Vertical dashed line: arbitrary 0.65 similarity cut-off value.

Figure 5.6 shows the biplot of the canonical correspondence analysis (CCA), which displays the species distribution in the different sites in relation to the environmental variables. The first two ordination axes explained 77.3% of total variance, with the first axis explaining 47.0% of the variance (Fig. 5.6).

The variable "Linear extension of the forest along the intertidal gradient" (IG) was associated with the "Areal extension of the forest" (AF), and these two variables were inversely correlated with the "Substrate type" (ST), suggesting that sites with fine substrates host larger forests, while small mangrove fringes are associated with coarser soil type. The variable "Insularity" (IN) was not correlated with the other parameters, suggesting that islands do not differ from mainlands in terms of forest size and substrate conditions (Fig. 5.6).

The different study sites are distributed along the axis 1, following a gradient of forest and sediment size, from smaller sites with coarser substrate (PM, PB, TT, on the left side of the graph), to sites hosting large forests on fine substrates (KS, PK, LK, on the right side of the plot). Sites Kuala Selangor and Pulau Kukup, which were plotted in the 1st quadrant of the biplot, have the same soil type conditions (mud, ST1) and are both large forests (AF3, IG3). Pulau Besar and Pulau Merambong were displayed in the 3rd quadrant, and they are both small insular mangrove sites with relatively coarse kind of substrate (AF1, IG1, ST3). Sites Tanjung Tuan and Langkawi were plotted in the 2nd and 4th quadrant, respectively. These two sites host the same soil conditions (mud and sand, ST2), but differ remarkably in the forest size and insularity conditions (Tanjung Tuan: AF1, IG2, IN1; Langkawi: AF3, IG3, IN2).

In general, the different species are scattered in the plot, showing that most of them follow distinct pattern of distribution (Fig. 5.6, but see Fig. 5.5 for groups of species with similar distribution).

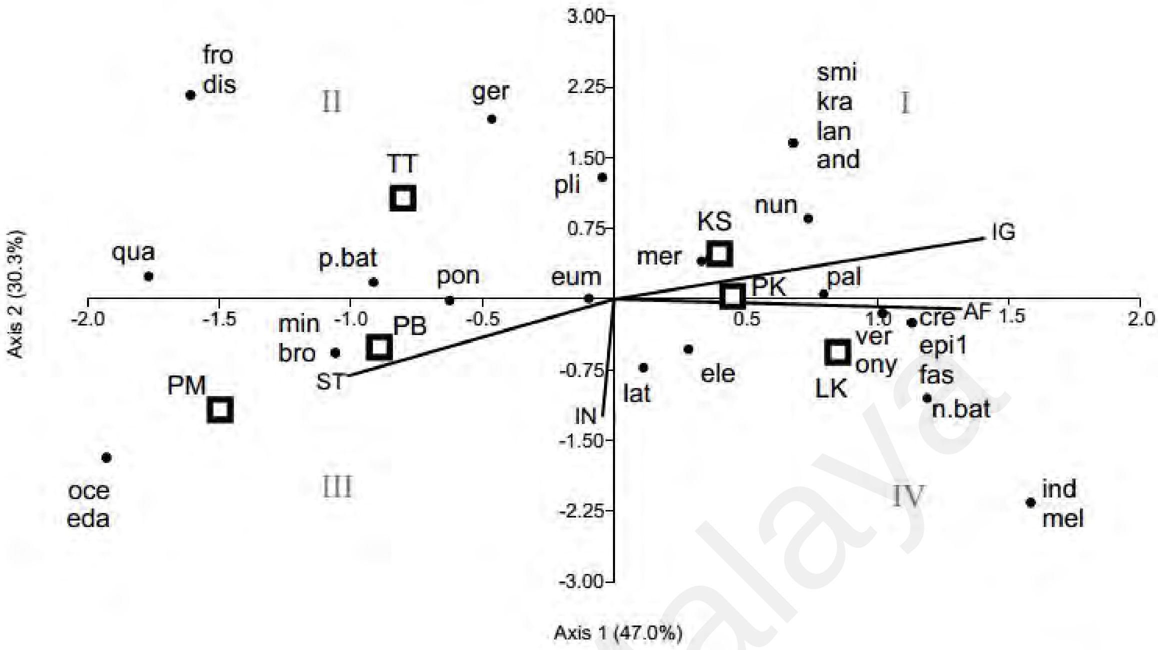

Figure 5.6: Canonical Correspondence Analysis (CCA) for the sites of Peninsular Malaysia. The triplot shows the positions of the species sampled in the different surveys. The species are plotted in the multivariate space defined by the environmental variables. The percent total variance explained by the first two axes is indicated in parentheses. Environmental variables are illustrated as vectors. Abbreviations as in Fig. 4.1, Tabs. 4.1, 5.2.

5.3.2 Brunei Bay

For the list of species found in this area, see Subchapter 4.3, and Tab. 4.2 (Chapter 4). Table 5.4 shows the number of specimens collected and the density (DsAT) of each species in each surveyed area.

The highest species richness was measured in site 4 (n = 12), followed by sites 1 and 2 (n = 11); the lowest richness was recorded in site 9 (n = 1), followed by sites 5 and 7 (n = 2), and site 8 (n = 3) (Tab. 4.2, Fig. 5.7a). The highest DsAT value was found in site 6 (n = 9.0), followed by site 3 (n = 7.7); the lowest value was recorded in sites 8 (n = 1.1), and 4 (n = 1.4) (Fig. 5.7c).

Sites 1, 2, and 4 have the highest number of effective species (S_{eff} = 7, 6, and 7, respectively), while sites 7 and 8 have the lowest S_{eff} values (S_{eff} = 2; Fig. 5.7b).

All the assemblages have evenness > 0.6, except sites 7 and 8 (Simpson 1-D < 0.5), which were dominated by a few species (Fig. 5.7d).

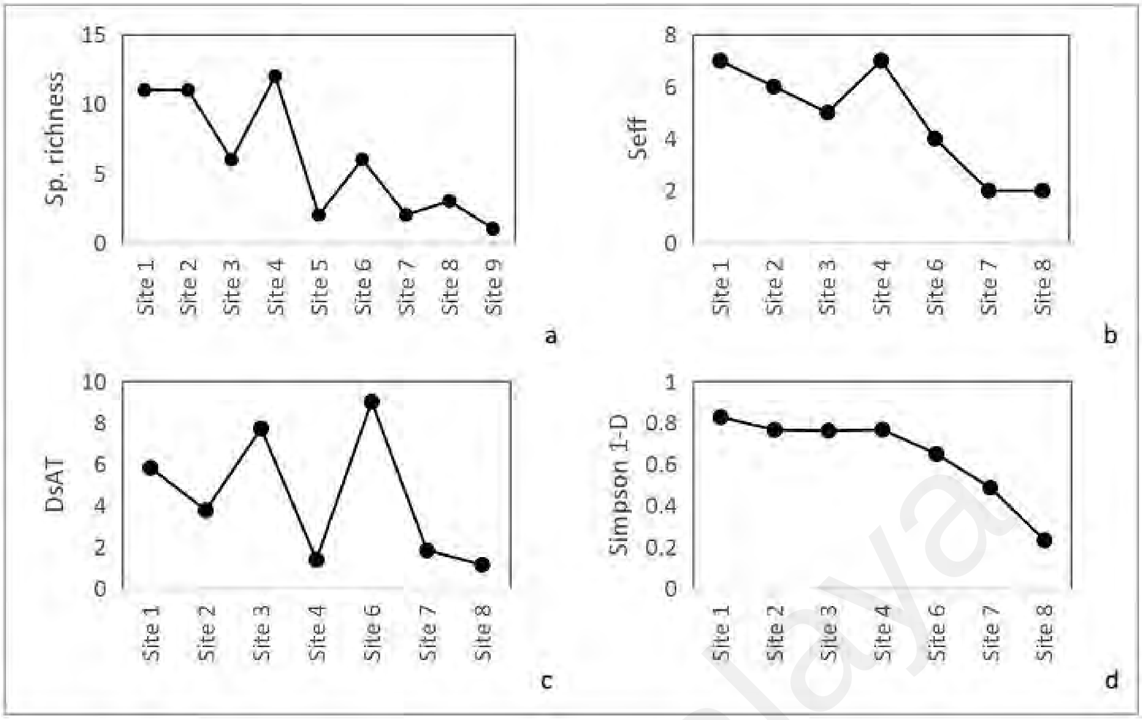

Figure 5.7: Species richness (a); effective number of species S_{eff} (b); density (DsAT, number of individuals per unit time and area) (c); and assemblage evenness (Simpson index 1-D) (d). In (b), (c) and (d), sites 5 and 9 are not included (sampling made by more than one researcher or different researchers). Juveniles specimens not identified at specific level have not been included in the graphics, except than in (c). See Figure 4.3 for sites numbers.

The Abundance-Distribution plot highlighted 3 groups of species (Fig. 5.8). Species plotted in quadrant A included 9 taxa which were found to be abundant (high DsAT) and uncommon (low frequency of occurrence), while quadrant B include 5 taxa abundant and common (high frequency of occurrence) (Fig. 5.8). The remaining 15 species were plotted in quadrant C, which included species uncommon and not abundant. Quadrant D (species common and not abundant) did not include any species (Fig. 5.8).

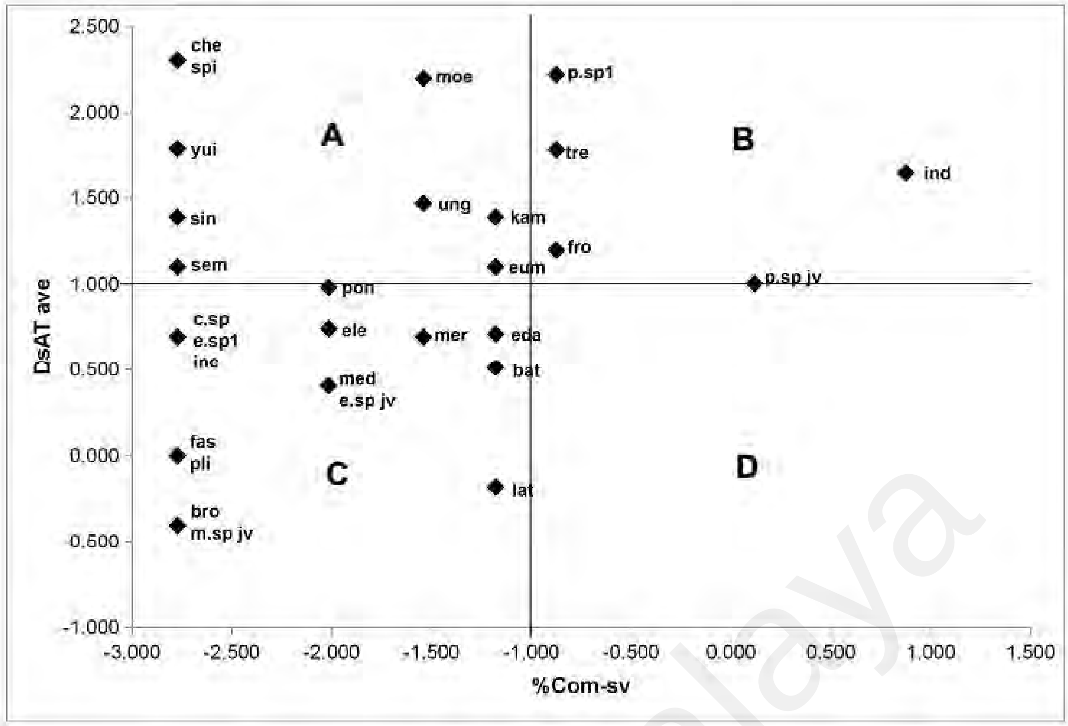

Figure 5.8: Distribution-Abundance plot. The abundance of each species, measured as log-transformed average DsAT (DsAT ave), has been plotted against its logit-transformed percentage commonness [%Com-sv = (number of surveys where the species occurs/ tot number of surveys)*100]. Quadrant A includes species relatively uncommon and abundant, quadrant B includes species common and abundant, quadrant C includes species uncommon and not abundant, quadrant D includes species common and not abundant. See Tab. 4.2 for species abbreviations.

Figure 5.9 shows the taxonomic composition of the different assemblages in the investigated area. In general, in every site 1-2 species dominated the assemblages, except than in site 1, where 4 species were dominant. In particular, in site 3, *M. tredecim* and *M. frontalis* represented >50% of the collected individuals, while *P. indiarum* dominated the assemblages in sites 1, 2, and 4. In general, in these sites the assemblages was composed by several species occurring in small densities. Site 6 was dominated by *P. moeschi* and *Parasesarma* sp.1, while in site 7 only two species were found, almost equally abundant, *H. kamora* and *N. spinicarpus.* Site 8 included 3 species only. One of these species, *Parasesarma* sp.1, was found also in sites 1 and 6, which hosted very different environmental conditions and vegetation types.

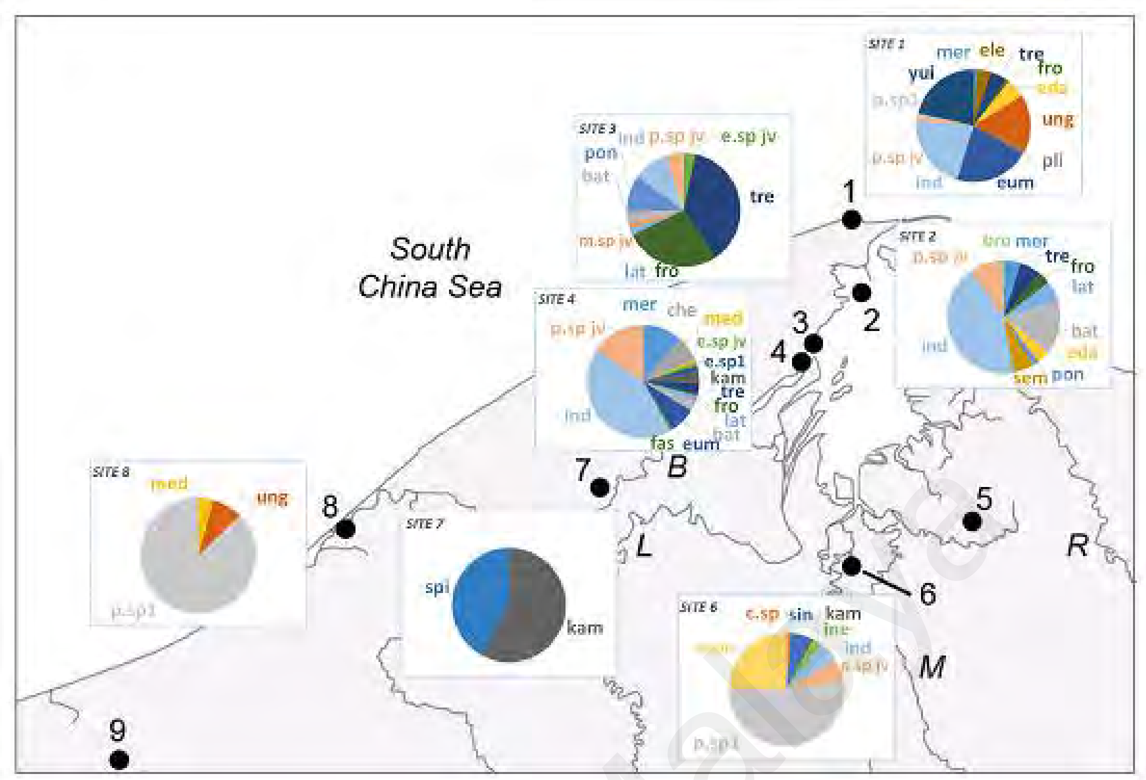

Figure 5.9: Map of the assemblages from the Brunei Bay. Percentage abundances of species in the different assemblages where quantitative measures of abundance (DsAT) were obtained. Abbreviations as in Fig. 4.3 and Tab. 4.2.

The canonical correspondence analysis (CCA) biplot of the species abundance for each survey in relation to the environmental variables is shown in Figure 5.10. The first two ordination axes explained 84.8% of total variance, with the first axis explaining 45.7% of the variance (Fig. 5.10).

The variables “Salinity” (SA) and “Type of sediment” (SD) varied inversely with the variable “Mean distance from the mangrove seaward fringe” (DM) and “Type and density of vegetation coverage” (DV) (Fig. 5.10). In particular, lower salinity values were associated with lower distance from the nearest water body, while coarser sediments are associated with higher salinity values and lower distance from the seaward fringe. The variables DM and DV mainly contributed to the first axis, while the other two variables (SA and SD) contributed to both the first and the second axis.

In general, sites 6, 7 and 8 separated from the other sampling sites (except for survey 8D), while the other four sampling sites included in the analysis were clustered together, except for survey 1C, which clearly separated from all the other surveys (Fig. 5.10). Sites 6 and 8 were found clustered together (except for surveys 6A and 8D) in the second and third quadrants, associated with higher values of DV and DM. Site 7 was found in the fourth quadrant, characterised by higher values of SD and SA, and low values of DV and DM. Most of the surveys of sites 1-4 were plotted in the first and fourth quadrants, and were clustered together, relatively close to the origin of the biplot (surveys 1A, 1B, 2A, 2B, 3A, 3B, 4A, 4B). These surveys generally corresponds to the lower intertidal areas of sites 1-4. In contrast, surveys 1C and 4C clearly separated from the other surveys, while surveys 2C and 4D were plotted in the second quadrant, close to survey 8D.

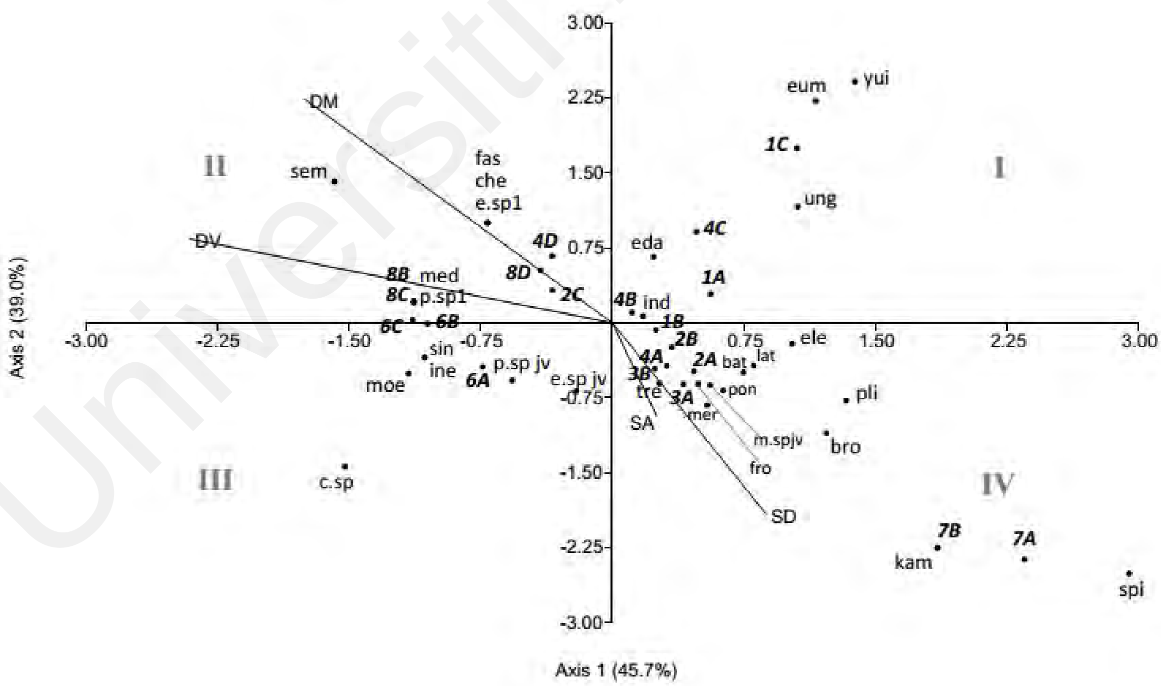

Figure 5.10: Canonical Correspondence Analysis (CCA). Triplot showing the positions of the species sampled in the different surveys. The species are plotted in the multivariate space defined by the environmental variables. The percent total variance explained by the first two axes is indicated in parentheses. Environmental variables are illustrated as vectors. Abbreviations as in Tabs. 4.2, 5.2, and Fig. 4.3).

The species distribution in the different sites and surveyed areas is summarised by the dendrograms of cluster analyses (Fig. 5.11).

Ten groups of species (Si1-Si10) were associated with different sampling sites (Fig. 5.11a), with each group including two or three species only. The species of the group Si1 (*Haberma kamora* and *Neosarmatium spinicarpus*) were collected from Sungai Brunei (site 7), and partly from Sungai Bunga (site 4) and Sungai Belayang (site 6), while group Si2 (*Clistocoeloma* sp., *Episesarma singaporense*, *Neosarmatium inerme*) included species found only in Sungai Belayang (site 6). The species of the group Si3 (*Parasesarma* sp.1, and *Pseudosesarma moeschi*) were found in Sungai Belayang (site 6), and partly in Pemburongunan Creek (site 1) and Sungai Tutong (site 8). Group Si4 (*Episesarma* sp. and *Metopograpsus* sp., both juvenile specimens) included species collected in Sungai Besar (site 3), and partly in Sungai Bunga (site 4). Species of the group Si5 (*Metaplax tredecim*, *Metopograpsus frontalis*, *Nanosesarma pontianacense*) were found in Pulau Bedukang and Sungai Besar (sites 2 and 3), and partly in Pemburongunan Creek and Sungai Besar (sites 1 and 4). Species of the group Si6 (*Perisesarma indiarum* and *Perisesarma* sp.) were collected from several sites, including Pemburongunan Creek (site 1), Pulau Bedukang (site 2), Sungai Besar (site 3), Sungai Bunga (site 4) and Sungai Belayang (site 6). Group Si7 (*Metopograpsus latifrons*, *Nanosesarma batavicum*) included species found in Pulau Bedukang (site 2), Sungai Besar (site 3), and Sungai Bunga (site 4). Group Si8 (*Metaplax elegans*, *Nanosesarma edamense*) included species found in Pemburongunan Creek (site 1), and partly in Pulau Bedukang (site 2). Species of the group Si9 (*Parasesarma ungulatum*, *Parasesarma eumolpe*, *Varuna yui*) were collected in Pemburongunan Creek (site 1), and partially in Sungai Bunga (site 4) and Sungai Tutong (site 8). Group Si10

Episesarma chentongense, *Episesarma* sp.1, *Fasciarma fasciatum*) included species found in Sungai Bunga (site 4), and partially in Pulau Bedukang (site 2).

Four groups of species (Su1-Su4) were associated with different surveys (Fig. 5.11b). Most of the species were not included in any group, and each group included two species only. Species of group Su1 (*Metaplax tredecim* and *Metopograpsus frontalis*) were recorded from several surveys, i.e. 1A, 2A, 3A, 3B, and partially from 4A and 4D. Group Su2 (*Parasesarma eumolpe* and *Varuna yui*) included species found in survey 1C, and partially in surveys 4B, 4C and 4D. Species of groups Su3 (*Episesarma* sp.1 and *Fasciarma fasciatum*) and Su4 (*Episesarma singaporense* and *Neosarmatium inerme*) have been reported from one survey only, i.e. surveys 4D and 6B, respectively.

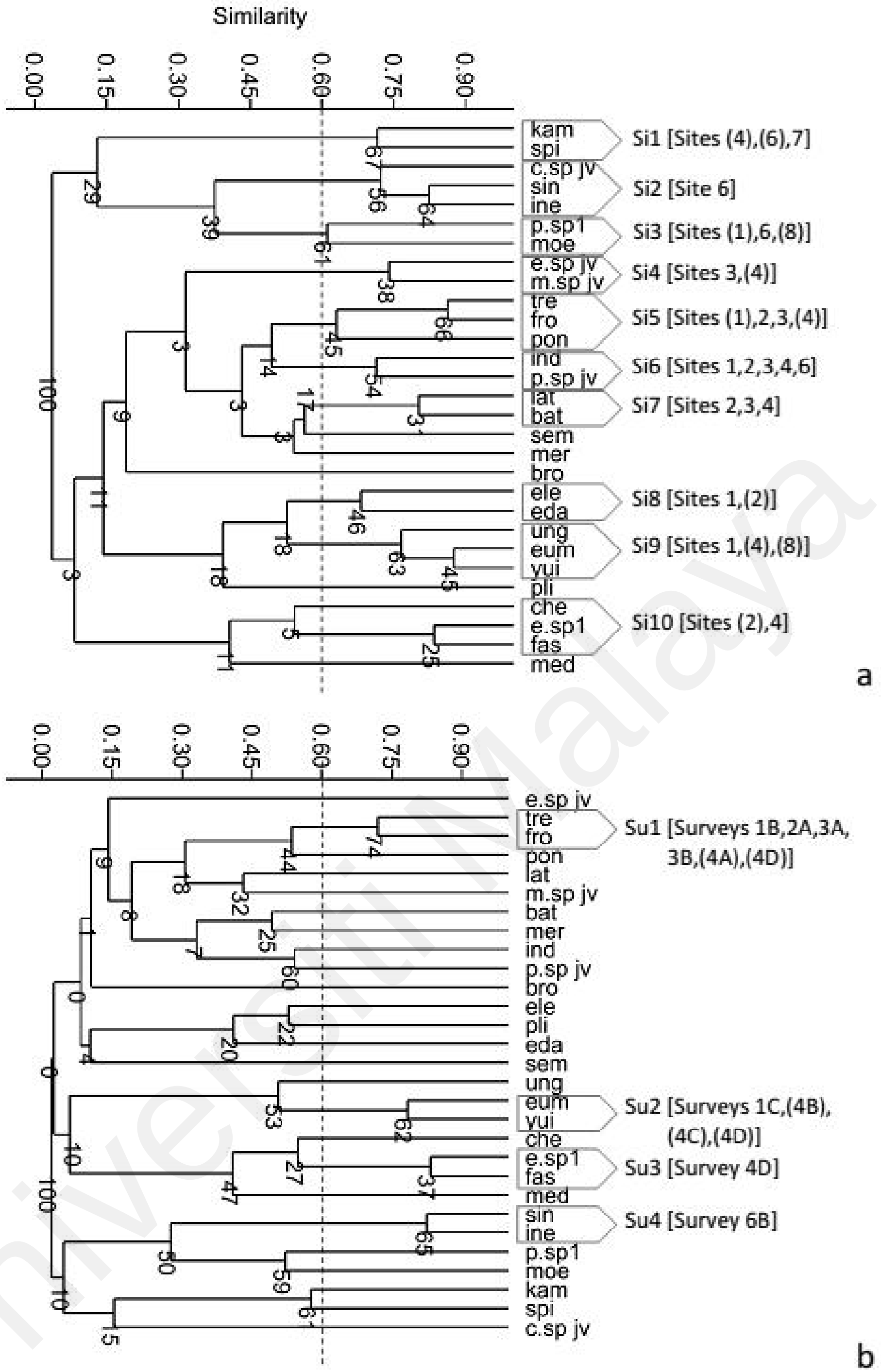

Figure 5.11: Hierarchical cluster analyses of grapsoid species relative to sampling sites (a), and surveys (b). In (a): 10 groups of species (Si1 - Si10) are associated with different sites; *in square parentheses*: sampling sites in which the group's components were found (abbreviations in Fig. 4.3), *in round parenthesis*: sites where only some of the species of the group were found; several of the species were not included in any group. In (b), 4 groups of species (Su1-Su4) are associated with different surveys; *in square parentheses*: surveys where the group's components were found, *in round parenthesis*: surveys where only some of the species of the group were found]. Vertical dashed lines: arbitrary 0.5 similarity cut-off value. Species' abbreviations as in Tab. 4.2.

Table 5.4: Numbers of collected crabs per survey (*n*), and estimated densities (DsAT). *Tot (ave)*: total number of collected crabs per species, and average density (*in parentheses*); *n tot*: total number of crabs per survey; *DsAT tot*: grand mean density per survey. Surveys not included in the analysis are not included in the table: 2D (1 *Episesarma chentongense*), 2E (1 *Parasesarma indiarum*, 1 *Metopograpsus latifrons*, 1 *Parasesarma* cf. *semperi*), 3C (1 *Metaplax tredecim*), 5B (2 *Pseudosesarma* sp.), 5C (1 *Pseudosesarma bocourti*), 5D (1 *Geosesarma gracillimum*), 5E (1 *G. gracillimum*), 9A (8 *G. gracillimum*), 9B (2 *G. gracillimum*). See Chapter 4 for details on the surveys.

Taxa	n,D	1A	1B	1C	2A	2B	2C	3A	3B	4A	4B	4C	4D	5A	6A	6B	6C	7A	7B	8A	8B	8C	8D
Clistocoeloma merguiense	n	1				1				4													
	DsAT	0.2				0.6				0.6													
Clistocoeloma sp. (juv)	n														1								
	DsAT														0.3								
Episesarma chentongense	n												10										
	DsAT												0.4										
Episesarma mederi	n												1										1
	DsAT												0.0										0.2
Episesarma singaporense	n															2							
	DsAT															1.5							
Episesarma sp. 1	n												2										
	DsAT												0.1										
Episesarma sp. (juv.)	n								2			1											
	DsAT								0.5			0.1											
Fasciarma fasciatum	n												1										
	DsAT												0.0										
Haberma kamora	n									1			1		1			12	1				
	DsAT									0.2			0.0		0.3			1.8	0.3				

Table 5.4, continued.

Taxa	n,D	1A	1B	1C	2A	2B	2C	3A	3B	4A	4B	4C	4D	5A	6A	6B	6C	7A	7B	8A	8B	8C	8D
Nanosesarma batavicum	n				1	3			2	1													
	DsAT				0.1	1.7			0.5	0.2													
Nanosesarma edamense	n	1	4		2		1																
	DsAT	0.2	0.8		0.2		0.2																
Nanosesarma pontianacense	n				2			6															
	DsAT				0.2			1.6															
Neosarmatium inerme	n															1							
	DsAT															0.7							
Neosarmatium spinicarpus	n																	10					
	DsAT																	1.5					
Parasesarma eumolpe	n			2							2	3	1										
	DsAT			3.8							0.2	0.2	0.0										
Parasesarma indiarum	n	8	3	1		6	7		6	8	10	1	2		3	1							
	DsAT	1.3	0.6	1.9		3.3	1.6		1.5	1.3	0.9	0.1	0.1		1.0	0.7							
Parasesarma plicatum	n	1																					
	DsAT	0.2																					
Parasesarma cf. *semperi*	n						3																
	DsAT						0.7																
Parasesarma cf. *ungulatum*	n	6		1																			2
	DsAT	1.0		1.9																			0.4
Parasesarma sp. 1	n	1													4	11	3			2	1	5	3
	DsAT	0.2													1.3	8.0	5.0			1.1	0.6	1.8	0.6
Parasesarma sp. (juv.)	n		1			1	2	2	1	2	5	1			5								
	DsAT		0.2			0.6	0.4	0.5	0.3	0.3	0.5	0.1			1.6								

Table 5.4, continued.

Taxa	n,D	1A	1B	1C	2A	2B	2C	3A	3B	4A	4B	4C	4D	5A	6A	6B	6C	7A	7B	8A	8B	8C	8D
Pseudosesarma moeschi	n													1	9	3	1						
	DsAT													0.2	2.9	2.2	1.7						
Selatium brockii	n				1																		
	DsAT				0.1																		
Metopograpsus frontalis	n		1		4			13	3				1										
	DsAT		0.2		0.4			3.5	0.8				0.0										
Metopograpsus latifrons	n				1	1		1			1												
	DsAT				0.1	0.6		0.3			0.1												
Metopograpsus sp. (juv.)	n							1															
	DsAT							0.3															
Metaplax elegans	n	3	1																				
	DsAT	0.5	0.2																				
Metaplax tredecim	n		4		7			8	14	1													
	DsAT		0.8		0.7			2.1	3.6	0.2													
Varuna yui	n			2																			
	DsAT			3.8																			
	n tot	21	14	6	18	12	13	31	28	17	18	6	19	1	23	18	4	22	1	2	1	5	6
	DsAT tot	3.5	2.8	11.3	1.8	6.7	2. 9	8.3	7.2	2.7	1.7	0.4	0.8	0.2	7.3	13.1	6.7	3.4	0.3	1.1	0.6	1.8	1.2

5.4 Discussion and Conclusions

5.4.1 Peninsular Malaysia

The species richness of most of the sites investigated in Peninsular Malaysia is comparable (Langkawi, Tanjung Tuan, Pulau Kukup and Pulau Besar; 8-12 species). However, Kuala Selangor and Pulau Merambong differ remarkably. In particular, Kuala Selangor hosts a relatively high number of species (19 species), which may be due to a role of the estuary. The input of freshwater from the Selangor River may provide additional spatial niches for freshwater and brackish water species, and also euryhaline species, increasing therefore the species richness of the assemblages. In Pulau Merambong, the reduced number of species(4 species) reported may be linked to the small size of the mangrove forest, and also to its uniformity, since the site hosts a continuous mangrove fringe which borders its western side. In fact, Pulau Besar and Pulau Merambong have a similar mangrove extension, but in the first site the mangrove fringe is scattered in three different sides of the island, exposed therefore to different hydrodynamic regimes, which are likely to provide a higher heterogeneity of environmental conditions and therefore can host a higher number of species.

While species richness is similar among sites, the taxonomic composition of the assemblages vary considerably, possibly due to the different eco-physiographic conditions of these systems.

Most of the recorded species have been found in less than half of the investigated sites, suggesting that habitats are patchily distributed, and that some species are either stenotypic, or they have a restricted geographic distribution. A similar pattern has been observed in other taxa, such as plants, intertidal invertebrates, terrestrial arthropods, and terrestrial vertebrates (Brown, 1984), and in other studies on grapsoid communities (e.g.

Tweedie, 1954; Ashton et al., 2003b; Salgado Kent & McGuinness, 2010). This pattern may be related either to adaptation to specific habitat conditions (niche specialization), or to competitive interactions between species that share the same ecological niche (competitive exclusion) (e.g. see Verberk 2011).

Only three species, i.e. *Clistocoeloma merguiense*, *Parasesarma eumolpe* and *Metaplax elegans*, were found to be relatively widely distributed and euritypic, occurring in more than half of the study sites, and in different environmental conditions. This result is not surprising, considering that these species are apparently common in this geographic area, (e.g. Tweedie, 1936; Sasekumar et al., 1974; Ashton et al., 2003a), and they also have a large distribution area, spreading throughout the whole Indo-West Pacific region (*C. merguiense* and *M. elegans*; e.g. Saba, 1972; Frusher et al., 1994; Ng, 2006; Nordhaus et al., 2009; Diele et al., 2013), or at least South East Asia (*P. eumolpe*; e.g. Frith et al., 1976; Ashton et al., 2003b; Pratiwi & Widyastuti, 2013).

The investigated assemblages are apparently not influenced by latitudinal or other geographic patterns; their taxonomic composition appears to be related to variables acting at the habitat scale, such as substrate type and forest area.

On the base of the environmental variables here considered, and the results from the CCA, the study sites can be tentatively subdivided in four groups, defined as (i) "large mangrove forests with fine substrate" (Kuala Selangor and Pulau Kukup), (ii) "mainland forests with intermediate areal extension and sediment size" (Tanjung Tuan), (iii) "large insular forests with mixed sediment size" (Langkawi), and (iv) "small insular forests with coarse sediment" (Pulau Besar and Pulau Merambong).

Although every site hosts distinct grapsoid communities, a few patterns in the assemblage structure relatively to habitat conditions can be identified. For instance, in sites of group (iv) the assemblages are characterised by the absence of large burrower species (e.g. *Episesarma* spp., *Neosarmatium smithi*, *Parasesarma onychophorum*), that were instead found in sites of group (i) and (iii). It is possible that the massive burrowing activity of these species requires a muddy substrate (i.e. cohesive enough), and enough space for the population to build its burrows network. In fact, Thongtham and Kristensen (2003) found out that *Episesarma versicolor* digs burrows in impermeable silt and fine sand, and the burrow structure is affected by the type of sediment (Thongtham & Kristensen, 2003).

In mangrove fringes of small islands (group iv; i.e. Pulau Besar and Pulau Merambong) the grapsoid community is mainly composed of algivorous and predator species (i.e. *Metopograpsus* spp., *Metaplax* spp., *Selatium brockii*; e.g. Fratini et al., 2000; Sivasothi, 2000; Ng, 2006; pers. obs.). The absence of large folivore and detritivore species (i.e. feeding on mangrove leaves and litter, e.g. *Parasesarma onychophorum*, *Episesarma* spp.; e.g. Malley, 1978; Sivasothi, 2000) is consistent with the small forest area of these sites, which may not provide enough food resources to sustain large populations of these species.

Genera with small-sized individuals are apparently more adaptable to different kind of environmental conditions. For instance, the genus *Nanosesarma* was found in several sites with different sediment type and forest size. *Nanosesarma* species were often found inside crevices in rotting wood (pers. obs.), which agrees with previous studies (e.g. Komai et al., 2004). The small size of these species probably allows them to easily occupy crevices and tunnels built by wood borers, which can act as a shelter from predators, and also provide better microhabitat conditions, in terms of lesser water evaporation and temperature fluctuations. This microhabitat can be found basically in every kind of mangrove site, thus explaining the ubiquitous presence of this genus.

However, within the genus an apparent differentiation in the species distribution could be observed, each of them being found in different sites, maybe related to competitive interactions among these species, which compete for the same spatial niche.

The presence of several species found both on mainland systems and islands indicates that in this area the early dispersalist stages (zoeal stages) can move both along the coast line and towards off-shore water. However, further investigations on patterns of larval dispersal would be useful to clarify the degree of connections between mainland and insular populations of the same species.

The field investigation conducted in this area provided information for some species whose autecological traits are practically unknown, since these taxa were reported only in a few studies, mainly involving only taxonomic aspects or distribution records. In particular, these species include *Nanosesarma edamense* (De Man 1887, 1888, Tweedie 1950a, Ng & Richer de Forges 2007), *N. nunongi* (Tweedie 1936), *Parasesarma batavianum* (De Man 1890, 1895, Tweedie 1936, Pratiwi & Rahmat 2015), and *P. lanchesteri* (Tweedie 1936, 1950a) (see also Chapter 3).

The results from this study updated also existing information on several species. For instance, *Fasciarma fasciatum* was found previously mainly on sandy substrate, in disturbed areas (Sasekumar, 1974; Guerao et al., 2004). In the present study, this species was found on muddy and sandy substrates in Langkawi, and on muddy substrate in Kuala Selangor, suggesting that this species can occur on different kinds of substrate.

Nanosesarma andersonii was previously recorded from a riverine mangrove system (De Man, 1887-1888), and also in different salinity conditions (Ravichandran et al., 2007), while no information on the substrate was previously reported. The present study recorded this species from Kuala Selangor on muddy substrate, confirming this species as an estuarine species, and providing first information on the kind of substrate where it occurs.

Nanosesarma minutum has been found in different types of coastal ecosystems and substrates (i.e. both mangrove forests on fine substrate, and unvegetated rocky shores; e.g. Lundoer, 1974; Ravichandran et al., 2007). In the present study, this species was found both in a large muddy mangrove forest (Kuala Selangor), and in small mangrove fringes on coarser substrate (Pulau Besar and Pulau Merambong), confirming this species as capable to adapt to different environmental conditions.

Nanosesarma pontianacense has been previously reported from a heavily impacted estuarine lagoon on muddy substrate (Indonesia, Nordhaus et al., 2009), while other authors reported it from several locations but did not provide information on the environmental conditions (e.g. De Man, 1895; Tweedie, 1940; Lundoer, 1974). The present study reported this species from Kuala Selangor and Pulau Besar, thus suggesting that this species can be found in different substrate conditions and forest types.

Neosarmatium smithi has been found on sandy substrates with high salinity values (Bosire et al., 2004). In the present study, this species was found in an estuarine mangrove forest on muddy substrate (Kuala Selangor), suggesting therefore that this species can cope with different substrate types and salinity conditions.

Parasesarma indiarum has been considered one of the dominant species in the mangrove assemblages of Singapore (Huang et al., 2008), and it has been reported also from Thailand (e.g. Frith, 1974) and from the northern part of Peninsular Malaysia (Penang and Pahang states; Tweedie, 1940). However, in the present study this species was found only in one site, in the northern portion of our study area (Langkawi), while it was absent in the other investigated sites. This suggests a patchy distribution of this species in this region, which may be attributed to specific habitat requirements of this species.

5.4.2 Brunei Bay

5.4.2.1 Diversity of the different ecosystems

Lower and middle intertidal mangrove sites dominated by *Rhizophora* forests (such as Pulau Bedukang and Sungai Bunga, sites 2 and 4), pioneer *Avicennia* and *Sonneratia* forests (Pemburongunan Creek and Sungai Besar, sites 1 and 3) and monotypic nipah forests (Sungai Belayang, site 6) hosted relatively highly diverse assemblages, both in term of species richness and evenness.

In contrast, high intertidal and supratidal ecosystems, such as the upper tract of a river (Sungai Brunei, site 7, 24 km from the river mouth), mangrove backforests, and peat swamps (Sungai Labu, Sungai Tutong and Badas, sites 5, 8 and 9) hosted peculiar communities, taxonomically distinct from the other sites, and including a few species only. It is likely that these semi-terrestrial systems host environmental conditions which are "extreme" for these marine taxa, especially in term of salinity (freshwater) and access to water bodies, allowing only a few species to occupy these ecological niches. The reduced competition may allow these species to thrive, as suggested by the facts that some of them were found in relatively high abundance of individuals (e.g. Sungai Brunei). Considering that the higher intertidal areas of tropical coastal wetlands are generally the most affected by reclamation for human activities (Lee et al., 2017), conservation measures are especially needed in order to preserve the unique assemblages of these systems.

Within the lower and middle intertidal mangrove sites (sites 1-4), Sungai Besar (site 3) hosted relatively low species richness, which may be explained by the very shortened intertidal gradient of this site (15 m, see Chapter 4). This site was dominated by two species, *Metaplax tredecim* and *Metopograpsus frontalis*, that have been found also in the other mangrove sites (sites 1, 2 and 4), although less abundant. These two species have been found to co-occur when considering the species associations at both site and survey levels (CA), suggesting that they may be associated with similar environmental conditions at both ecosystem and habitat/microhabitat levels.

Sungai Belayang (site 6) too hosted lower diversity levels compared to mangrove sites (1-4), both in term of richness and evenness of the assemblages. Moreover, the taxonomic composition of its grapsoid community differed quite remarkably from those of other sites (see CCA). In particular, this site is located in the middle/upper intertidal tract of a river delta, and it is dominated by a monotypic nipah forest, and characterised by low salinity values, which can explain the peculiarity of the grapsoid assemblages. In particular, *Episesarma singaporense* and *Neosarmatium inerme* have been found in this site only, while the assemblage was numerically dominated by two species, *Pseudosesarma moeschi* and *Parasesarma* sp.1.

Ecological studies on the brachyuran communities of nipah forests are basically unknown (but see Udoidiong & Ekwu, 2011), although several grapsoid species have been reported from this kind of systems (e.g. *Bresedium sedilense*, *Neosarmatium spinicarpus*, *Pseudosesarma crassimanum*, *P. granosimanum*, *P. moeschi*, Tweedie 1940, see also Davie, 1994; *Labuanium politum*, Ng et al., 2015).

When considering mangrove sites (1-4), the CCA plot showed an overlapping of these sites in the biplot, suggesting that assemblages of these sites are more similar among each other than within them. Moreover, for these sites the plot showed a separation between assemblages of lower and upper intertidal areas, which is consistent with results from other studies (e.g. Sasekumar, 1974; Frusher et al., 1994).

In particular, surveys from the lower intertidal zones (1A, 1B, 2A, 2B, 3A, 3B, 4A, 4B) were closely clustered together, indicating a similarity in their assemblages. Assemblages of the upper zones were instead more dispersed in the plot, indicating that the higher intertidal zone of each site differs remarkably from those of other sites. For instance, while surveys 2C, 4D, and 8D were plotted close to each others, surveys 1C and 4C clearly separated from other surveys.

These two surveys (1C, 4C) were conducted in areas with peculiar environmental conditions, especially in terms of vegetation type (see also Tabs. 5.2, 5.3, Fig. 5.1 and Subchapter 4.2.1.2). In particular, survey 1C was dominated by grasses, intersperse with large tidepools, few stunted trees and numerous dead trees, while area of survey 4C included *Acrostichum* ferns and *Acanthus* sp. Additionally, this surveyed area (4C) was also colonised by *Thalassina* mounds, which may play a role in its differentiation from other surveys. For instance, Sivasothi (2000) found that the presence of *Thalassina* mounds can influence the distribution of *Episesarma* species, with *E. singaporense* being particularly abundant in *Thalassina* areas, while the congeneric *E. versicolor* mainly colonised areas without mounds.

5.4.2.2 Spatial ecology and distribution of the species

In general, the investigated community was found to be composed of several "specialist/stenotypic" species, which occurred in only a few of the studied sites, and a few "generalist/euritypic" species (*Parasesarma indiarum*, *Metaplax tredecim, Metopograpsus frontalis*), which have been found in several sites. The same trend was observed when considering the frequency of occurrence of the species at survey level, with most of the species occurring in a restricted number of surveys.

Specialist species were generally not abundant, except for a few species (9 species, see Fig. 5.8), which have been recorded in relatively large numbers of individuals where they occur. These species seem to be well adapted to specific environmental conditions, where they can thrive. They are instead excluded from most of the other surveyed areas, due possibly to unsuitable environmental conditions or competitive interactions. For instance, *Haberma kamora* was found particularly abundant in site 7, where it was collected from a meadow where grass had been recently cut, while this species was present also in other sites, although not abundant. Our data confirm previous information for this genus, since the conspecific *Haberma nanum* was to be more abundant in disturbed areas, such as soil-covered man-made debris around a ruined building (Ng & Schubart, 2002).

Several studies found that natural assemblages are usually composed of many rare species and a few common ones, and widespread species also occur in higher densities (abundance per unit of space), compared to species with a restricted distribution (Verberk, 2011). This pattern has been widely observed in natural assemblages across several taxa, including plants, intertidal invertebrates, terrestrial arthropods, and terrestrial vertebrates (Brown, 1984). Other studies on grapsoid crabs reported similar patterns, in which most of the species were recorded in restricted areas, or in peculiar environmental conditions only (e.g. Tweedie, 1954; Ashton et al., 2003a; Salgado Kent & McGuinness, 2010).

The restricted distribution of most of the species indicates that each site hosts a peculiar brachyuran assemblage, with the different species being adapted to different environmental conditions. This emphasizes the importance of preserving the diversity of different habitat types in conservation plans and management of these coastal wetlands.

In fact, the dendrograms of the cluster analyses highlighted how the different species follow apparently independent distribution patterns, and only a few of them are co-occurring in the same sites or surveyed area. In particular, when considering the dendrogram of the species relatively to the surveyed areas, most of the species were not included in any group of similarity, suggesting that at habitat level each species occupy a different spatial niche.

Maintaining a certain degree of connectivity between different kind of ecosystems (e.g. the transition mangrove - back forest - peat swamp/freshwater swamp), and within the ecosystems (e.g. the transition from low to high intertidal zone within mangrove forests) is important to ensure that all the species can find a suitable ecological niche, and therefore have “enough habitat” to survive. This goal can be achieved for instance by protecting biodiversity corridors, especially along the intertidal gradient, to ensure connectivity between populations (mangrove systems cannot become isolated patches), and to preserve the natural continuum of species occurring along this gradient.

5.4.2.3 Update and new findings on species autecological traits

This study provides new information on the autecology of these species, which in some cases have not been previously investigated in ecological studies. Ecological data on grapsoid species in the IWP are in many cases fragmentary and limited to specific areas or species (Lee, 1998, 2008).

In particular, *Nanosesarma edamense*, *N. pontianacense* and *Neosarmatium spinicarpus* have been previously reported only in taxonomic studies (De Man, 1887; Tweedie, 1940, 1950a,b; Davie, 1994), or in distribution records (De Man, 1888; Nobili, 1903; Tesch, 1917; Tweedie, 1940, 1950a; Lundoer, 1974; Ng & Richer De Forges, 2007).

Episesarma species are differentially distributed along the intertidal zone (Sivasothi, 2000), although no quantitative studies are available in the literature. In the present study, all *Episesarma* species were found on brackish mud, but *E. singaporense* was found associated with freshwater, in the upper zone of a *Nypa* forest along Sungai Belayang (site 6). *E. mederi* and *E. chentongense* were found instead in middle and lower intertidal zones, in *Rhizophora* marine pioneer shores (Pulau Bedukang and Sungai Bunga, sites 2 and 4), in brackish conditions. In general, *Episesarma* species were absent from relatively open areas (Pemburongunan Creek and Sungai Brunei, sites 1 and 7) and from sites with reduced intertidal extension (Sungai Besar, site 3).

Haberma kamora was recently described from Irian Jaya (Rahayu and Ng, 2005), where it was found on the muddy banks of a river and on hard substrates in the upper intertidal zone of a mangrove forest. This species was also reported from a heavily impacted lagoon in Indonesia (Nordhaus et al., 2009). In this study, this species was found on muddy substrates in both freshwater and brackish conditions, in a mangrove forest (Sungai Bunga, site 4), in an artificial grass meadow near a river bank (Sungai Brunei, site 7), and in a *Nypa* forest (Sungai Belayang, site 6). The present finding confirms this species can adapt to different habitat conditions, and is able to colonise impacted and altered areas.

The genus *Pseudosesarma* is currently under revision (Ng et al., 2008). *P. bocourti* is widely distributed throughout South East Asia, although morphological intraspecific variation occurs among different assemblages (Ng 1995a), prompting for a revision of this species (Yeo et al., 1999). *P. moeschi* has been reported in mangrove swamps and *Nypa* forests from Thailand, Peninsular Malaysia, and Indonesia (Guerao et al., 2007), and it has been documented to be highly euryhaline (McLauglin et al., 1996). In this study, this species was found in a *Nypa* forest (Sungai Belayang), in freshwater conditions, but on brackish mud.

In lower intertidal areas, a few species have been exclusively found inside dead wood (pers. obs., *Nanosesarma pontianacense*, *Metopograpsus frontalis*, *M. latifrons*). This specific habitat may offer suitable microhabitat conditions for these species, increasing water availability during low tide, and buffering daily temperature fluctuations. In fact, the seaward edge of mangrove forests is generally more exposed to direct sunlight, compared to more shaded habitats, such as the mid-intertidal and high-intertidal forest (pers. obs., unpublished data). Dead wood also likely offers protection from both terrestrial and aquatic predators.

Geosesarma gracillimum was found in pitcher plants of the genus *Nepenthes*, and inside the soil litter. Species of this genus are known to be nepentophilous (e.g. Ng & Lim, 1987), and our record confirms this habitat type for this species, as also recently reported by Ng (2017).

Within the mangrove sites, several species were found to be associated to specific sites or surveyed areas. For instance, *M. elegans*, *P. plicatum* and *Varuna yui* have been found only in Pemburongunan Creek (site 1), a site with relatively low density of vegetation coverage, suggesting that these species prefer open areas. In particular, *P. plicatum* have been found to feed mainly on microphytobenthos (Bouillon et al., 2004), more abundant in unvegetated or scarcely vegetated areas.

A few species have been reported from one of the investigated sites only, i.e. *P. semperi* and *S. brockii* have been recorded from Pulau Bedukang (site 3) only, while *Episesarma* sp.1 and *F. fasciatum* have been found in Sungai Bunga (site 4) only. In contrast, *M. tredecim*, *M. frontalis* and *P. indiarum* have been reported from more than four of the investigated sites, and they can therefore be considered as opportunistic species, able to live in different systems within the studied geographic area. Salgado Kent and McGuinness (2010) found *M. frontalis* in lower intertidal areas, often inundated by tides, suggesting that tidal flow or elevation gradient may be important factors for this species. *P. indiarum* has been considered one of the dominant species in mangrove assemblages of Singapore (Huang et al., 2008), while in another northern Borneo, Ashton et al. (2003a) reported this species from only one of their surveyed plots. In fact, Shahdadi et al. (2018) has recently splitted this species, by describing a new species (*P. peninsulare*) for samples reported from Peninsular Malaysia and Singapore. The specimens collected in this study could be therefore belonging to the new species. However, since a re-examination of the samples has not been possible, the previous name was maintained.

Davie (1994) pointed out how *Neosarmatium inerme* and *N. spinicarpus* are considered as aberrant species within the genus *Neosarmatium*: both these species were found in nipah forests (Tweedie, 1940, current study), which may indicate they have adapted to these kind of environment, in contrast with other *Neosarmatium* species. In this study, however, *Neosarmatium spinicarpus* has been recorded only from Sungai Brunei, in an artificial meadow, thus suggesting that this species may be able to colonise also areas anthropically altered.

CHAPTER 6: CONCLUSIONS

The present study investigated the composition and structure of several sesarmid assemblages in Peninsular Malaysia and northern Borneo, updating the knowledge on the diversity of these dominant mangrove macrofaunal taxa, and providing datasets for several previously unexplored sites. Checklists and species inventories are fundamental tools in the management of natural resources, and can be utilised to highlight the value of local ecosystems and promote their conservation.

A comprehensive review of the state of knowledge of these crabs has been provided, including any information available for the species reported from the investigated area (Peninsular Malaysia, Singapore, northern Borneo). The review revealed a diverse species pool in this area, which seems to be relatively unexplored. In fact, for several species the autecological traits are still largely unknown.

The field studies (West coast of Peninsular Malaysia and Brunei Bay) revealed that local mangrove systems host peculiar communities, which differ considerably among each others in their taxonomic composition, and are probably influenced by soil conditions, salinity, forest size, position along the intertidal gradient, and type of vegetation.

In this area several mangrove forests and other wetlands have been converted to other uses without a prior assessment of their diversity (e.g. Malacca city land reclamation projects, Pengarang Iskandar Johor), with the risk that some of the species may have already become locally extinct. The variety of communities needs therefore to be taken into consideration in management plans, to prevent extinctions and further loss of biodiversity.

The results from this study suggested that most of the species are either stenotypic or have a patchy areal distribution. Therefore, it is advisable to identify and protect the diversity of the assemblages, and especially endemic species (e.g. *Nanosesarma nunongi*, which has been found only in the Malay Peninsula). Because of their restricted distribution area, these species may be particularly vulnerable to anthropic impacts on the ecosystem, such habitat loss or physico-chemical alterations. A change in the habitat conditions may create unsuitable conditions for certain species, e.g. changes in salinity may affect the community, that will lose stenohaline species, resulting in an impoverishment of the original diversity.

Considering that different kinds of mangroves provide also different goods and services (Ewel et al., 1998), protecting and enhancing the diversity of mangrove sites will have positive benefit on the long run, for both the ecosystems and the local and global human communities.

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PUBLICATIONS AND PAPERS PRESENTED

PAPERS PRESENTED

Ribero, L., Lim, P. E., & Polgar, G. (2013). Mangrove and other peritidal communities of grapsoid crabs (Brachiura: Grapsoidea) and oxudercine gobies (Gobiidae: Oxudercinae), along the west coast of the Malay Peninsula, with special reference to islands. *Port Dickson International Conference on Sustainable Development of Tropical Coastal Zones, 5-6 September 2013,* (oral presentation), Port Dickson, Malaysia

APPENDICES

Appendix 1 - List of the specimens deposited in Museum collections (Muzium Zoologi, University of Malaya; Lee Kong Chian Natural History Museum, Singapore).

Selection of specimens deposited in Lee Kong Chian Natural History Museum (ZRC), collected from the Brunei Bay. Measurements of carapace width (CW) are reported to the nearest 0.1 mm. All specimens were collected by GP and LR, unless noted. All specimens were fixed in 70% ethanol, unless noted, and preserved in 70% ethanol. CD = Claas Damken, GP = Gianluca Polgar. See Chapter 4 for the descriptions of the sampled areas (surveys).

The samples collected in Peninsular Malaysia have been deposited in the Museum Zoologi of the University of Malaya: for these specimens, however, a reference number is not available yet, since the catalogue process by the museum is still in progress.

Grapsidae:

Metopograpsus frontalis: ZRC 2018.0845, female, 12.3 mm CW, Pulau Bedukang, survey 2A, 13 October 2013. ZRC 2018.0861, male, 13.4 mm CW, Pulau Bedukang, survey 2A, 13 October 2013. ZRC 2018.0864, ovigerous female, 21.4 mm CW, Pemburongunan Creek, survey 1B, 1 December 2013. ZRC 2018.0859, male, 9.9 mm CW, Sungai Besar, survey 3A, 10 October 2013. ZRC 2018.0870, female, 20.1 mm CW, Sungai Besar, survey 3A, 10 October 2013.

Metopograpsus latifrons: ZRC 2018.0869, male, 20.3 mm CW, Pulau Bedukang, survey 2A, 13 October 2013. ZRC 2018.0871, female, 18.5 mm CW, Sungai Besar, survey 3A, inside dead wood, 10 October 2013.

Sesarmidae:

Clistoceloma merguiense: ZRC 2018.0876, male, 7.7 mm CW, Pulau Bedukang, survey 2B, 13 October 2013. ZRC 2018.0858, ovigerous female, 11.6 mm CW, Pemburongunan Creek, survey 1A, 1 December 2013. ZRC 2018.0862, female, 9.4 mm CW, Sungai Bunga, survey 4A, on leaf axil of *N. fruticans*, 8 October 2013, fixed in 5% formalin.

Episesarma chentongense: ZRC 2018.0875, male, 41.8 mm CW, Pulau Bedukang, survey 2D, 27 May 2013, coll. GP. ZRC 2018.0840, male, 40.1 mm CW, Sungai Bunga, survey 4D, 11 October 2013. ZRC 2018.0857, female, 25.6 mm CW, Sungai Bunga, survey 4D, 11 October 2013.

Episesarma mederi: ZRC 2018.0853, ovigerous female, 30.5 mm CW, Sungai Bunga, survey 4D, 11 October 2013.

Episesarma singaporense: ZRC 2018.0918, male, 33.3 mm CW, Sungai Belayang, survey 6B, 15 October 2013.

Fasciarma fasciatum: ZRC 2018.0848, female, 10.4 mm CW, Sungai Bunga, survey 4D, 11 October 2013.

Geosesarma gracillimum: ZRC 2018.0842, male, 9.0 mm CW, Badas, survey 9A, 18 May 2013, coll. GP. ZRC 2018.0880, male, 12.5 mm CW, Sungai Labu (Labu forest reserve), survey 5D, 26 February 2014, coll. CD, fixed in 100% propylene glycole.

Haberma kamora: ZRC 2018.0925, male, 5.1 mm CW, Sungai Belayang, survey 6A, 15 October 2013. ZRC 2016.0380, male, 6.8 mm CW, Sungai Brunei, survey 7A, 10 October 2013. ZRC 2018.0881, female, 8.2 mm CW, Sungai Brunei, survey 7A, 10 October 2013. ZRC 2018.0878, male, 4.5 mm CW, Sungai Bunga, survey 4A, 8 October 2013. ZRC 2018.0850, female, 5.4 mm CW, Sungai Bunga, survey 4D, specimen with exuvia, 11 October 2013.

Nanosesarma batavicum: ZRC 2016.0383, Pulau Bedukang, male, 4.8 mm CW, survey 2A, 13 October 2013. ZRC 2016.0382, ZRC 2016.0385, ZRC 2016.0386, 3 males, 4.2−5.9 mm CW, Pulau Bedukang, survey 2B, 13 October 2013. ZRC 2016.0381, ZRC 2016.0384, 2 females, 5.7, 5.9 mm CW, Sungai Besar, survey 3B, 10 October 2013. ZRC 2016.0387, ovigerous female, 5.2 mm CW, Sungai Bunga, survey 4A, 8 October 2013.

Nanosesarma edamense: ZRC 2016.0391, ZRC 2016.0393, 2 males, 5.5−6.6 mm CW, Pulau Bedukang, survey 2A, 13 October 2013. ZRC 2016.0392, male, 6.4 mm CW, Pulau Bedukang, survey 2C, 13 October 2013. ZRC 2016.0389, male, 3.0 mm CW, Pemburongunan Creek, survey 1A, 1 December 2013. ZRC 2016.0388, ZRC 2016.0390, ZRC 2016.0394, ZRC 2016.0395, 1 female, 3 males, 3.4-5.2 mm CW, Pemburongunan Creek, survey 1B, 1 December 2013.

Nanosesarma pontianacense: ZRC 2018.0877, ovigerous female, 4.9 mm CW, Pulau Bedukang, survey 2A, 13 October 2013. ZRC 2018.0866, ovigerous female, 5.4 mm CW, Sungai Besar, survey 3A, inside dead wood, 10 October 2013.

Neosarmatium inerme: ZRC 2016.0396, female, 14.0 mm CW, Sungai Belayang, survey 6B, 15 October 2013.

Neosarmatium spinicarpus: ZRC 2018.0874, female, 10.7 mm CW, Sungai Brunei, survey 7A, 10 October 2013. ZRC 2016.0397, male, 9.9 mm CW, Sungai Brunei, survey 7A, 10 October 2013.

Parasesarma eumolpe: ZRC 2018.0865, female, 13.9 mm CW, Pemburongunan Creek, survey 1C, 1 December 2013. ZRC 2018.0844, female, 15.9 mm CW, Sungai Bunga, survey 4D, 11 October 2013.

Parasesarma indiarum: ZRC 2018.0867, ovigerous female, 15.5 mm CW, Pulau Bedukang, survey 2C, 13 October 2013. ZRC 2018.0868, male, 13.1 mm CW, Pulau Bedukang, survey 2C, 13 October 2013. ZRC 2018.0841, male, 9.9 mm CW, Pemburongunan Creek, survey 1A, 1 December 2013. ZRC 2018.0843, female, 11.9 mm CW, Pemburongunan Creek, survey 1A, 1 December 2013. ZRC 2018.0919, female, 12.8 mm CW, Sungai Belayang, survey 6A, 15 October 2013. ZRC 2018.0922, male, 11.4 mm CW, Sungai Belayang, survey 6B, 15 October 2013. ZRC 2018.0873, male, 10.7 mm CW, Sungai Besar, survey 3B, 10 October 2013. ZRC 2018.0855, male, 12.1 mm CW, Sungai Bunga, survey 4A, 8 October

2013. ZRC 2018.0924, female, 16.7 mm CW, Sungai Bunga, survey 4D, 11 October 2013.

Parasesarma plicatum: ZRC 2018.0856, male, 19.1 mm CW, Pemburongunan Creek, survey 1A, 1 December 2013.

Pseudosesarma bocourti: ZRC 2018.0879, male, 28.5 mm CW, Sungai Labu (Labu forest reserve), survey 5C, 28-30 March 2014, coll. CD, fixed in 100% propylene glycole.

Pseudosesarma moeschii: ZRC 2018.0920, female, 13.1 mm CW, Sungai Belayang, survey 6A, 15 October 2013. ZRC 2018.0921, ovigerous female, 9.9 mm CW, Sungai Belayang, survey 6A, 15 October 2013. ZRC 2016.0405, male, 13.5 mm CW, Sungai Belayang, survey 6B, 15 October 2013. ZRC 2018.0923, male, 12.0 mm CW, Sungai Labu, survey 5A, exuvia, 29 November 2013, coll. LR.

Selatium brockii: ZRC 2018.0847, female, 25.4 mm CW, Pulau Bedukang, survey 2A, inside a hole in a branch of *Sonneratia* sp., 13 October 2013.

Varunidae:

Metaplax elegans: ZRC 2018.0839, male, 11.2 mm CW, Pemburongunan Creek, survey 1A, 1 December 2013.

Metaplax tredecim: ZRC 2018.0849, male, 11.8 mm CW, Pulau Bedukang, survey 2A, 13 October 2013. ZRC 2018.0860, ovigerous female, 11.0 mm CW, Pulau Bedukang, survey 2A, 13 October 2013. ZRC 2018.0854, ovigerous female, 14.2 mm CW, Pemburongunan Creek, survey 1B, 1 December 2013. ZRC 2018.0863, male, 19.5 mm CW, Pemburongunan Creek, survey 1B, 1 December 2013. ZRC 2018.0852, female, 10.4 mm CW, Sungai Besar, survey 3A, 10 October 2013. ZRC 2018.0872, ovigerous female, 13.3 mm CW, Sungai Besar, survey 3B, 10 Oct. 2013. ZRC 2018.0846, male, 13.8 mm CW, Sungai Bunga, survey 4A, 8 October 2013.

Varuna yui: ZRC 2018.0851, male, 18.3 mm CW, Pemburongunan Creek, 1C, 1-12-13.

Appendix 2 - Examined comparative material from the crab collection of the Lee Kong Chian Natural History Museum of Singapore (ZRC).

Grapsidae:

Metopograpsus frontalis: ZRC 2008.0213, 1 male and 1 female, Singapore.

Metopograpsus latifrons: ZRC 2001.2296, 1 male, Singapore.

Metopograpsus oceanicus: ZRC 2003.0716, 1 male, Indonesia (Anambas Island).

Sesarmidae:

Episesarma chentongense: ZRC 1997.699, 1 male, Singapore. ZRC 1987.458-459, 1 male and 1 female, Singapore.

Episesarma lafondii: ZRC 2004.0468, 1 male, Philippines.

Episesarma mederi: ZRC 2004.0469, 1 male and 1 female, Philippines. ZRC 2008.1292, 1 female, Singapore.

Episesarma palawanense: ZRC 1967.7.15.3, 1 male, Singapore.

Episesarma singaporense: ZRC 2011.0173, 1 male and 1 female, Singapore. ZRC 2011.0190, 2 males, Singapore. ZRC 2012.0314, 1 male, Singapore. ZRC 1999.1141, 1 male, Malaysia (Sarawak). ZRC 1998.1177, 1 male and 1 female, Thailand.

Episesarma versicolor: ZRC 1996.218-220, 1 male and 1 female, Singapore. ZRC 2001.1068, 1 male, Thailand (Phuket). ZRC 2000.2624, 1 male and 1 female, Thailand (Phuket). ZRC 2012.0339, 1 male and 1 female, Singapore. ZRC 2012.0279, 1 male, Singapore.

Fasciarma fasciatum: ZRC 1965.8.2.146-155, 1 male and 1 female, Labuan.

Geosesarma peraccae: ZRC 2009.0311, 1 male, Singapore.

Nanosesarma batavicum: ZRC 1964.9.3.46-56, 1 male and 1 female, Malaysia (Penang).

Nanosesarma minutum: ZRC 2009.0325, 1 male and 1 female, Taiwan.

Nanosesarma pontianacense: ZRC 2001.2281, 1 female, Singapore. ZRC 1999.1166, 1 male and 1 female, Singapore.

Neosarmatium fourmanoiri: ZRC 2002.0180, 1 male and 1 female, Guam.

Neosarmatium indicum: ZRC 2000.1842, 1 male, Taiwan.

Neosarmatium malabaricum: ZRC 1972.12.4.1-10, 1 male and 1 female, Sri Lanka.

Neosarmatium meinerti: ZRC 1997.660, 1 male and 1 female, Taiwan.

Neosarmatium punctatum: ZRC 2000.0104, 1 male, Taiwan.

Neosarmatium rotundifrons: ZRC 1997.657, 1 male and 1 female, Taiwan.

Neosarmatium smithi: ZRC 2012.0276, 1 male, Singapore.

Neosarmatium spinicarpus: ZRC 1964.9.3.502-503, 1 male, Malaysia (Sarawak).

Neosarmatium trispinosum: ZRC 2002.0178, 1 male, Guam.

Parasesarma batavianum: ZRC 1972.1.29.1, 1 male, Indonesia (Muara Baru). ZRC 1964.8.12.161-169, 2 males, Singapore.

Parasesarma bengalense: ZRC 2001.0994, 1 male, India.

Parasesarma bidens: ZRC 2012.0030, 1 male and 1 female, Hong Kong. ZRC 1975.6.30.11, 1 male, Japan.

Parasesarma brevicristatum: ZRC 1972.3.7.3, 1 male, Australia (Queensland).

Parasesarma eumolpe: ZRC 2009.0324, 2 males and 2 females, Singapore. ZRC 170209, 1 male, Singapore. ZRC 1972.3.6.9, 1 female, Singapore. ZRC 1993.238-239, 1 male, Singapore. ZRC 2012.0282, 3 males, Singapore. ZRC 1965.8.2.158-160, 2 males and 1 female, Malaysia (Pahang).

Parasesarma foresti: ZRC 2002.0608, 1 male, Indonesia (Papua, Portsite, Tipocka).

Parasesarma guttatum: ZRC 2003.0204, 1 male, Kenya.

Parasesarma indiarum: ZRC 1995.450, 1 male, Singapore. ZRC 2000.1658, 1 male and 1 female, Malaysia (Sabah). ZRC 2012.0243, 1 male, Singapore.

Parasesarma lepidum: ZRC 1964.9.3.466-487, 1 male, Malaysia (Labuan).

Parasesarma maipoense: ZRC 2009.0800, 1 male and 1 female, Vietnam.

Parasesarma melissa: ZRC 1967.11.20.6, 1 male, Singapore.

Parasesarma cf. *messa*: ZRC 2003.0483, 1 male and 1 female, Indonesia (Irian Jaya).

Parasesarma onychophorum: ZRC 2000.1766, 2 males and 1 female, Malaysia (Johor). ZRC 2000.1434, 2 males and 3 females, Malaysia (Penang).

Parasesarma pictum: ZRC 2000.2049, 1 male, Indonesia (Guam).

Parasesarma plicatum: ZRC 1969.1.4.1, 1 male, India (Bombay). ZRC 1999.0566, 1 male, Indonesia. ZRC 2010.0078, 1 male and 1 female, Pakistan.

Parasesarma rutilimanum: ZRC 2000.1907, 3 males and 3 females, Thailand.

Parasesarma semperi: ZRC 2003.0485, 1 male and 1 female, Indonesia (Irian Jaya).

Parasesarma ungulatum: ZRC 1999.0566, 1 male and 1 female, Thailand. ZRC 2008.0903, 1 male and 3 females, Philippines.

Perisesarma dussumieri: ZRC 1965.8.2.68-69, 1 male and 1 female, Singapore. ZRC 2000.1435, 1 female, Malaysia (Penang). ZRC 1987.558-559, 1 male, Malaysia (Langkawi).

Pseudosesarma bocourti: ZRC 1995.225, 1 male, Malaysia (Sarawak). ZRC 1996.1724, 1 male and 1 female, Malaysia (Tioman Island). ZRC 2000.0952, 1 male, Thailand.

Pseudosesarma crassimanum: ZRC 1999.0957, 2 males and 1 female, Malaysia (Tioman Island).

Pseudosesarma edwardsii: ZRC 2003.0084, 1 male, Singapore.

Pseudosesarma patshuni: ZRC 2012.0032, 1 male and 1 female, Hong Kong.

Selatium brockii: ZRC 2011.0181, 2 males and 1 female, Singapore. ZRC 2012.0323, 2 males and 2 females, Singapore. ZRC 2012.0350, 1 male and 1 female, Singapore.

Selatium elongatum: ZRC 2008.0481, 1 male and 1 female, Indonesia (North Sulawesi). ZRC 2009.0567, 1 male, Papua.

Varunidae:

Metaplax crenulata: ZRC 1997.696, 1 male and 1 female, Singapore.

Metaplax elegans: ZRC 2011.0193, 1 male and 1 female, Singapore.

Varuna yui: ZRC 2008.1258, 1 male, Taiwan.