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Systematic studies on the major groups
of stomatopods (Crustacea: Malacostraca:
Hoplocarida) from Indo-West Pacific region

인도-서태평양 해역에 서식하는 주요 구각류
(갑각아문: 연갑강: 자하아강)의 계통분류학적 연구

2019 년 08 월

서울대학교 대학원

생명과학부

황희승

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**Systematic studies on the major groups
of stomatopods (Crustacea: Malacostraca: Hoplocarida)
from Indo-West Pacific region**

**A dissertation submitted in partial fulfillment
of the requirement for the degree of**

**DOCTOR OF PHILOSOPHY
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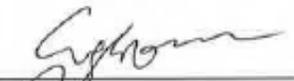
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ABSTRACT

Systematic studies on the major groups of stomatopods (Crustacea: Malacostraca: Hoplocarida) from Indo-West Pacific region

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Among stomatopods from the Indo-West Pacific region, systematic studies were conducted on the major groups that use main identification key characters requiring taxonomic revision (telson tooth, rostral plate, and carina). For the comparison of morphological characters, the Korean specimens were collected from the intertidal zones and subtidal zones of the continental shelf between the year 1991 and 2019 and the overseas specimens were loaned from fourteen museums worldwide and were observed. For the comparison of molecular characters, mitochondrial COI gene sequences were used. In chapter 1, the taxonomic reviews of the genus *Taku* and *Chorisquilla* as the group related to telson tooth were conducted. First, genus *Taku* from throughout its range based on morphological and

molecular data was reconsidered and it has revealed the presence of two discrete species: *T. spinosocarinatus* sensu stricto and *T. pruvotae* which are removed from the synonymy of *T. spinosocarinatus*. As a result of the taxonomic review of *Chorisquilla* species, a species known as *C. spinosissima* in Korea was identified as new species, *C. orientalis* and *C. mehtae* which has not been adequately illustrated, was redescribed. In chapter 2, the taxonomic reviews of the genus *Gonodactylaceus* and *Gonodactylus* as the group related to rostral plate were conducted. In particular, *Gonodactylaceus falcatus* from throughout its range using morphological and molecular data, the species was newly identified as four discrete species: *G. falcatus* sensu stricto, *G. siamensis*, *G. gravieri*, *G. mutatus*, *G. insularis*. In chapter 3, the taxonomic reviews of seven genera (*Oratosquilla*, *Levisquilla*, *Anchisquilla*, *Cloridopsis*, *Miyakella*, *Squilloides*, and *Kempella*) belonging to Squilloids, one genus *Faughnia* belonging to Parasquilloids, two genera (*Acaenosquilla* and *Acanthosquilla*) belonging to Lysiosquilloids as the group related to carina were conducted. In chapter 4, the systematic study of Korean stomatopods was conducted and it resulted in discovery six first records of species from Korean waters: four Squilloids (*Levisquilla inermis* (Manning, 1965), *Levisquilla jurichi* (Makarov, 1979a), *Anchisquilla fasciata* (de Haan, 1844), and *Cloridopsis scorpio* (Latreille, 1828)) and two Lysiosquilloids which also reported for the first time from Korean waters (*Acaenosquilla latifrons* (de Haan, 1844), *Acanthosquilla multifasciata* (Wood-Mason, 1895)). These species were described with taxonomic remarks and illustrated with photographs. As a result of this study, fourteen species of thirteen genera belonging to the seven families of four superfamilies were identified. The keys of all genus and checklist covered in the present study have been updated.

Keywords: Stomatopoda, mantis shrimp, DNA Barcoding, Systematic study, taxonomy, Korean fauna

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CONTENTS

ABSTRACT	i
CONTENTS	v
LIST OF TABLE AND FIGURES	viii
INTRODUCTION	1
STOMATOPOD MORPHOLOGY	5
MATERIALS AND METHODS	9
CHAPTER 1. TAXONOMIC REVISION OF THE SELECTED STOMATOPOD GROUP RELATED TO TELSON TOOTH	
BACKGROUND	15
1-1. TAXONOMIC REVIEW OF THE GENUS <i>TAKU</i> (GONODACTYLOIDEA: TAKUIDAE)	18
INTRODUCTION	18
RESULTS	20
SYSTEMATIC ACCOUNTS	21
DISCUSSION	38
1-2. TAXONOMIC REVIEW OF THE GENUS <i>CHORISQUILLA</i> (GONODACTYLOIDEA: PROTOSQUILLIDAE)	39
INTRODUCTION	39
MATERIALS AND METHODS	39
RESULTS	40

SYSTEMATIC ACCOUNTS 42

CHAPTER 2. TAXONOMIC REVISION OF THE SELECTED STOMATOPOD GROUP RELATED TO ROSTRAL PLATE

2-1. TAXONOMIC REVIEW OF THE GENUS *GONODACTYLACEUS* (GONODACTYLOIDEA: GONODACTYLIDAE) 93

INTRODUCTION 93

MATERIALS AND METHODS 93

SYSTEMATIC ACCOUNTS 96

DISCUSSION 139

2-2. TAXONOMIC REVIEW OF THE GENUS *GONODACTYLUS* (GONODACTYLOIDEA: GONODACTYLIDAE) 141

INTRODUCTION 141

MATERIALS AND METHODS 142

SYSTEMATIC ACCOUNTS 143

CHAPTER 3. TAXONOMIC REVISION OF THE SELECTED STOMATOPOD GROUP RELATED TO CARINA

3-1. TAXONOMIC REVIEW OF THE SEVEN GENERA (SQUILLIOIDEA: SQUILLIDAE) 161

INTRODUCTION 161

MATERIALS AND METHODS 161

RESULTS 166

3-2. TAXONOMIC REVIEW OF THE GENUS <i>FAUGHNIA</i> (PARASQUILLIOIDEA: PARASQUILLIDAE)	230
INTRODUCTION	230
MATERIALS AND METHODS	230
SYSTEMATIC ACCOUNTS	231
3-3. TAXONOMIC REVIEW OF THE GENUS <i>ACANTHOSQUILLA</i> (LYSIOSQUILLIOIDEA: NANOSQUILLIDAE) AND THE GENUS <i>ACAENOSQUILLA</i> (LYSIOSQUILLOIDEA: TETRASQUILLIDAE)	242
INTRODUCTION	242
MATERIALS AND METHODS	242
SYSTEMATIC ACCOUNTS	243
CHAPTER 4. FAUNAL STUDY OF KOREAN STOMATOPODS	
INTRODUCTION	268
MATERIALS AND METHODS	268
SYSTEMATIC ACCOUNTS	275
DISCUSSION	319
CONCLUSION	320
REFERENCES	323
ABSTRACT(KOREAN)	341

LIST OF TABLE AND FIGURES

Table 1. Detailed collection localities in Korea

Fig. 1. Morphological terms used in descriptive accounts for a generalized stomatopod

Fig. 2. Morphology of anterior cephalon

Fig. 3. Carinal terminology used in descriptive accounts, principally applicable to squillids.

Fig. 4. Morphological terms used in descriptive accounts for raptorial claw and endopod of pleopod 1

Fig. 5. Map showing previously recorded locations and new collecting sites

Fig. 6. Abdominal somite 6 and telson of *Dictosquilla miles*, *Squillodies leptosquilla*, *Ahchisquilloides mcneilli*, *Cloridina verrucosa*, *Harpiosquilla stephensoni*, *Oratosquilla stephensoni*

Fig. 7. Neighbor-joining topology of *T. spinosocarinatus* (Fukuda, 1909) and *T. pruvotae* (Gravier, 1930)

Fig. 8. Telson teeth of *Gonodactyloideus rubrus* Ahyong, 2004 and *Taku spinosocarinatus* (Fukuda, 1909)

Fig. 9. *Taku spinosocarinatus* (Fukuda, 1909)

Fig. 10. *Taku spinosocarinatus*, female

Fig. 11. Distribution of *Taku spinosocarinatus* (Fukuda, 1909)

Fig. 12. Distribution of *Taku pruvotae* (Gravier, 1930)

Fig. 13. *Taku pruvotae* (Gravier, 1930), female

Fig. 14. Neighbor-joining topology of *Chorisquilla orientalis* and other *Chorisquilla* species based on COI sequences

Fig. 15. *Chorisquilla mehtae* Erdmann & Manning, 1998.

Fig. 16. Distribution of *Chorisquilla orientalis* Hwang, Ahyong & Kim, 2018

Fig. 17. *Chorisquilla orientalis* Hwang, Ahyong & Kim, 2018

Fig. 18. *Chorisquilla orientalis* male.

Fig. 19. *Chorisquilla orientalis* juvenile male paratype

Fig. 20. Distribution of *Chorisquilla mehtae* Erdmann & Manning, 1998

- Fig. 21.** *Chorisquilla mehtae* Erdmann & Manning, 1998
- Fig. 22.** Distribution of *Chorisquilla brooksii* (de Man, 1888)
- Fig. 23.** *Chorisquilla brooksii* (de Man, 1888)
- Fig. 24.** Distribution of *Chorisquilla andamanica* Manning, 1975
- Fig. 25.** Distribution of *Chorisquilla convoluta* Ahyong, 2001
- Fig. 26.** Distribution of *Chorisquilla excavata* (Miers, 1880)
- Fig. 27.** Distribution of *Chorisquilla convoluta* Ahyong, 2001
- Fig. 28.** Distribution of *Chorisquilla gyrosa* (Odhner, 1923)
- Fig. 29.** *Chorisquilla gyrosa* (Odhner, 1923)
- Fig. 30.** Distribution of *Chorisquilla kroppi* Ahyong & Erdmann, 2003
- Fig. 31.** Distribution of *Chorisquilla pococki* Manning, 1975
- Fig. 32.** *Chorisquilla pococki* Manning, 1975.
- Fig. 33.** Distribution of *Chorisquilla quinquelobata* (Gordon, 1935)
- Fig. 34.** *Chorisquilla quinquelobata* (Gordon, 1935)
- Fig. 35.** Distribution of *Chorisquilla similis* Ahyong, 2002
- Fig. 36.** Distribution of *Chorisquilla spinosissima* (Pfeffer, 1888)
- Fig. 37.** *Chorisquilla spinosissima* (Pfeffer, 1888).
- Fig. 38.** Distribution of *Chorisquilla hystrix* (Nobili, 1899)
- Fig. 39.** *Chorisquilla hystrix* (Nobili, 1899)
- Fig. 40.** Distribution of *Chorisquilla tweediei* (Serène, 1950)
- Fig. 41.** *Chorisquilla tweediei* (Serène, 1950)
- Fig. 42.** Distribution of *Chorisquilla trigibbosa* (Hansen, 1926)
- Fig. 43.** Distribution of *Chorisquilla tuberculata* (Borradaile, 1907)
- Fig. 44.** Cephalon of *Gonodactylaceus falcatus* (Forskål, 1775) and *Gonodactylaceus insularis* Manning & Reaka, 1982
- Fig. 45.** Anterior cephalon and rostral plate of *Gonodactylaceus falcatus* (Forskål, 1775) and *Gonodactylaceus insularis* Manning & Reaka, 1982
- Fig. 46.** Ventral of telson of *Gonodactylaceus siamensis* Manning & Reaka and *Gonodactylaceus insularis* Manning & Reaka, 1982

- Fig. 47.** Abdominal somites 5–6, telson and uropod of *Gonodactylaceus insularis* Manning & Reaka, 1982 and *Gonodactylaceus siamensis* Manning & Reaka
- Fig. 48.** Neighbor-joining (NJ) tree of COI sequences from four nominal species of *Gonodactylaceus falcatus*, four *Gonodactylaceus* species, and outgroup.
- Fig. 49.** Distribution of *Gonodactylaceus falcatus* (Forskål, 1775)
- Fig. 50.** *Gonodactylaceus falcatus* (Forskål, 1775), female
- Fig. 51.** Distribution of *Gonodactylaceus siamensis* Manning & Reaka, 1981
- Fig. 52.** *Gonodactylaceus siamensis* Manning & Reaka, 1981
- Fig. 53.** *Gonodactylaceus siamensis* Manning & Reaka, 1981, male
- Fig. 54.** Distribution of *Gonodactylaceus insularis* Manning & Reaka, 1982
- Fig. 55.** *Gonodactylaceus insularis* Manning & Reaka, 1982
- Fig. 56.** *Gonodactylaceus insularis* Manning & Reaka, 1982, female
- Fig. 57.** Distribution of *Gonodactylaceus mutatus* Lanchester, 1903
- Fig. 58.** Rostral plate and telson of *Gonodactylaceus mutatus* Lanchester, 1903
- Fig. 59.** Distribution of *Gonodactylaceus glabrous* (Brooks, 1886)
- Fig. 60.** *Gonodactylaceus glabrous* (Brooks, 1886)
- Fig. 61.** Distribution of *Gonodactylaceus ternatensis* (de Man, 1902)
- Fig. 62.** *Gonodactylaceus ternatensis* (de Man, 1902)
- Fig. 63.** Distribution of *Gonodactylaceus graphurus* (Miers, 1875)
- Fig. 64.** *Gonodactylaceus graphurus* (Miers, 1875)
- Fig. 65.** Distribution of *Gonodactylaceus randalli* (Manning, 1978)
- Fig. 66.** *Gonodactylaceus randalli* (Manning, 1978)
- Fig. 67.** Distribution of *Gonodactylus childi* Manning, 1971
- Fig. 68.** *Gonodactylus childi* Manning, 1971
- Fig. 69.** Distribution of *Gonodactylus chiragra* (Fabricius, 1781)
- Fig. 70.** *Gonodactylus chiragra* (Fabricius, 1781)
- Fig. 71.** Distribution of *Gonodactylus platysoma* Wood-Mason, 1895
- Fig. 72.** *Gonodactylus platysoma* Wood-Mason, 1895
- Fig. 73.** Distribution of *Gonodactylus smithii* Pocock, 1893

- Fig. 74.** *Gonodactylus smithii* Pocock, 1893
- Fig. 75.** Distribution of *Gonodactylus acutirostris* de Man, 1898
- Fig. 76.** Distribution of *Gonodactylus botti* Manning, 1975
- Fig. 77.** Anterior cephalon of *Oratosquilla fabricii* (Holthuis, 1941)
- Fig. 78.** Lateral processes of thoracic somites 5–8 of *Oratosquilla fabricii* (Holthuis, 1941)
- Fig. 79.** Raptorial claw carpus of *Oratosquilla fabricii* (Holthuis, 1941)
- Fig. 80.** Neighbor-joining (NJ) tree of COI sequences from 18 Korean *Oratosquilla oratoria* and Outgroup
- Fig. 81.** Distribution of *Oratosquilla oratoria* (De Haan, 1844)
- Fig. 82.** *Oratosquilla oratoria* (De Haan, 1844)
- Fig. 83.** Distribution of *Oratosquilla fabricii* (Holthuis, 1941)
- Fig. 84.** Distribution of *Oratosquilla mauritania* (Kemp, 1913)
- Fig. 85.** Distribution of *Levisquilla inermis* (Manning, 1965)
- Fig. 86.** *Levisquilla inermis* (Manning, 1965)
- Fig. 87.** Distribution of *Levisquilla inermis* (Manning, 1965)
- Fig. 88.** *Levisquilla inermis* (Manning, 1965)
- Fig. 89.** Distribution of *Levisquilla minor* (Jurich, 1904)
- Fig. 90.** Telson, ventral view of *A. subfasciata* (Tate, 1883), *A. fasciata* (de Haan, 1844), and *A. chani* Ahyong, 2001
- Fig. 91.** Distribution of *Anchisquilla fasciata* (de Haan, 1844)
- Fig. 92.** *Anchisquilla fasciata* (de Haan, 1844)
- Fig. 93.** Ventral telson of *Anchisquilla fasciata* (de Haan, 1844)
- Fig. 94.** Distribution of *Anchisquilla subfasciata* (Tate, 1883)
- Fig. 95.** *Anchisquilla subfasciata* (Tate, 1883)
- Fig. 96.** Distribution of *Anchisquilla chani* Ahyong, 2001
- Fig. 97.** *Anchisquilla chani* Ahyong, 2001
- Fig. 98.** Distribution of *Anchisquilla chani* Ahyong, 2001
- Fig. 99.** *Anchisquilla chani* Ahyong, 2001
- Fig. 100.** Lateral process of thoracic somite 5 of *Squilloides leptosquilla*

- Fig. 101.** Telson variation of *Squilloides leptosquilla*
- Fig. 102.** Distribution of *Squilloides leptosquilla* (Wood-Mason, 1891)
- Fig. 103.** Distribution of *Squilloides tenuispinis* (Wood-Mason, 1891)
- Fig. 104.** Distribution of *Kempella mikado* (Kemp & Chopra, 1921)
- Fig. 105.** *Kempella mikado* (Kemp & Chopra, 1921)
- Fig. 106.** Distribution of *Kempella stridulans* (Wood-Mason, in Alcock, 1894)
- Fig. 107.** *Kempella stridulans* (Wood-Mason, in Alcock, 1894)
- Fig. 108.** *Cloridopsis scorpio* (Latreille, 1828)
- Fig. 109.** Distribution of *Cloridopsis scorpio* (Latreille, 1828)
- Fig. 110.** *Cloridopsis scorpio*, female
- Fig. 111.** Distribution of *Cloridopsis terrareginensis* (Stephenson, 1953).
- Fig. 112.** *Cloridopsis terrareginensis* (Stephenson, 1953).
- Fig. 113.** Distribution of *Cloridopsis immaculata* (Kemp, 1913)
- Fig. 114.** *Cloridopsis immaculata* (Kemp, 1913)
- Fig. 115.** Distribution of *Cloridopsis gibba* (Nobili, 1903)
- Fig. 116.** Distribution of *Cloridopsis bengalensis* (Tiwari & Biswas, 1952)
- Fig. 117.** Distribution of *Cloridopsis dubia* (H. Milne Edwards, 1837)
- Fig. 118.** Distribution of *Miyakella nepa* (Latreille, 1828)
- Fig. 119.** *Miyakella nepa* (Latreille, 1828)
- Fig. 120.** Distribution of *Miyakella holoschista* (Kemp, 1911)
- Fig. 121.** *Miyakella holoschista* (Kemp, 1911)
- Fig. 122.** Distribution of *Faughnia formosae* Manning & Chan, 1997
- Fig. 123.** *Faughnia formosae* Manning & Chan, 1997.
- Fig. 124.** Distribution of *Faughnia haani* (Holthuis, 1959)
- Fig. 125.** *Faughnia haani* (Holthuis, 1959).
- Fig. 126.** Distribution of *Faughnia serenei* Moosa, 1982
- Fig. 127.** *Faughnia serenei* Moosa, 1982
- Fig. 128.** Distribution of *Faughnia profunda*
- Fig. 129.** Distribution of *Acaenosquilla brazieri* (Miers, 1880)

- Fig. 130.** Distribution of *Acaenosquilla latifrons* (de Haan, 1844)
- Fig. 131.** *Acaenosquilla latifrons* (de Haan, 1844)
- Fig. 132.** Distribution of *Acanthosquilla derijardi* Manning, 1970
- Fig. 133.** *Acanthosquilla derijardi* Manning, 1970
- Fig. 134.** Distribution of *Acanthosquilla multifasciata* (Wood-Mason, 1895)
- Fig. 135.** *Acanthosquilla multifasciata* (Wood-Mason, 1895)
- Fig. 136.** Distribution of *Acanthosquilla melissae* Ahyong, 2008
- Fig. 137.** *Acanthosquilla melissae* Ahyong, 2008
- Fig. 138.** Distribution of *Acanthosquilla manningi* Makarov, 1979b
- Fig. 139.** Distribution of *Acanthosquilla crosnieri* Ahyong, 2002
- Fig. 140.** Distribution of *Acanthosquilla tigrina*
- Fig. 141.** Distribution of *Acanthosquilla wilsoni* Moosa, 1973
- Fig. 142.** Distribution of *Acanthosquilla multispinosa* Blumstein, 1974
- Fig. 143.** Distribution of *Acanthosquilla multifasciata* (Wood-Mason, 1895) in Korea
- Fig. 144.** *Acanthosquilla multifasciata* (Wood-Mason, 1895)
- Fig. 145.** Distribution of *Acaenosquilla latifrons* (de Haan, 1844) in Korea
- Fig. 146.** *Acaenosquilla latifrons* (de Haan, 1844)
- Fig. 147.** Distribution of *Levisquilla inermis* (Manning, 1965) in Korea
- Fig. 148.** *Levisquilla inermis* (Manning, 1965)
- Fig. 149.** Distribution of *Levisquilla jurichi* (Makarov, 1979a) in Korea
- Fig. 150.** *Levisquilla jurichi* (Makarov, 1979a)
- Fig. 151.** Distribution of *Anchisquilla fasciata* (de Haan, 1844) in Korea
- Fig. 152.** *Anchisquilla fasciata* (de Haan, 1844)
- Fig. 153.** Distribution of *Cloridopsis scorpio* (Latreille in Latreille et al., 1828) in Korea
- Fig. 154.** *Cloridopsis scorpio* (Latreille in Latreille et al., 1828)
- Fig. 155.** Distribution of *Kempella mikado* (Kemp & Chopra, 1921) in Korea
- Fig. 156.** Distribution of *Oratosquilla oratoria* (De Haan, 1844) in Korea
- Fig. 157.** *Oratosquilla oratoria* (De Haan, 1844)
- Fig. 158.** Distribution of *Squilloides leptosquilla* (Brooks, 1886) in Korea

- Fig. 159.** Distribution of *Gonodactylaceus falcatus* (Forskål, 1775) in Korea
- Fig. 160.** *Gonodactylaceus falcatus* (Forskål, 1775)
- Fig. 161.** *Gonodactylaceus falcatus*, male
- Fig. 162.** Distribution of *Taku spinosocarinatus* (Fukuda, 1909) in Korea
- Fig. 163.** *Taku spinosocarinatus* (Fukuda, 1909)
- Fig. 164.** Distribution of *Chorisquilla orientalis* Hwang, Ah Yong & Kim, 2018 in Korea.
- Fig. 165.** *Chorisquilla orientalis* Hwang, Ah Yong & Kim, 2018
- Fig. 166.** *Chorisquilla orientalis* Hwang, Ah Yong & Kim, 2018, postlarvae
- Fig. 167.** Distribution of *Odontodactylus japonicus* (de Haan, 1844)
- Fig. 168.** Distribution of *Faughnia formosae* Manning & Chan, 1997 in Korea.
- Fig. 169.** *Faughnia formosae* Manning & Chan, 1997
- Fig. 170.** *Faughnia formosae* Manning & Chan, 1997, male

INTRODUCTION

The order Stomatopoda belonging to the subphylum Crustacea is one of the most morphologically diverse taxa, and the members are aggressive predators. Stomatopods occupy a wide range of continental shelf or slope habitats, from the shore down to about 1500 m. They are common and conspicuous on coral reefs and abundant on soft, level substrates. Although most speciose in tropical and subtropical waters, some stomatopods occur in temperate and even subantarctic waters (Ahyong, 2012). Their trademark morphological features are the second maxilliped modified as large raptorial appendages and highly specialized eyes, which may be the most complex of any invertebrate. Since the last three segments of the second maxilliped fold against each other forming a raptorial claw resembles the forelegs of the praying mantis insect, the common name is mantis shrimp (Ahyong, 2001). Prey is captured by “spearing” or “smashing” according to whether the dactylus of the raptorial claw is extended or held folded during the strike. The movement is one of the fastest known animal movements and these two methods of prey capture distinguished two broad functional groups: the “spearers” and the “smashers” (Caldwell & Dingle, 1976).

A number of species are commercially exploited in several countries of the world. The most fisheries are *Oratosquilla oratoria* (De Haan, 1844) in Japan of East Asia and *Squilla mantis* (Linnaeus, 1758) in the Mediterranean Sea, with artisanal fisheries for catching various squillids and lysiosquillids in the Indo-Pacific region. Recently, it turned out to be a useful bioindicator of marine pollution stress on coral reefs (Erdmann & Caldwell, 1997; Erdmann & Sisovann, 1998) and it is considered an ecologically important group.

WORLD STUDIES

The taxonomy of the Stomatopoda has been extensively conducted over the past four decades worldwide. Like most other invertebrate groups, the diversity of the stomatopod Crustacea is highest in the Indo-West Pacific region and contains the

largest proportion (67%) of world stomatopods (Ahyong, 2001, 2012). The foundations of the study of the Indo-West Pacific Stomatopods were conducted by Kemp (1913) who recognized 139 species worldwide, and 98 from the Indo-West Pacific region. Moosa (1986, 1991) made major studies of New Caledonia and Philippine stomatopods, and Manning (1995) revised the Vietnamese fauna. Ahyong (2001) revised the Australian fauna, recognizing 146 species and Hamano (2005) and Ahyong (2012) listed 68 species of Stomatopoda from Japan. 72 species are recorded from New Caledonia (Moosa 1991; Ahyong, 2007), 63 species from Taiwan (Ahyong et al., 2008) and at least 104 species from China Seas (Wang & Liu, 2008), 20 species from New Zealand (Ahyong, 2012). Currently, about 330 species are known from the Indo-West Pacific region, with new species regularly discovered. Consequently, more than 450 species have been described worldwide in 7 superfamilies and 17 families (Ahyong 2001, 2012).

PREVIOUS KOREA STUDIES

Before this systematic study of stomatopod was conducted, only 3 species have previously been recorded in Korean waters: *Oratosquilla oratoria* (De Haan, 1844), *Taku spinosocarinatus* (Fukuda, 1909), and *Chorisquilla spinosissima* (Pfeffer, 1888) (see Kim and Rho, 1969; The Korean Society of Systematic Zoology, 1997). Also, these species have only been reported without taxonomic remarks, including descriptions and illustration. Since then, Hwang et al., (2013) reported that Korean unrecorded species *Faughnia formosae* and Kang et al., (2016) reported that Korean unrecorded species *Kempella mikado* and *Squilloides leptosquilla*. It was only then that the report, including detailed descriptions and illustration, was made. After, Hwang et al., (2018) reported that Korean unrecorded species *Gonodactylaceus falcatus* additionally. Up to date, 7 species of stomatopods are now recorded in the Korean fauna. The number of Korean stomatopod species is less than 2 % of the worldwide stomatopod species. Compared to the reported species of neighboring countries such as 68 species from Japan and 63 species from Taiwan, the research on the Korean stomatopods is relatively poorly studied. Still, numerous Korean

stomatopods remained undiscovered and undescribed. Revisions that reflect the latest taxonomic ranks and classification system are required.

PRESENT STUDIES

For the systematic study of stomatopods, some stomatopod groups from Indo-Pacific region were required taxonomic revision on the identification key characters. In identification of the stomatopod species, 'primary teeth' (submedian, intermediate, and lateral teeth) on telson, rostral plate, a median carinule on the sixth abdominal somite, postanal carina on the telson ventral surface, and carina and groove on the dorsal surface of telson were used. In the case of primary teeth, similar size and shape of spine and denticle between primary teeth can be interpreted as the primary teeth. The identification of the stomatopods can be changed according to the different interpretation of the primary teeth. In some protosquillids, similar size and shape of spine and denticle between primary teeth can be interpreted as the primary teeth. According to Ahyong's comment (2001), the term is applied to all large teeth or processes of the telson margin despite the fact that they may not have been derived in same way. More accurate examination and solid definition of the terminology are necessary. In the case of rostral plate, the characters of the rostral plate generally can be changed according to allometric growth in the relative length of rostral plate and anterior margins of basal portion. The rostral spine is proportionally longest in small specimens and becomes shorter with increasing body size and can become proportionally thicker. Also, the anterior margin of basal portion of the rostral plate slopes more posteriorly in smaller specimens and become transverse or even slightly concave with increasing body size. More accurate examination of the character based on a number of specimens is necessary. Lastly, carina and groove on the dorsal surface of telson also can be misinterpreted. In some Lysiosquillids, the member has very low carina or boss. It can be interpreted as if it does not exist. Therefore, additional morphological traits must be added for accurate identification.

The purpose of this study is to conduct systematic taxonomy studies both for stomatopod species including Korean species that have not been discovered and studied in detail and reexamination of main identification key characters. To

accomplish this, three groups of stomatopods requiring taxonomic revision on the identification key character from Indo-Pacific region were selected. After morphological analysis, then they were examined by DNA barcoding method additionally. Especially, DNA barcoding is useful for identification of organisms that are very rare or young, where morphological identification is challenging. After that, the main identification key characters were re-examined and make clear the terminology definition and morphological traits variation. Consequently, the purpose of this study is to conduct the taxonomic revision and review of the three selected groups of stomatopods from Indo-Pacific region. In each chapter, the taxonomic studies for three stomatopod groups were conducted based on morphological and molecular data, respectively. The contents of each chapter are summarized in the following. Chapter 1 covers the taxonomic study for two stomatopod group identified by terminology ‘primary teeth’ of telson. Chapter 2 provides a taxonomic review of stomatopod group identified by rostral plate. Chapter 3 describes a taxonomic study of stomatopod group identified by carina on the dorsal surface of carapace and telson. Lastly, chapter 4 focuses on the systematic study of Korean stomatopod fauna.

STOMATOPOD MORPHOLOGY

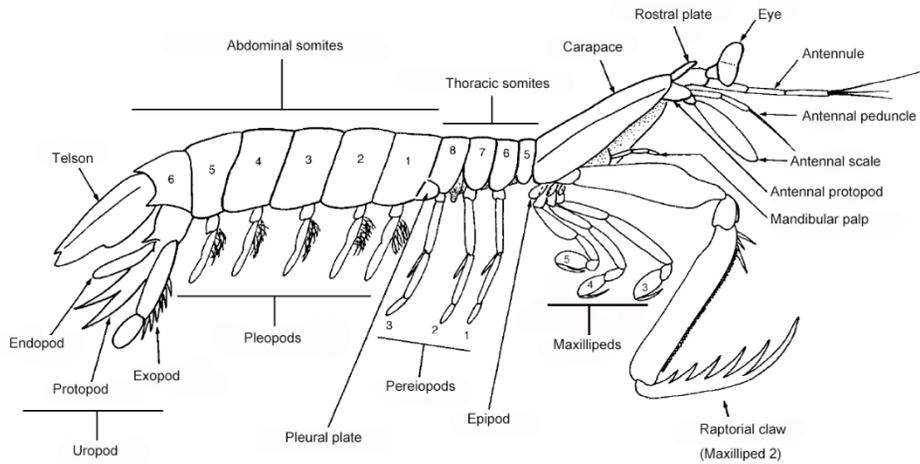


Fig. 1. Morphological terms used in descriptive accounts for a generalized stomatopod. Modified from Ahyong (2001).

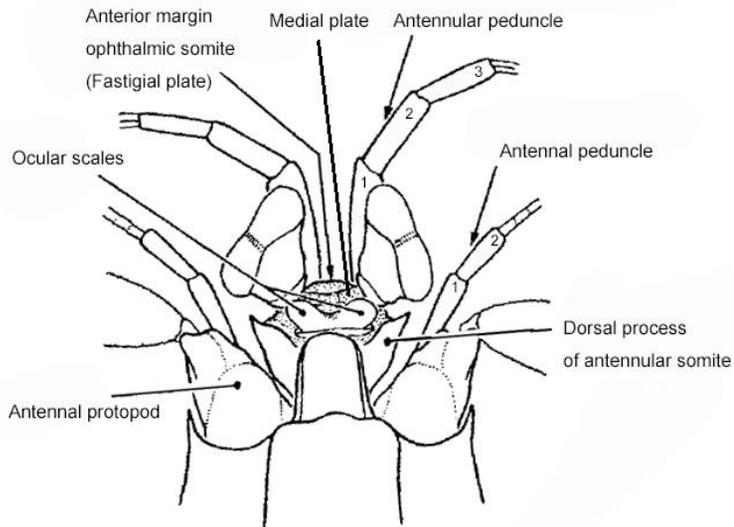


Fig. 2. Morphology of anterior cephalon. Modified from Ahyong (2001).

CEPHALOTHORAX

The cephalothorax consists of a head with ophthalmic somite bearing the eyes, five cephalic somites bearing the antennae, antennules, mandibular palp, maxillae, maxillules, and five thoracomeres bearing maxillipeds 1–5. The anterior cephalon consists of three main plates (fastigial plate, medial plate, and ocular scales). The rostral plate usually conceals the antennular somite and its lateral margins are expanded to form anterolaterally lobes called as “dorsal processes”. In some gonodactyloids, it has a “tri-spinous” form consisting of the slender median spine and a short, broad basal portion in which the anterolateral margins are variable and it is used as key characters in the identification of the species. The carapace is divided longitudinally into three regions by the gastric grooves. The dorsal pit is present in the midline of the carapace. The cervical groove is marked transversely.

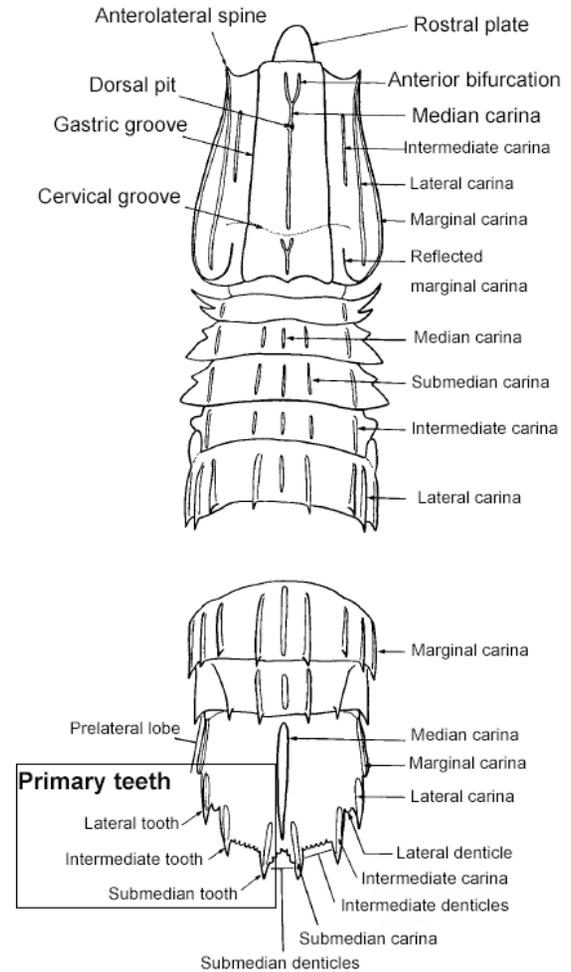


Fig. 3. Carinal terminology used in descriptive accounts, principally applicable to squillids. Modified from Ahyong (2001).

THORAX

Thoracic somites 5–8 are freely articulated. Especially, thoracomere 5 is the shortest of the thoracic somites and carries maxilliped 5. Thoracic somites 6–8 each bear a pair of walking legs termed pereopods 1–3, respectively. In some Squillids, lateral process of the thoracic somites 5–8 is bilobed, or single and it is used as key characters in the identification of the species.

PLEON

The pleon comprise six abdominal somites and a telson. The abdominal somites are wider than the thoracic somites. The dorsal carination of the respective abdominal somites usually has four pairs of dorsal carinae, termed intermediate, submedian, lateral, and marginal. The sixth abdominal somite generally has bosses or carinae. The uropods that articulate laterally are located separately. The pleura is well developed and its first somite carries a rounded, anteriorly projection lobe called a pleural plate. Ventrally, the abdominal somites 1–5 each have paired pleopods. The telson usually has a median carina or boss on the dorsal surface, along with three pairs of teeth that are intervened by rows of small denticles. The three pairs of teeth are distinct in both larvae and adults and are collectively termed primary teeth. Especially, the term is applied to all large teeth or processes of the telson margin despite the case that they may not have been derived in the same way (Ahyong, 2001). The margins between the submedian teeth sometimes have a row of denticles, called as submedian denticles. The intermediate denticles are present on the margin between the intermediate and lateral teeth, and lateral denticles can be present between the intermediate and lateral teeth. Besides telson teeth, the prelateral lobe is present along the anterolateral margin of the telson anterior to the lateral tooth (Ahyong, 2005).

RAPTORIAL CLAW

Among maxillipeds, maxilliped 2 has become enlarged as a powerful raptorial claw. The raptorial claw part is divided into the following parts: ischium, merus, carpus, propodus, and dactylus. The ischium, considerably shorter than the merus, articulates at the proximal end of the merus, called as a terminal articulation. The occlusal margin of the propodus is unarmed or sparsely pectinate and there may be one or two proximal movable spines.

SEXUAL DIMORPHISM

Sexual dimorphism is generally expressed in more accentuated or inflated in male than females. The endopod of pleopod 1 is modified for copulation termed petasma.

The most distinct and important characters of the petasma are flattened and an elongated part called a tube process, an opposing hook process and a flap-like part termed posterior endite. The role of the tube process is unclear, but the hook process is known to be used for a clasp for orientation of the penes during the copulation (Tirmizi & Kazmi, 1984). Depending on the presence or absence of this hook process, gender can be distinguished.

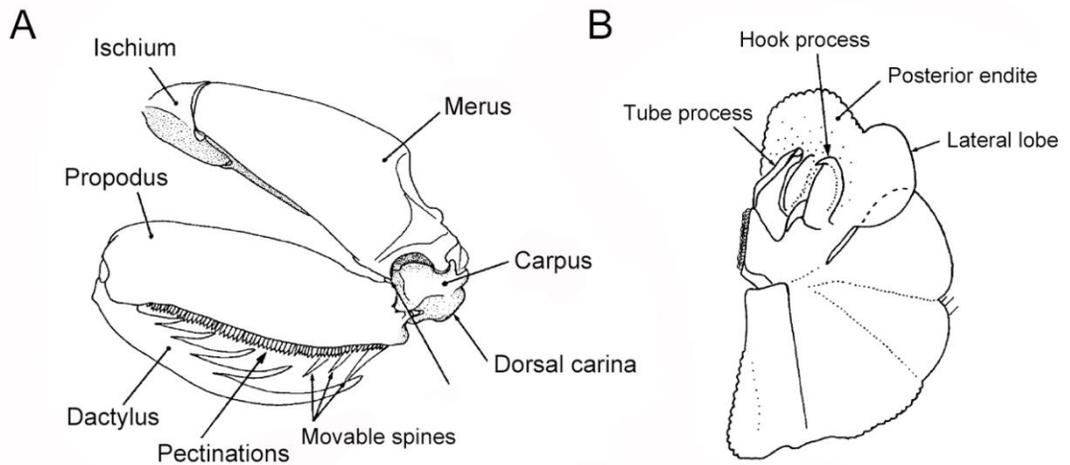


Fig. 4. Morphological terms used in descriptive accounts. A, Raptorial claw; B, endopod of pleopod 1. Modified from Ahyong (2001).

MATERIALS AND METHODS

1. Morphological taxonomic study

Collection and Examination

The Korean specimens examined in this study have been collected in the littoral zone from 1991 to 2019. During the period March 2010 to April 2019, 543 individuals were collected, and remaining specimens are deposited in the Marine Arthropod Depository Bank of Korea (MADBK), Seoul National University from 1991 to 2019. A total of 47 collecting sites were marked on the map along with the previously recorded locations (Fig. 5). Specimens were collected by hands or commercial fishing trawlers or SCUBA diving on the preformed cavities in rubble and reef rock (including mollusk tubes) in coral reefs. All specimens were preserved in 95% ethanol.

All specimen measurements are given in millimeters (mm). Body length, or total length (TL), was measured along the dorsal midline from the apex of the rostral plate to the apex of the submedian teeth of the telson. Carapace length (CL) was measured along the dorsal midline and excluded the rostral plate. The abdominal-width-carapace-length index (AWCLI) is given as $100 \times \text{abdominal somite 5 width} / \text{carapace length}$.

A stereomicroscope (MZ8; Leica, Wetzlar, Germany) was used for observation and sorting. Illustrations were made by a compound microscope equipped with a camera lucida. Photographs of specimens were recorded using a Nikon D200 digital camera and processed with the focus stacking program Helicon Focus (Helicon Soft, Kharkov, Ukraine).

Morphological terminology and size descriptors generally follow Ahyong (2001, 2012).

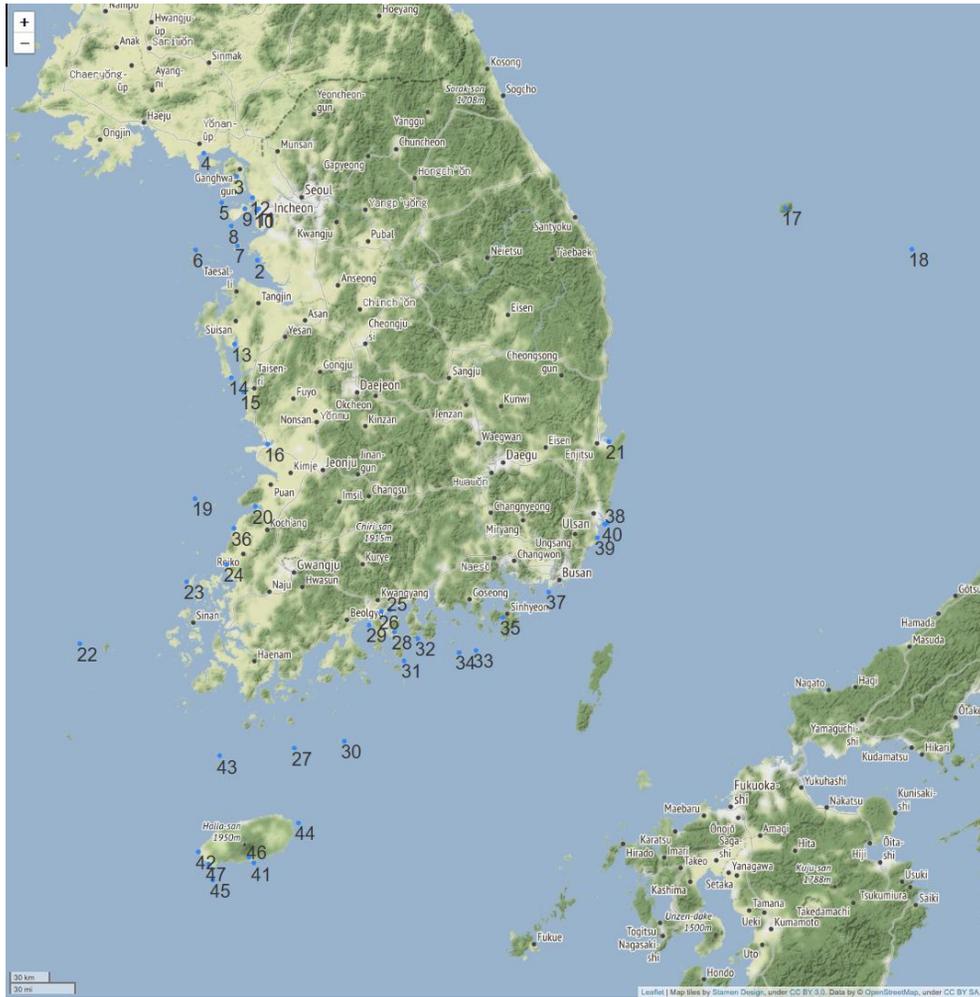


Fig. 5. Map showing previously recorded locations and new collecting sites in the study

Table 1. Detailed collection localities from 1991 to 2019 in Korea

	Collection locality	Latitude (N)	Longitude (E)
Gyeonggi-do			
1	Si-hwa lake, Ansan-si	37°19'26.3"N	126°36'50.9"E
2	Jebudo-Island, Seosin-myeon, Hwaseong-si	37°10'23.7"N	126°37'27.3"E
Incheon			
3	Ganghwado-Island, Ganghwa-gun	37°43'47.4"N	126°27'17.6"E
4	Ganghwa-gun	37°45'57.1"N	126°22'11.2"E
5	Jangbongdo-Island, Ongjin-gun	37°32'16.8"N	126°20'10.8"E
6	Deokjeokdo-Island, Ongjin-gun	37°12'17.5"N	126°12'43.5"E
7	Yeongheungdo-Island, Ongjin-gun	37°15'45.0"N	126°27'42.2"E
8	Muuido-Island, Jung-gu	37°22'16.2"N	126°24'43.7"E
9	Yeongjongdo-Island, Jung-gu	37°30'08.9"N	126°32'05.2"E
10	Dong-gu	37°29'25.1"N	126°37'10.2"E
11	Bukhang, Seo-gu	37°30'22.0"N	126°38'00.1"E
12	Seo-gu	37°34'47.9"N	126°37'36.0"E
Chungcheongnam-do			
13	Seosan-si	36°50'38.3"N	126°19'58.3"E
14	Tae-an-gun	36°40'58.2"N	126°08'39.8"E
15	Daecheon Port, Boryeong-si	36°19'43.0"N	126°30'37.2"E
Chungcheongbuk-do			
16	Gunsan-si	35°55'54.2"N	126°43'55.1"E
17	Ulleungdo-Island, Ulleung-gun	37°30'26.4"N	130°51'23.3"E
18	Dokdo-Island, Ulleung-gun	37°14'27.4"N	131°51'53.3"E
19	Buan-gun	35°37'59.6"N	126°31'15.6"E
20	Gomso Port, Buan-gun	35°35'17.9"N	126°36'16.0"E
21	Pohang-si	36°07'06.4"N	129°24'51.5"E
Jeollanam-do			
22	Hongdo-Island, Sinan-gun	34°41'54.1"N	125°12'03.1"E
23	Injado-Island, Sinan-gun	35°05'07.3"N	126°04'52.9"E
24	Suldo Port, Yeonggwang-gun	35°12'45.6"N	126°22'32.1"E

25	Gwangyang Port, Gwangyang-si	34°55'00.9"N	127°40'52.4"E
26	Gwangyang-si	34°55'03.0"N	127°42'51.8"E
27	Yeoseodo-Island Wando-gun	33°59'11.4"N	126°55'18.7"E
Gyeongsangnam-do			
28	Baekdo-Island, Yeosu-si	34°19'25.7"N	127°28'11.6"E
29	Yeosu-si	34°44'08.3"N	127°44'01.8"E
30	Geomundo-Island, Yeosu-si	34°03'36.3"N	127°19'00.4"E
31	Dolsando-Island, Yeosu-si	34°37'59.7"N	127°45'50.8"E
32	Sejondo-Island, Namhae-gun	34°43'22.5"N	128°00'13.2"E
33	Tongyeong-si	34°50'32.7"N	128°26'06.0"E
34	Yokji-Island, Tongyeong-si,	34°38'15.5"N	128°14'58.8"E
35	Geoje-si	34°51'20.4"N	128°36'00.2"E
36	Gusifo Beach, Gochang-gun	35°26'37.9"N	126°26'04.7"E
Busan			
37	Saha-gu	35°02'54.2"N	128°58'19.4"E
Ulsan			
38	Bangeojin Port, Dong-gu	35°29'07.8"N	129°25'38.9"E
39	Jinha-beach, Ulju-gun	35°23'07.6"N	129°20'38.5"E
40	Ulju-gun	35°19'49.3"N	129°18'24.2"E
Jeju-do			
41	Samdo-Island, Jeju-si	33°31'03.5"N	126°31'27.5"E
42	Chagwido-Island, Jeju-si	33°18'40.5"N	126°08'56.7"E
43	Chujado-Island, Jeju-si	33°57'09.9"N	126°19'14.7"E
44	Udo-Island, Jeju-si	33°29'57.1"N	126°57'11.9"E
45	Marado-Island, Seogwipo-si	33°07'18.3"N	126°16'00.7"E
46	Munseom-Island, Seogwipo-si	33°13'47.1"N	126°33'58.7"E
47	Moseulpo port, Seogwipo-si	33°13'06.4"N	126°15'02.2"E

The overseas specimens examined herein are deposited in the following institutions.

AM	Australian Museum, Sydney, Australia
FLMNH	Florida Museum of Natural History, USA
MNHN	Muséum national d'Histoire naturelle, Paris
MZC	University Museum of Zoology, Cambridge, England
NIBR	National Institute of Biological Resources, Incheon, Korea
NIWA	National Institute of Water and Atmospheric Research, New Zealand
NSMT	National Science Museum, Tokyo, Japan
QM	Queensland Museum, Brisbane, Australia
RMNH	Leiden National Natuurhistorische Museum, National Museum of Natural History Naturalis, Darwinweg 2, Leiden, Netherlands
SMF	Natur-Museum und Forschungsinstitut Senckenberg, Frankfurt am Main, Germany
TM	Tasmanian Museum, Hobart, Australia
USNM	National Museum of Natural History, Smithsonian Institution, Washington D.C. USA
WAM	Western Australian Museum, Perth, Australia
ZRC	Zoological Reference Collection of the Lee Kong Chian Museum of Natural History, Singapore

2. Molecular taxonomic study

Sample collection, DNA extraction, amplification, and sequencing

Stomatopod specimens examined in the present study were sequenced for the DNA Barcoding after morphological identification of species. A total of 68 species representing 14 genera of superfamily Squilloidea, Parasquilloidea, Lysiosquilloidea, and Gonodactyloidea were sampled. They were collected by hands or commercial fishing trawlers or SCUBA diving and were primarily obtained from the collections which are deposited in the Marine Arthropod Depository Bank of Korea (MADBK),

Seoul National University. They were preserved directly in 95% ethyl alcohol after collection. Information on the examined samples with accession numbers is shown in Table 1. The materials for DNA extraction were excised from muscle tissue or gills, or last pleopods. Genomic DNA was extracted using the Qiagen DNeasy Blood and Tissue kit according to the manufacturer's instructions. The primers used for the PCR were LCO1490 (5'-GGT CAA CAA ATC ATA AAG ATA TTG G-3') and HCO2198 (5'-TAA ACT TCA GGG TGA CCA AAA AAT CA-3') for COI (Folmer et al., 1994). All reactions carried out for the amplification of the COI-5' region were run by the following thermal cycling program: 5 min at 94°C followed by 40 cycles of 1 min at 94°C, 1 min at 40°C, 2 min at 72°C, and a final extension of 72°C for 10 min. The 25 µL PCR reaction mix included 15.7 µL ultrapure water, 5 µL of 5× PCR buffer, 2 µL of each primer (10 µM), 1 µL of dNTP (10 mM), 0.3 µL of Taq polymerase (5 U), and 1 µL of the DNA template. PCR products were purified using the QIAquick PCR Purification Kit (Qiagen). Sequencing reactions were resolved on an ABI 3730 automated DNA sequencer. Sequences were aligned using MUSCLE software (Edgar, 2004). Sequence divergences among individuals were quantified with the Kimura 2-parameter (K2P) distance model (Kimura, 1980) It is known that K2p model offers the best metric when genetic distances are low (Nei & Kumar, 2007). A neighbor-joining (NJ) tree of K2P distances was created in MEGA version 4.0.2 (Tamura et al., 2007). In respective chapters, a molecular taxonomic study was conducted on the respective selected group. The sequences of overseas specimens were downloaded from Genbank. They were selected as outgroups because of the close relationship between the groups which were wanted to compare.

CHAPTER 1.

TAXONOMIC REVISION OF THE SELECTED STOMATOPOD GROUP RELATED TO TELSON TOOTH

BACKGROUND

Telson morphological character can be used as key characters in the identification of the species. Especially, the margins of the telson are usually armed and fundamentally comprise three pairs of teeth. The three pairs of teeth are distinct in both larvae and adults, and are collectively termed primary teeth (submedian, intermediate, and lateral teeth) used as key characters and varies according to genus and family.

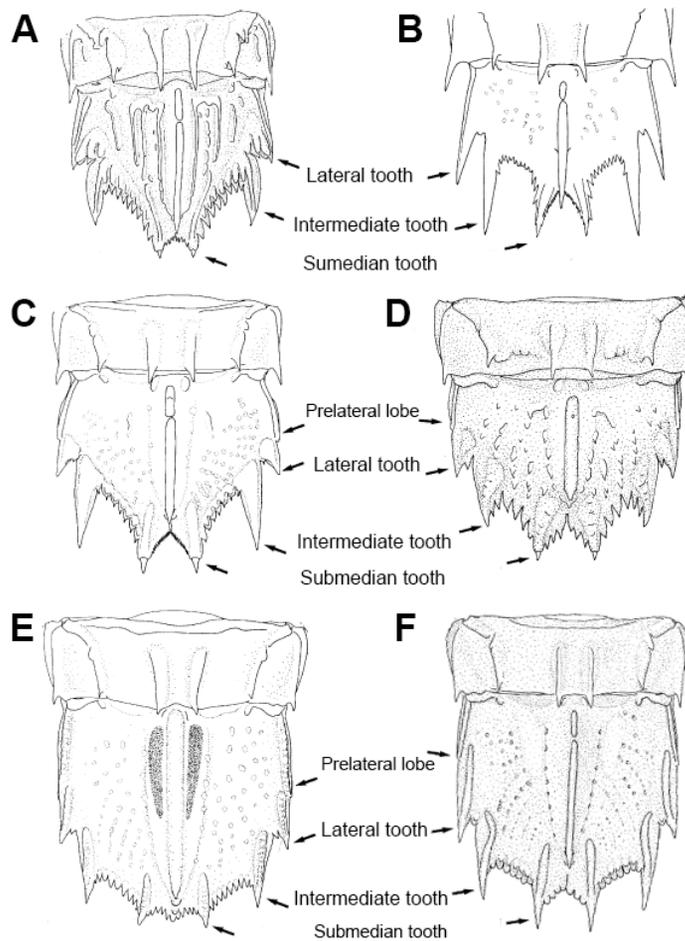


Fig. 6. Abdominal somite 6 and telson. A, *Dictosquilla miles*; B, *Squillodites leptosquilla*. C, *Ahchisquilloides mcneilli*; D, *Cloridina verrucosa*; E, *Harpiosquilla stephensoni*; F, *Oratosquilla stephensoni*. Modified from Ahyong (2005).

On the margin of their telson, similar size and shape of spine and denticle between primary teeth can be interpreted as the primary teeth. According to Ahyong's comment (2001), the term is applied to all large teeth or processes of the telson margin despite the fact that they may not have been derived in same way. The identification of the stomatopods can be changed according to the different interpretation of the primary teeth. In general, the tooth is not easily distinguished from spine and denticle. In case of spine, its shape is sharp-form and it is just projected on the surface, while denticle between primary teeth has relatively blunt shape-form. More accurate examination and solid definition of the 'primary teeth' are necessary.

The takuids and protosquillid species fall under the case. The species *Taku spinosocarinatus* belonging to family Takuidae has generally three pairs of primary teeth (submedian, intermediate teeth, lateral teeth) and 9 appressed carinae on the dorsal surface. The genus *Taku*, was considered monotypic, containing only *T. spinosocarinatus* Fukuda, 1909 [type locality: Okinawa, Japan], but with two primary synonyms, *Gonodactylus strigatus* Hansen, 1926 [type locality: Sulawesi, Indonesia], and *Gonodactylus demani* var. *pruvotae* Gravier, 1936 [type locality: Isle of Pines, New Caledonia]. However, the specimens of *T. spinosocarinatus* from Korea, Vietnam, Indonesia, Taiwan seem to be different species from Australian specimens. Asian samples from Korea, Vietnam, Indonesia, Taiwan show morphological difference from Australian ones in bearing a very tiny tooth and it is considered as lateral tooth among primary teeth. Accordingly, further taxonomic studies on *Taku* species are essential.

Also, the species *Chorisquilla brooksii* belonging to family protosquillidae has generally two pairs of primary teeth (submedian and intermediate teeth) and 4–6 spines on lateral margin. In the specimens, if the lateral tooth is not considered, there are 9–10 spines showing the variation of *C. brooksii* or they could be undescribed species. If the most distal spine is considered as the lateral tooth, the numbers of spines on lateral margin become 7–8 and fall in the range of 6–10 spines on lateral margin and 3 primary teeth on telson of *C. mehtae*. In the case of *C. mehtae*, the species has been reported once from only Indonesia, and only one figure exists. In

the figure, lateral tooth is only indicated as a tiny spine which slightly set off from outline of telson, distinguishing from the lateral 6–10 spines. But the lateral tooth can be easily interpreted as one of the lateral spines, then the number of lateral spines falls in the variation of that of *C. brooksii*. Accordingly, further taxonomic studies on *Chorisquilla* species are necessary.

To accomplish more accurate examination and establish exact definition of the ‘primary teeth’, a taxonomic review of the mantis shrimp genus *Taku* Manning, 1995 is conducted based on morphological and molecular data in the first section of chapter 1. As the other part of chapter 1, a taxonomic review of the mantis shrimp genus *Chorisquilla* Manning, 1969 is conducted based on morphological and molecular data. In respective section, some aspects of telson terminology are clarified about the telson teeth.

1-1. Taxonomic review of the genus *Taku* (Gonodactyloidea: Takuidae)

INTRODUCTION

Taku Manning, 1995, is one of three genera of the Takuidae Manning, 1995, removed from Gonodactylidae Giesbrecht, 1910, chiefly on the basis of their unique uropod form. In takuids, the posterior three spines on the outer margin of the proximal article of the uropodal exopod are immovable and anteriorly recurved – in all other stomatopods, these spines are directed posteriorly and articulated. Like *Mesacturoides* Manning, 1978, *Taku* has well-developed and widely separated submedian teeth on the telson, contrasting with the slender, medially appressed submedian processes of *Mesacturus* Miers, 1880. *Taku* is most closely related to *Mesacturoides* (see Ah Yong & Harling, 2000) but distinguished by the obscure instead on prominent intermediate primary teeth of the telson. *Taku* has long been considered to be monotypic with a wide range in the western Pacific: Japan to New Caledonia, Australia, Indonesia and Vietnam with two nominal species in its synonymy (Ah Yong et al., 2018). In the present study, the taxonomic revision of the mantis shrimp genus *Taku* were conducted and reviewed this genus from throughout its range using both morphological and molecular data, showing the presence of two distinct forms that it can be recognized as two separate species.

MATERIALS AND METHODS

Taku specimens from throughout its range were examined, including type material. The Korean stomatopod specimens were collected by SCUBA diving on the preformed cavities in rubble and reef rock including mollusc tubes in shallow water (intertidal to 35 m) from 2001 to 2015. 34 undamaged individuals of *Taku spinosocarinatus* were sampled and then preserved in 95% ethanol and are deposited in the Marine Arthropod Depository Bank of Korea, Seoul National University,

Seoul, Korea (MADBK) and National Institute of Biological Resources, Incheon, Korea (NIBRIV). For comparison about morphological character, overseas specimens were loaned and the specimens examined herein were deposited Australian Museum, Sydney, Australia (AM); Muséum national d'Histoire naturelle, Paris (MNHN); Natur-Museum und Forschungsinstitut Senckenberg, Frankfurt am Main (SMF); Queensland Museum, Brisbane (QM); and the Zoological Reference Collection of the Lee Kong Chian Museum of Natural History (ZRC).

For comparison about molecular character, the barcoding region of the mitochondrial cytochrome oxidase subunit 1 gene was sequenced from 7 Korean specimens of *T. spinosocarinatus*. Also, 7 sequences from Korean *T. spinosocarinatus* specimens (MADBK 600101_015, MADBK 600101_018, MADBK 600101_019, MADBK 600101_020, MADBK 600101_022, MADBK 600101_029, MADBK 600101_030) are registered in GenBank (Acc. nos. MH137215–MH137221). And they were compared with two published sequences from the Great Barrier Reef, Australia, previously identified as *T. spinosocarinatus* (Acc. nos. HM138811.1, AF205257.1). Additionally, two published sequences from *Gonodactylaceus falcatus* (Forskål, 1775) belonging to Gonodactylidae were selected as the outgroup owing to the close relationship between Takuidae and Gonodactylidae (Ahyong & Harling 2000; Ahyong & Jarman 2009; Porter et al. 2010). Their GenBank Accession numbers are KM 982433.1 and KM 982437.1.

RESULTS

Molecular data

Sequences from Korean specimens and sequences from Australian specimens form two reciprocally monophyletic groups, with internal divergence in COI of 0.0–2.0 % (Korea) and 1.0% (Australia), respectively (Fig. 7). Mean divergence between the Korean group and Australian group lades was 11%, corresponding to separate species. Observed intra-specific and inter-specific divergences among the two species of *Taku* are consistent with those observed for other species of Stomatopoda at <2.4%, >3.0%, respectively (Tang et al. 2010). The group of Korean specimens corresponds to *T. spinosocarinatus* sensu stricto, and the group of Australian specimens to *Gonodactylus demani* var. *pruvotae*, herein removed from synonymy as *Taku pruvotae* (Gravier, 1930) comb. nov.

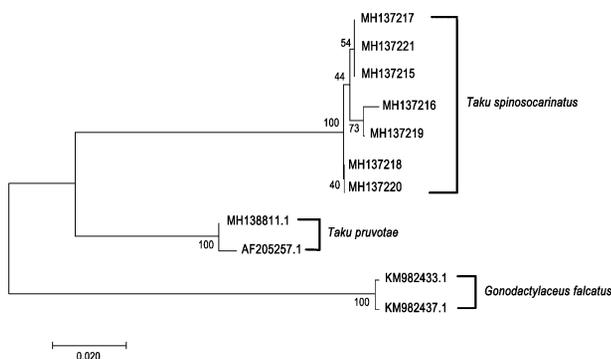


Fig. 7. Neighbor-joining topology of *T. spinosocarinatus* (Fukuda, 1909) and *T. pruvotae* (Gravier, 1930) comb. nov. based on COI sequences, rooted to *Gonodactylaceus falcatus*.

SYSTEMATIC ACCOUNTS

Order Stomatopoda Latreille, 1817

Family Takuidae Manning, 1995

Genus *Taku* Manning, 1995

Taku Manning, 1995: 119 (Type species: *Gonodactylus spinosocarinatus* Fukuda, 1909, by original designation and monotypy).

Diagnosis. Carapace anterolateral angles broadly rounded, extending anteriorly beyond base of rostral plate. Mandibular palp 2-segmented. Maxilliped 1–5 with epipod. Telson wider than long; submedian primary teeth well formed, widely separated, with movable spines; submedian denticles present; intermediate and lateral teeth indistinct, indicated by shallow notch in telson margin; dorsal surface with broad, low median carina flanked by 4 or 5 low, curved, appressed longitudinal carinae (median, accessory medians present or absent, submedian, intermediate, lateral, marginal), occupying almost entire dorsal surface except surface of submedian teeth; median carina more than twice width of submedian, intermediate and lateral carinae; marginal carina distinctly narrower than lateral carina. Uropodal endopod laminar, held horizontally, margins with single row of setae; lacking dorsal or ventral setae.

Composition. *Taku spinosocarinatus* (Fukuda, 1909); *T. pruvotae* (Gravier, 1930).

Remarks. *Taku* was considered to be monotypic, containing only *T. spinosocarinatus* (Fukuda, 1909), with two nominal species in its synonymy: *Gonodactylus strigatus* Hansen, 1926 (Zuid Island, near Saleyer, Indonesia), and *Gonodactylus demani* var. *pruvotae* Gravier, 1930 (Isle of Pines, New Caledonia).

In the present study, two species are recognized in the genus: the type species, *T. spinosocarinatus* (Fukuda, 1909), and *T. pruvotae* (Gravier, 1930).

Telson tooth terminology in *Taku*

Whereas most gonodactyloids have prominent submedian and intermediate teeth, and a clearly indicated lateral tooth on the telson, (Fig. 8A), the marginal armature of the telson in *Taku* is clearly evident only in the well-developed submedian teeth. In *Taku*, the intermediate denticles, intermediate teeth, and lateral teeth are present, but not prominent, being appressed to the telson margins (Fig. 8B): the intermediate denticles immediately precede the low intermediate tooth, and the lateral tooth is indicated by a very short notch.

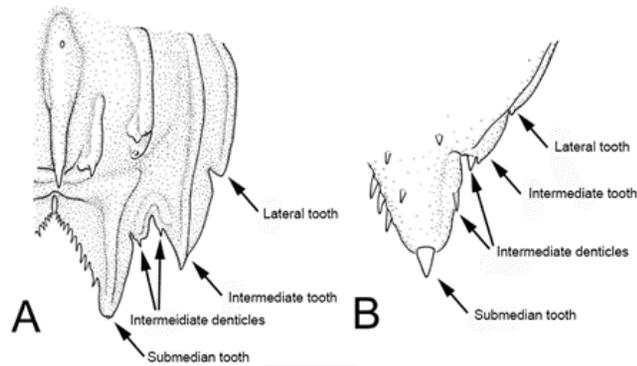


Fig. 8. Telson teeth. *Gonodactyloideus rubrus* Ahyong, 2004, female holotype, TL 48 mm, Philippines, ZRC 2002.0470 (A). *Taku spinosocarinatus* (Fukuda, 1909), male neotype, TL 12 mm, Okinawa, AM P60104 (B). smt, submedian tooth; id, intermediate denticles; it, intermediate tooth; lt, lateral tooth. Scale bars: A = 2.0 mm, B = 0.5 mm.

Key to the species of *Taku* Manning, 1995

1. Telson with well-defined accessory median carinae. Proximal dorsal surface of uropodal protopod with 4 small spines. Rostral plate with anterior margins of basal portion distinctly concave *T. pruvotae*
- Telson without accessory median carinae. Proximal dorsal surface of uropodal protopod with 3 small spines. Rostral plate with anterior margins of basal portion straight to faintly concave, almost transverse *T. spinosocarinatus*

1. *Taku spinosocarinatus* (Fukuda, 1909) (Figs. 9–10)

Gonodactylus spinosocarinatus Fukuda, 1909: 54–56, pl. 5, figs 2, 2a [type locality: Nakamoto, Kuroshima Island, Taketomi Town, Okinawa Prefecture, by neotype designation, Ahyong, 2001]; Fukuda, 1910: 143–145, pl. 4 figs 2, 2a; Serène, 1952: 14–16, figs 28–32; Serène, 1954: 6, 7, 10, 11, fig. 13-10.

Gonodactylus spinosocarinatus: Kemp, 1913: 173–174; 1927: 340–341.

Gonodactylus strigatus Hansen, 1926: 31, pl. 2, fig. 2 [type locality: near Saleyer, Sulawesi, Indonesia]; Serène, 1949: 225–231.

Mesacturus spinosocarinatus: Manning, 1969: 151, 153; Hamano, 1987: 209; Hamano, 1988: 28, fig. 13c–e.

Mesacturoides spinosocarinatus: Manning, 1978: 3.

Taku spinosocarinatus: Manning, 1995: 10, 11, 21, 120–121, figs. 9j, 65, 66, pl. 23; Moosa, 2000: 427, tab. 1; Ahyong & Davie, 2002: 86 [unnumbered fig.]; Schram & Müller, 2004: 85 [part]; Hamano, 2005: 13, 38–39, fig. 2–9e–g; Ďuriš, 2007: 126; Yeh & Hsueh, 2010: 370–372, fig. 1; Ahyong, 2012b: 247.

Materials examined

Type material

Neotype: AM P60104, male neotype (TL 12 mm), Nakamoto, Kuroshima Island, Taketomi Town, Okinawa Prefecture, Japan, 24°19'N, 124°05'E, coll. K. Nomura, 24 September 1987.

Non type materials

KOREA: Ulleung Island, Dodong-ri, Ulleung-eup, Ulleung-gun, Gyeongsangbuk-do, 37°31'27.69"N, 130°48'22.11"E: MADBK 600101_001, female (TL 28 mm), 26 July 2001; MADBK 600101_002, female (TL 23 mm), 28 July 2001; MADBK 600101_003, female (TL 26 mm), coll. S.H Kim, 19 October 2001; MADBK 600101_006, female (TL 27 mm), 22 January 2006; MADBK 600101_007, female (TL 28 mm), 21 June 2006; MADBK 600101_013, female (TL 26 mm), 25 June 2007; MADBK 600101_015, female (TL 28 mm), 10m, 25 June 2009; MADBK 600101_022, male (TL 25 mm), 8 m, 8 June 2015; MADBK 600101_029, male (TL 19mm), 20m, 26 July 2016; MADBK 600101_030, female (TL 29 mm), 20 m, 26 July 2016.

Dokdo Island, Dokdo-ri, Ulleung-eup, Ulleung-gun, Gyeongsangbuk-do, 37°29'44.93"N, 130°55'51.38"E: NIBRIV0000044635, female (TL 21 mm), coll. I.S Seo, 25 July 2001; MADBK 600101_005, female (TL 18 mm), 20 m, 21 June 2005; MADBK 600101_008, female (TL 24 mm), 21 June 2006; MADBK 600101_014, female (TL 18 mm), 9 October 2008; NIBRIV0000300402, male (TL 24 mm), 18 June 2014; NIBRIV0000300401, female (TL 18 mm), 18 June 2014; NIBR0000300400, female (TL 24 mm), 19 June 2014; MADBK 600101_021, female (TL 31 mm), coll. J.H Park, 4 June 2015; MADBK 600101_023, female (TL 21 mm), 6 July 2016; MADBK 600101_026, female (TL 24 mm), 9 June 2016; MADBK 600101_027, female (TL 19 mm), 9 June 2016; MADBK 600101_028, female (TL 23 mm), 22 June 2016.

Geomundo Island, Geomun-ri, Sasam-myeon, Yeosu-si, Jeollanam-do, 34°02'54.77"N, 127°19'6.01"E: MADBK 600101_004, female (TL 28 mm), 21 June 2002.

Yeondo-ri, Nam-myeon, Yeosu-si, Jeollanam-do, 34°26'04.0"N, 127°48'24.1"E: MADBK 600101_009, female (TL 7 mm), 10 October 2006; MADBK 600101_010,

male (TL 9 mm), 10 October 2006; MADBK 600101_011, male (TL 8 mm), 10 October 2006; MADBK 600101_012, male (TL 9 mm), 10 October 2006.

Seodo-ri, Nam-myeon, Yeosu-si, Jeollanam-do, 34°02'24.3"N, 127°17'22.9"E: MADBK 600101_018, female (TL 32 mm), 24 April 2013.

Baekdo-Island, Geomun-ri, Sasam-myeon, Yeosu-si, Jeollanam-do, 34°01'46.5"N, 127°18'56.2"E: MADBK 600101_017, male (TL 24 mm), 17 April 2012; MADBK 600101_019, female (TL 13 mm), 02 July 2014; MADBK 600101_020, female (TL 19 mm), 02 July 2014.

Munseom- Island, Seogwipo-dong, Seogwipo-si, Jeju Island, 33°14'02.4"N, 126°33'57.6"E: MADBK 600101_016, female (TL 17 mm), 35 m, 14 March 2012.

Nodae-ri, Yokji-myeon, Tongyeong-si, Gyeongsangnam-do, 34°40'55.7"N, 128°14'45.2"E: MADBK 600101_024, female (TL 27 mm), 15 July 2015; MADBK 600101_025, female (TL 26 mm), 20 August 2015.

TAIWAN: ZRC 2009.0573–0574, 1 male (TL 13 mm), 1 female (TL 9 mm), Wanlitong, Pingtung County, 21°59.44'N, 121°42.16'E, inside dead coral rock, lower intertidal coral reefs, coll. P.-W. Hsueh, 15 December 2007.

VIETNAM: AM P12155, 1 female (TL 15 mm), Île Tré, Dam Tré, Cauda Bay, 12°13'N, 109°16'E, coll. R. Serène, 23 August 1949; MNHN Sto742, 1 female (broken, TL 14 mm), Culao, Nhatrang Bay, reefs, coll. W. Dawydoff, June–September 1934.

INDONESIA: USNM 274329, 2 males (TL 10–18 mm), 5 females (TL 9–17 mm), Gili Meno, Lombok, Indonesia, 8°21'68"S, 116°03'83"E, coll. M. Erdmann, August 1994.

Description. Eye (Figs. 9, 10A) elongate, cornea subglobular, reaching almost to or slightly beyond antennular peduncle article 3. Ocular scales, separate, narrower than base of rostral spine, rounded to subtruncate.

Rostral plate (Figs. 9, 10A, C, M–O) with trapezoid basal portion, lateral margins strongly divergent, slightly convex, anterior margin distinctly concave at all sizes, apices sharp but not spiniform; median spine slightly compressed laterally, ventral margin obtusely angular, apex not reaching to proximal margin of cornea.

Antennular peduncle 0.40–0.76 CL. Antennal scale 0.18–0.28 CL.

Raptorial claw (Fig. 10E) propodus occlusal margin sparsely pectinate proximally, without movable spine. Dactylus with shallow basal notch; outer proximal margin strongly inflated; distal occlusal margin minutely serrated.

Thoracic somites (Figs. 9, 10F) 6–8 smooth, with low marginal ridge; somites 6–7 lower lateral margins subtruncate; somite 8 lower lateral margin irregularly rounded.

Male pleopod 1 endopod (Fig. 10H) with posterior endite, lateral lobe absent.

Abdominal somites 1–5 (Figs. 9, 10G, H) smooth dorsally, each with marginal ridge; posterolateral corners rounded, unarmed. Abdominal somite 6 (Fig. 3G) with 6 broad, unarmed, longitudinal carinae (paired submedian, intermediate, lateral); submedian carinae slightly wider than intermediates or laterals. Lateral carina posteriorly, blunt, rounded, slightly produced. AWCLI 718–781.

Telson (Figs. 9, 10G, I) as long as wide, with 8–14 (usually 12 or 13) spiniform submedian denticles. Dorsal surface in specimens \geq TL 15 mm with small scattered spinules along mesial margin of lateral carina, mesial and lateral margins of submedian and intermediate carinae, posterior (especially posterolateral) surfaces of median carinae and few scattered spinules on dorsal surface of submedian teeth, usually also on proximal lateral surfaces of telson including single spinule usually on anterior surface of lateral carina. Median carina low, widest anteriorly, reaching posteriorly to or almost to base of posterior sinus of telson; proximal dorsal pit; accessory median carinae absent; specimens \geq TL \sim 20 mm with margins of posterior half to two-thirds excavated, minutely spinulose, appearing “pinched”.

Uropodal (Figs. 9, 10G, J) exopod proximal article with 6 spines on outer margin, proximal 3 spines straight, articulated, anteriormost spine smallest, distal 3 spines always fixed, recurved anteriorly, anterior spine largest. Protopod without lobes between terminal spines; outer terminal spine longer, wider than inner; dorsal surface with spine above exopod articulation in addition to row of 2–4 (usually 3) blunt spinules or tubercles proximally. Endopod (Figs. 9, 10G, J) outer margin lined with plumose setae; inner margin with 1–4 minute simple setae, usually decreasing in number with increasing body size; length 2.79–4.40 \times width.

Coloration. Color-in-life mostly ivory to light brown. Antennal protopod, pereopod, antennal and antennular peduncle ivory. Rostral plate, most of carapace, thoracic and abdominal somites, and telson largely ivory to light brown. Dactylus of raptorial claw and median boss of telson pink to red.

Measurements. Male (N = 6) TL 8–24 mm, female (N = 28) TL 7–32 mm.

Habitat. Coral reef from preformed cavities in rubble and reef rock including mollusc tubes; intertidal to 35 m.

Remarks. *Taku spinosocarinatus* (as *Gonodactylus*) was originally described from “Jogashima, Sagami” (=Kanagawa Prefecture), Japan, based on two females, TL 15 and 28.5 mm (Fukuda, 1909). Fukuda’s original type material is now lost, and a neotype from Okinawa was designated by Ahyong (2001). *Taku spinosocarinatus* is readily separated from *T. pruvotae* comb. nov. by the absence of the accessory median carinae on the telson, which are well-developed by about TL 15 mm in the latter species; the deep, spinule-lined grooves demarcating the accessory medians, evident in *T. pruvotae*, are absent in *T. spinosocarinatus*. In large specimens (typically > TL 20 mm) of *T. spinosocarinatus*, however, the margins of the posterior half of the median carina in the position of the accessory medians in *T. pruvotae* are weakly excavated, often with denser spinule coverage (giving the posterior half of the median carina a “pinched” appearance) (as can be seen in Fukuda’s original figures, albeit over-emphasized). As a result, Fukuda’s (1909) stylized rendering of the telson of *T. spinosocarinatus* has been misinterpreted as showing eleven dorsal carinae (e.g., Hansen, 1926; Serène, 1952), rather than nine. The absence of accessory median carinae, however, is clear from Fukuda’s (1909) description indicating presence of only nine dorsal carinae (including the marginal carinae). This misinterpretation of the number of dorsal carinae in large specimens of *T. spinosocarinatus*, in combination the only other Japanese specimen reported to date measuring TL 12 mm (Ahyong, 2001), may explain why the distinctness of *T.*

pruvotae has gone unrecognized until now. Other distinctions between *T. spinosocarinatus* and *T. pruvotae* are outlined under the account of the latter. In addition to Gravier's *T. pruvotae* (now recognized as valid), *Gonodactylus strigatus* Hansen, 1926, has also been regarded as a junior synonym of *T. spinosocarinatus* since Serène (1952) synonymized the two nominal species. Given its small size (TL 10 mm), the holotype of *G. strigatus* does not exhibit the full telson ornamentation of larger specimens, complicating assignment to either *T. spinosocarinatus* or *T. pruvotae*. Notably, however, Hansen (1926) emphasized the absence of dorsal telson spinulation in the holotype of *G. strigatus*, which is consistent with similarly-sized *T. spinosocarinatus* but not *T. pruvotae*, in which the spinulation is clearly evident even at TL 9 mm. Additionally, material examined from Vietnam and Serène's (1949) account of an 18 mm female from the same locality (as *G. strigatus*) agree well with *T. spinosocarinatus* sensu stricto. As such, *G. strigatus* is regarded herein as a junior synonym of *T. spinosocarinatus* pending re-examination of the holotype of *G. strigatus* and availability of other Indonesian specimens. The revised distribution of *T. spinosocarinatus*, following recognition of *T. pruvotae*, now includes Japan, Korea, Taiwan, Vietnam and northern Indonesia, whereas *T. pruvotae* is a more southerly occurring species, apparently restricted to the Coral Sea, from New Caledonia to the Great Barrier Reef, Australia.

Allometric variation in *T. spinosocarinatus* is largely evident in the increasing degree of dorsal telson spinulation and general reduction in the number of minute setae on the inner margin of the uropodal endopod: usually 3 or 4 in the smallest specimens, usually 1 or 2 in the largest specimens, although in some specimens, the pattern may be reversed. The telson carinae of *T. spinosocarinatus* are unarmed at TL 10 mm, but by TL 12 mm the margins of the median and inner margins of the submedian carinae have spinules in addition to a few scattered spinules on the intermediate carinae. By about TL 20 mm, the posterior half of the lateral margins of the median carina are slightly excavated and multi-spinulose.

Taku spinosocarinatus evidently matures at a small size, with the penes and modified pleopod 1 endopod well developed even in the smallest males examined (TL 8 mm).



Fig. 9. *Taku spinosocarinatus* (Fukuda, 1909), female, TL 28 mm, Korea, MADBK 600101_015 (preserved coloration).

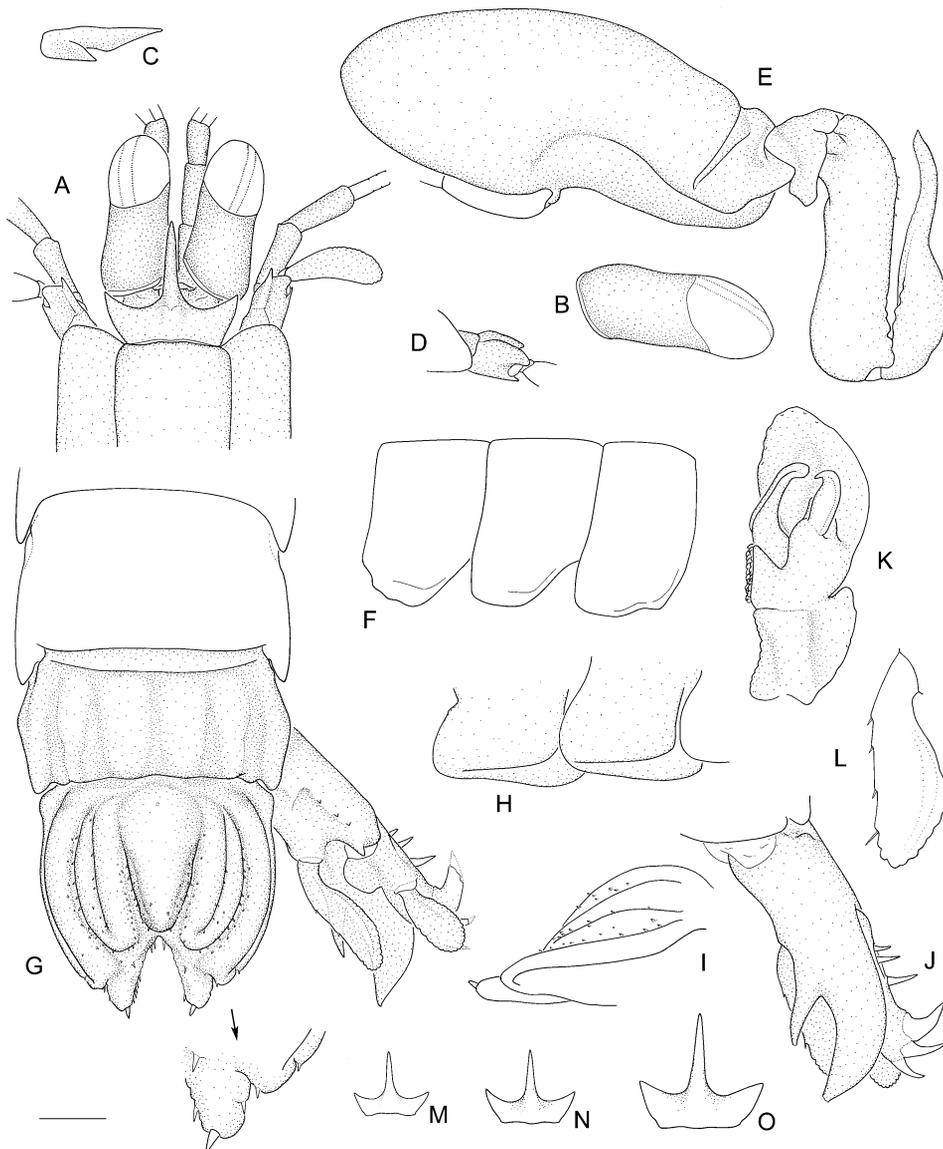


Fig. 10. *Taku spinosocarinatus*. A–K: male, TL 24 mm, Korea, NIBRIV0000300402. L–M: male neotype, TL 12 mm, Japan, AM P60104. N: male, TL 15 mm, Japan, AM P100680. O: female, TL 25 mm, Korea, AM P100684. A, anterior cephalothorax, dorsal view; B, right eye, lateral view; C, rostral plate, right lateral view; D, right antennal protopod, lateral view; E, right raptorial claw; F, thoracic somites 6–8, lateral view; G, posterior abdominal somites, telson and right uropod; H, abdominal somites 4–5, right lateral view; I, telson, right lateral view; J, left uropod, ventral view; K, right pleopod 1 endopod, anterior view; L, right uropodal endopod, dorsal view; M–O, Rostral plate. Scale bars: A–J, M–O = 1.0 mm, K–L = 0.5 mm.

Distribution. Japan, Taiwan, Vietnam, northern Indonesia, and Korea



Fig. 11. Distribution of *Taku spinosocarinatus* (Fukuda, 1909). Legend: star = type locality; circle = distribution in worldwide.

2. *Taku pruvotae* (Gravier, 1930) (Figs. 12–13)

Gonodactylus demani var. *pruvotae* Gravier, 1930: 214, fig. 1 [type locality: Isle of Pines, New Caledonia, by lectotype selection, Moosa, 1991]

Gonodactylus spinosocarinatus: Serène, 1952: 1, 14–16 [part, Australian specimens only].

Mesacturoides spinosocarinatus: Moosa, 1991: 161.

Taku spinosocarinatus: Ahyong & Harling, 2000: app. 1, fig. 3D; Ahyong, 2001: 125–127, fig. 62; Ahyong & Davie, 2002: 87 [Australian and New Caledonian records]; Schram & Müller, 2004: 85 (part); Ahyong, 2007: 335.

Materials examined.

Type material

Lectotype: MNHN Sto128, male (TL 22 mm), Isle of Pines, New Caledonia, coll. Mme Pruvot, 1927.

Non type materials

AUSTRALIA, QUEENSLAND: AM P58562, 1 female (TL 10 mm), West Cay, Diamond Islets, Coral Sea, 13°11'S, 143°43'E, intertidal beach rock pools, coll. D. McMichael & J. Yaldwyn, 23 October 1964; AM P81354, 1 male (TL 10 mm), S of Bird Island, Lizard Island, 14°42'S, 145°24'E, reef crest, 0 m, coral rubble, coll. M. Porter et al., 7 September 2009; AM P81355, 1 male (TL 12 mm), S of Bird Island, Lizard Island, 14°42'S, 145°24'E, reef crest, 0 m, coral rubble, coll. M. Porter et al., 7 September 2009; USNM 1154639, 1 female (TL 12 mm), Lizard Island, coll. N.J. Marshall, 1992; USNM 1154649, 2 females (TL 16 mm), Lizard Island, coll. N.J. Marshall, 7 April 1994; USNM 1154839, 2 males (TL 7–9 mm), 1 female (TL 9 mm), Lizard Head, Lizard Island, 2 m, rubble zone, JDT LIZ-15, coll. J. Thomas & J. Clark, 31 January 1989; USNM 1154840, 1 female (TL 13 mm), Lizard Head, Lizard Island, 2 m, from small rubble pieces on sand, JDT LIZ-19, coll. J. Thomas & J. Clark, 31 January 1989; USNM 1154841, 1 male (TL 8 mm), S of Lizard Head Peninsula, Lizard Island, 2 m, rubble zone, JDT LIZ-14, coll. J. Thomas & J. Clark, 29 January 1989; USNM 1154842, 4 males (TL 8–11 mm), 2 females (TL 9–12 mm), Lizard Island, 1.5 m, rubble zone, unconsolidated coral covered rubble, JDT LIZ-17, coll. J. Thomas & J. Clark, 1 February 1989; AM P56157, 1 female (TL 10 mm), Northeast Cay, Herald Group, Coral Sea, 17°20'S, 148°28'E, dead coral, coll. D. McMichael & J. Yaldwyn, 9 November 1964; AM P56178, 1 male (TL 9 mm), Northeast Cay, Herald Group, Coral Sea, 17°20'S, 148°28'E, coral rock workings, coll. D. McMichael & J. Yaldwyn, 6 November 1964; AM P10372, 1 male (TL 19 mm), 1 female (TL 17 mm), Northwest Islet, 23°30'S, 152°00'E, reef, coll. F. McNeill, December 1931; AM P60073, 3 females (TL 16–19 mm), One Tree Island, 23°30'S, 152°05'E; QM W22269, 1 female (TL 24 mm), Polomaise Reef, 6 km W of Masthead Island, 23°34'S, 151°41'E, littoral, under rocks, coll. P. Davie & D. Potter, 10 February 1986; AM P80952, 1 male (TL 10 mm), Queensland, no data.

Description. Eye (Fig. 13A) elongate, cornea subglobular, reaching almost to or slightly beyond antennular peduncle article 3. Ocular scales, separate, narrower than base of rostral spine, rounded to subtruncate.

Rostral plate (Fig. 13B) with trapezoid basal portion, lateral margins strongly divergent, convex, anterior margins concave in specimens to TL 12 mm, straight to faintly concave, almost transverse in specimens exceeding TL 12 mm, apices angular but not spiniform; median spine slightly compressed laterally, ventral margin obtusely angular, apex not reaching proximal margin of cornea.

Antennular peduncle 0.50–0.66 CL. Antennal scale 0.17–0.23 CL.

Raptorial claw (Fig. 13C) propodus occlusal margin sparsely pectinate proximally, without movable spine. Dactylus with shallow basal notch; outer proximal margin strongly inflated; distal occlusal margin minutely serrated.

Thoracic somites 6–8 (Fig. 13D) smooth, with low marginal ridge; somites 6–7 lower lateral margins subtruncate; somite 8 lower lateral margin irregularly rounded.

Male pleopod 1 endopod (Fig. 13I) with posterior endite, lateral lobe absent. Abdominal somites 1–5 (Figs. 13E, F) smooth dorsally, each with marginal ridge; posterolateral corners rounded, unarmed. Abdominal somite 6 (Fig. 5E) with 6 broad, unarmed, longitudinal carinae (paired submedian, intermediate, lateral); submedian carinae slightly wider than intermediates or laterals. Lateral carina posteriorly, blunt, rounded, slightly produced. AWCLI 652–859.

Telson (Figs. 13E, G) as long as wide, with 8–14 (usually 11 or 12) spiniform submedian denticles. Dorsal surface in specimens \geq TL 10 mm with small spinules along mesial margin of lateral carina, mesial and lateral margins of submedian and intermediate carinae, median carina (especially posterolaterally) and few scattered spinules on dorsal surface of submedian teeth, usually also on carinal surfaces including single spinule on anterior surface of lateral carina. Median carina low, widest anteriorly, reaching posteriorly to base of posterior sinus of telson; proximal dorsal pit; accessory median carinae present in specimens \geq TL \sim 10 mm, separated from median carina by distinct spinule-lined groove.

Uropodal (Figs. 13E, F, H) exopod proximal article with 5–8 (usually 6) spines on outer margin, proximally with 2–5 (usually 3) straight, articulated spines, anteriormost spine smallest, distal 3 spines always fixed, recurved anteriorly, anterior spine largest. Protopod without lobes between terminal spines; outer terminal spine longer and wider than inner; dorsal surface with spine above exopod articulation in

addition to row of 3–7 (usually 4) small spines proximally. Endopod (Fig. 5E, F, H) outer margin lined with plumose setae; inner margin with 1–4 minute simple setae, usually decreasing in number with increasing body size; length $2.74\text{--}4.14 \times$ width.

Coloration. Color in life mostly blue to green. Largest specimen was faded to dull olive green (Ahyong, 2001, as *Taku spinosocarinatus*).

Measurements. Male ($N = 10$) TL 7–19 mm, female ($N = 14$) TL 9–24 mm.

Habitat. Coral reef from preformed cavities in rubble and reef rock including mollusc and worm tubes; intertidal to shallow sublittoral depths.

Remarks. Serène (1952) was first to report *Taku spinosocarinatus* (as *Gonodactylus*) from Australia and in so doing, placed *Gonodactylus demani* var. *pruvotae* Gravier, 1930, and *G. strigatus* Hansen, 1926 in synonymy. With recognition of Gravier's species as valid, previous records of *T. spinosocarinatus* from the Coral Sea and Great Barrier Reef are all referable to *T. pruvotae*. The Australian specimens of *T. pruvotae* agree well with the lectotype from New Caledonia, showing the well-developed accessory median carinae in specimens TL 15 mm and larger (absent at all sizes in *T. spinosocarinatus*). Smaller specimens of *Taku pruvotae*, having undifferentiated accessory median carinae, may be difficult to distinguish from size-matched *T. spinosocarinatus*. At any given size, however, *T. pruvotae* is more spinose than *T. spinosocarinatus*, with the dorsal spinules on the telson carinae being larger and more numerous. Specimens of *T. pruvotae* as small as TL 7 mm have spinules (albeit few) lining the margins of the median and inner margins of the submedian carinae, and by TL 10–12 mm, all margins of the median, submedian and intermediate carinae, and usually also the inner margins of the lateral carinae are spinulose. In contrast, the telson carinae of *T. spinosocarinatus* are unarmed at TL 10 mm, by TL 12 mm the margins of the median and inner margins of the submedian carinae have spinules in addition a few scattered spinules on the intermediate carinae. The rostral shape of the plate differs between *T. pruvotae* and *T. spinosocarinatus* in

specimens above TL 12 mm: the anterior margins of the basal portion of the rostral plate in *T. pruvotae* are straight to faintly concave, almost transverse. In *T. spinosocarinatus*, the anterior margins of the basal portion of the rostral plate are distinctly concave in specimens of all sizes. The spination of the proximal dorsal surface of the uropodal protopod also differs between *T. spinosocarinatus* and *T. pruvotae*. Both species have two or three small spines in specimens to TL 10 mm (as well as at larger size in *T. spinosocarinatus*). *Taku pruvotae* above TL 10 mm, however, has four to six (usually four) spines.

Taku pruvotae exhibits similar allometric variation to *T. spinosocarinatus*, most evident in the general reduction in minute setae on the inner margin of the uropodal endopod, with four in the smallest specimens and one in the largest. Similarly, the uropodal endopod becomes proportionally longer with increasing body size. Males as small as TL 7 mm have fully developed penes and a fully modified pleopod 1 endopod.

Like *T. spinosocarinatus*, spination on outer margin of the proximal article of the uropodal exopod in *T. pruvotae* is remarkably consistent, with three movable spines preceding the three fixed spines. One specimen *T. pruvotae* (male, TL 10 mm, AM P81354), however, is atypical in having two and five movable spines on right and left uropods, respectively.

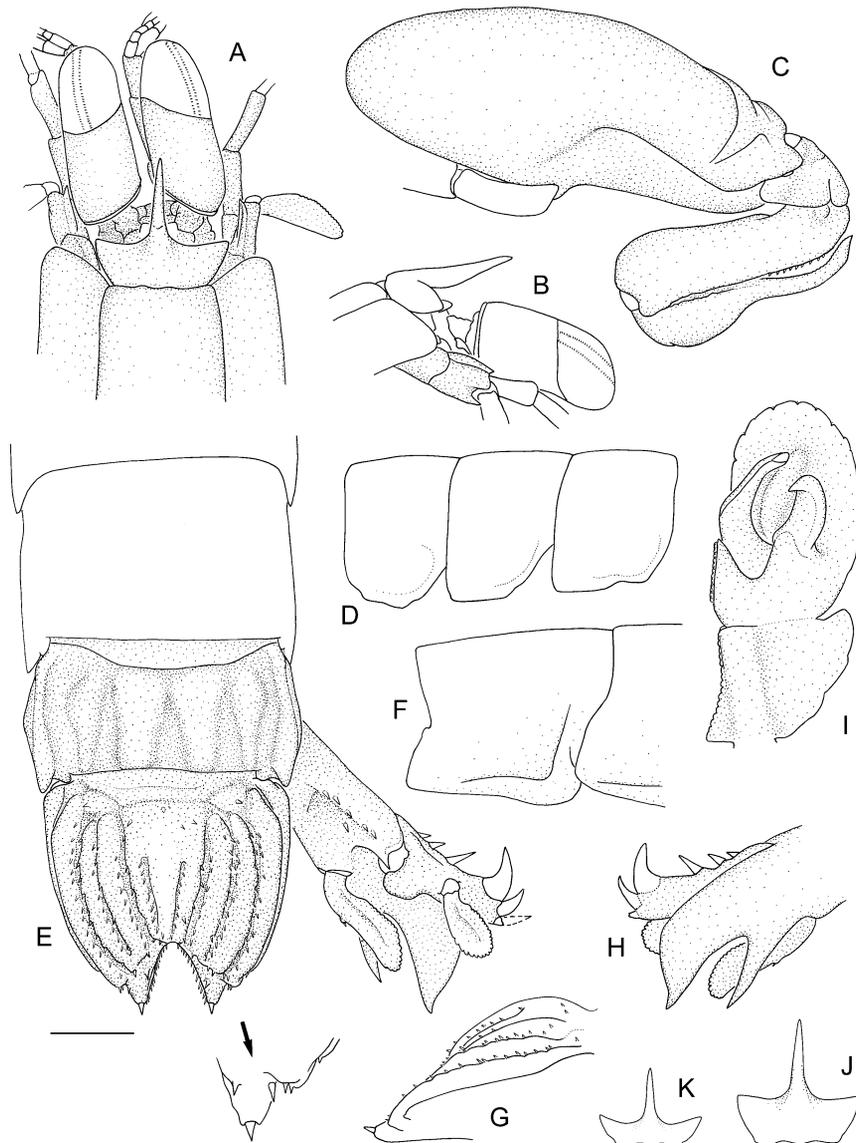


Fig. 13. *Taku pruvotae* (Gravier, 1930) comb. nov., Australia. A–H: female, TL 24 mm, QM W22269. I–J: male, TL 19 mm, AM P10372. K: male, TL 12 mm, Australia, AM P81355. A, Anterior cephalothorax, dorsal view; B, Anterior cephalothorax, right lateral view; C, Right raptorial claw; D, Thoracic somites 6–8, right lateral view; E, Posterior abdominal somites, telson and right uropod; F, Abdominal somites 4–5, right lateral view; G, Telson, right lateral view; H, Right uropod, ventral view; I, Right pleopod 1 endopod, anterior view; J–K, Rostral plate. Scale bars: A–H, J–K = 1.0 mm, I = 0.5 mm.

DISCUSSION

Prior to the present study, *Taku* was considered monotypic, containing only *T. spinosocarinatus* Fukuda, 1909 [type locality: Okinawa, Japan], but with two primary synonyms, *Gonodactylus strigatus* Hansen, 1926 [type locality: Sulawesi, Indonesia], and *Gonodactylus demani* var. *pruvotae* Gravier, 1936 [type locality: New Caledonia]. As such, *T. spinosocarinatus* has been afforded a wide distribution in the western Pacific, from Japan to northern Indonesia and Vietnam, and northeastern Australia to New Caledonia. Reconsideration of *Taku* from throughout its range based on both morphological and molecular data revealed the presence of two geographically discrete species: *T. spinosocarinatus* sensu stricto, ranging from Japan to northern Indonesia and Vietnam, and for the first time from Korea; and *Taku pruvotae*, occurring in the Coral Sea, ranging from New Caledonia to the Great Barrier Reef, Australia, herein removed from the synonymy of *T. spinosocarinatus*. *Gonodactylus strigatus*, however, is retained in synonymy based on Hansen's (1926) account of the 10 mm holotype, which agrees well with similarly sized *T. spinosocarinatus*; direct study of the Indonesian specimen, however, is required for confirmation. At present, Hansen's specimen represents the only record of *T. spinosocarinatus* from Indonesian waters; further sampling is required to better determine the distribution of *Taku* in southeast Asia.

1-2. Taxonomic review of the genus *Chorisquilla* (Gonodactyloidea: Protosquillidae)

INTRODUCTION

The mantis shrimp family Protosquillidae includes more than 35 species in six genera, of which five genera (*Chorisquilla* Manning, 1969, *Echinosquilla* Manning 1969, *Haptosquilla* Manning, 1969, *Rayellus* Ahyong, 2010, and *Siamosquilla* Naiyanetr, 1989) occur only in the Indo-West Pacific region (Ahyong 2010). Among protosquillid genera, *Chorisquilla* can be easily distinguished from other genera by the presence of following characteristics: (1) the presence of an articulated pleural plate on abdominal somite 1 and the presence of a deep V-shaped posterior median fissure on the telson. Among *Chorisquilla* species, characteristics of telson are used as the main identification keys and the identification of the stomatopods can be changed according to the different interpretation of these characteristics of telson. In this part, telson tooth of the all species of the genus *Chorisquilla* and terminology for telson tooth were examined.

MATERIALS AND METHODS

Chorisquilla specimens from throughout its range were examined, including type material. The Korean stomatopod specimens were collected by SCUBA diving on the preformed cavities in rubble and reef rock in shallow water (intertidal to 25 m) from 1991 to 2018. 32 undamaged individuals of *Chorisquilla orientalis* were sampled and then preserved in 95% ethanol and are deposited in the Marine Arthropod Depository Bank of Korea, Seoul National University, Seoul, Korea (MADBK) and National Institute of Biological Resources, Incheon, Korea (NIBRIV). For comparison about morphological character, overseas specimens were loaned and the specimens examined herein were deposited Australian Museum,

Sydney, Australia (AM); Muséum national d'Histoire naturelle, Paris (MNHN); Natur-Museum und Forschungsinstitut Senckenberg, Frankfurt am Main (SMF); Queensland Museum, Brisbane (QM).

For comparison about molecular character, the barcoding region of the mitochondrial cytochrome oxidase subunit 1 gene was sequenced from 4 Korean specimens of *Chorisquilla orientalis*. And four sequences from Korean *Chorisquilla orientalis* were compared with four published sequences from the species identified as *Chorisquilla spinosissima* (Acc. nos. AF205254.1), *Chorisquilla* sp. (Acc. nos. DQ440591.1), *Chorisquilla excavata* (Acc. nos. AF205253.1 and HM138776.1) Additionally, six published sequences from *Taku spinosocarinatus* and *Taku pruvotae* belonging to Takuidae were selected as the outgroup owing to the close relationship between Takuidae and Protosquillidae (Ahyong & Harling 2000; Ahyong & Jarman 2009; Porter et al. 2010). Its GenBank Accession numbers of *Taku pruvotae* is AF205257.1 and sequences of *Taku spinsocarinatus* were from Korean specimens (MADBK 600101_016, MADBK 600101_017, MADBK 600101_021, MADBK 600101_023, MADBK 600101_024).

RESULTS

Molecular data

Within *Chorisquilla* species, telson characteristics are used as key characters in the identification of the species and a more comprehensive interpretation is needed. Usually, in *C. brooksii*, there are two pairs of primary teeth (submedian and intermediate teeth) and 4–6 spines on lateral margin and *C. mehtae* has 6–10 spines on lateral margin. *Chorisquilla orientalis*, however, shows allometric changes in the spination of the telson. The number of lateral spines of the telson also increases with body size. Four lateral marginal spines are present on the telson by TL 11 mm (Fig.

19B), 8–13 spines by TL 20–48 mm (Figs. 18G), and 14 spines by TL 49 mm. A sequence (HS 2) from a specimen of TL 11 mm and three sequences (HS1, 5, 6) from specimens of TL 20–48 mm show that internal divergence in COI of 0.0–2.8%. Mean divergence between *Chorisquilla orientalis* group and other *Chorisquilla* species group lades was 8–12%, corresponding to separate species (Fig. 14). Observed intra-specific and inter-specific divergences among the two species of *Chorisquilla* are consistent with those observed for other species of Stomatopoda at <2.4%, >3.0%, respectively (Tang et al., 2010). The sequence of the specimen which has four telson lateral spines and the sequences of 8–13 lateral spines are the same, it can be regarded as a growth variation of the same species. More accurate examination of telson characteristics is necessary.

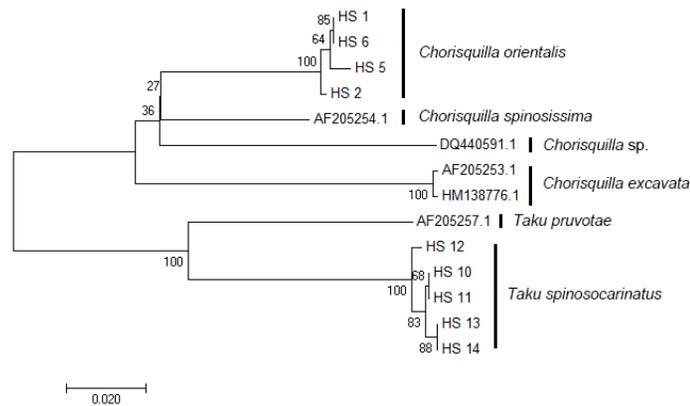


Fig. 14. Neighbor-joining topology of *Chorisquilla orientalis* and other *Chorisquilla* species based on COI sequences, rooted to *Taku spinosocarinatus* and *Taku pruvotae*.

SYSTEMATIC ACCOUNTS

Order Stomatopoda Latreille, 1817

Family Protosquillidae Manning, 1980

Genus *Chorisquilla* Manning, 1969

Chorisquilla Manning, 1969: 157 (type species *Gonodactylus excavatus* Miers, 1880, by original designation. Gender feminine).

Diagnosis. Cornea flattened dorsally, broadened laterally. Rostral plate trispinous. Mandibular palp 2-segmented. Maxillipeds 1–5 with epipod. Abdominal somite 1 with small, articulated, pleural plate anterolaterally. Abdominal somite 6 fused with telson but usually demarcated by dorsal groove. Telson posterior margin divided by deep V- or U-shaped median emargination. Uropodal endopod without dorsal spines.

Composition. *C. andamanica* Manning, 1975; *C. brooksii* (de Man, 1888); *C. convoluta* Ah Yong, 2001; *C. excavata* (Miers, 1880); *C. gyrosa* (Odhner, 1923); *C. hystrix* (Nobili, 1899); *C. kroppi* Ah Yong & Erdmann, 2003; *C. mehtae* Erdmann & Manning, 1998; *C. orientalis* Hwang, Ah Yong & Kim, 2018; *C. pococki* Manning, 1975; *C. quinquelobata* (Gordon, 1935); *C. similis* Ah Yong, 2002; *C. spinosissima* (Pfeffer, 1888); *C. trigibbosa* (Hansen, 1926); *C. tweediei* (Serène, 1950); and *C. tuberculata* (Borradaile, 1907).

Remarks. *Chorisquilla* species is morphologically similar to *Protosquilla* species in having the telson posterior margin divided by a narrow fissure but differs in having the articulated pleural plate on abdominal somite 1. Also, it can be easily distinguished from other protosquillid genera by the combination of following

characteristics: (1) the presence of a broadened cornea, and (2) the presence of a deep, V- or U-shaped posterior median fissure on the telson.

Manning (1969, 1995) regarded *C. tweediei* as a synonym of *C. trigibbosa*, and *C. hystrix* as a synonym of *C. spinosissima*. However, Ahyong (2001) removed synonymies of *C. spinosissima* with *C. hystrix* and *C. tweediei* with *C. trigibbosa* based on characteristics of abdominal somite 6 and telson. Similarly, *Chorisquilla andamanica* and *C. pococki*, which were synonymized with *C. excavata* by Moosa (1986), are both removed the synonymy. Up to date, seventeen species of *Chorisquilla* are recorded worldwide. Among them, a taxonomic review was carried out through morphological re-examination including telson primary teeth which is the main identification key.

Telson tooth terminology in *Chorisquilla*

Most species of *Chorisquilla* have only two pairs of well-developed primary teeth evident on the telson (submedian and intermediate), whereby the third primary teeth (lateral), present in the larvae, are completely suppressed in adults. In others, such as *C. trigibbosa* (Hansen, 1926) and *C. tweediei* (Serène, 1952), the submedian and intermediate teeth are prominent, but the lateral tooth is also present in adults, but as a small lobe, though clearly discernible because the lateral margin of the telson lacks spines or other acute ornamentation. Still others, those with spinose telson margins and surfaces, namely *C. brooksii* (De Man, 1887), *C. hystrix* (Nobili, 1899), *C. kroppi* Ahyong & Erdmann, 2003, and *C. spinosissima* (Pfeffer, 1888), also retain the lateral primary telson teeth in adults, but these are obscured by, and difficult to distinguish from, other prominent spines along the lateral margin of the telson. In these spinose-telson species, the lateral tooth is clearly evident in postlarvae and early juveniles because the row of lateral marginal spines is not fully developed. In adults, however, the lateral primary tooth is similar in size and form to others in the spine row lining the lateral margins of the telson (Ahyong 2001). Thus, for taxonomic convenience, *C. brooksii*, *C. hystrix*, *C. kroppi*, and *C. spinosissima* have often been treated as having only two pairs of primary telson teeth (submedian, intermediate) despite the homologue of the lateral tooth being present (Manning

1969, 1995; Ahyong, 2001). In *C. mehtae* and *C. orientalis* Hwang, Ahyong & Kim, 2018 described herein, three pairs of the primary telson teeth are present (submedian, intermediate and lateral) in adults and described as such, but as in other spinose-telson species, the lateral tooth is of similar form to others in the spine row lining the lateral margins of the telson. In *C. mehtae* and *C. orientalis* Hwang, Ahyong & Kim, 2018, the lateral tooth is the posteriormost spine in the lateral row of telson spines (Figs. 15H, J; lt) and is demarcated from the preceding spines by a short, convex margin. A minute lateral denticle may be present at the base of the lateral tooth (Fig. 15J; ld).

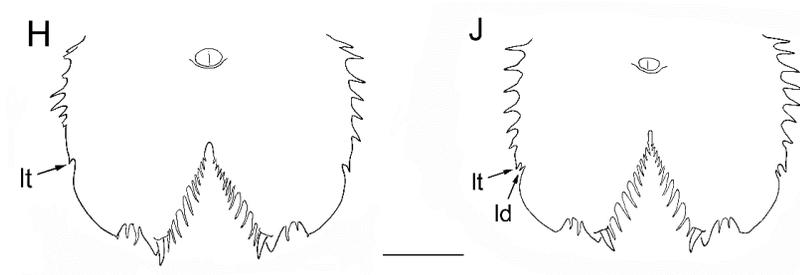


Fig. 15. *Chorisquilla mehtae* Erdmann & Manning, 1998. H, telson, ventral view; J, telson, ventral view (lt = lateral tooth; ld = lateral denticle). Scale bars: H–J = 1.0 mm.

Key to the species of *Chorisquilla* Manning, 1969

1. Telson with 2 pairs of primary teeth 5
- Telson with 3 pairs of primary teeth 2
2. Abdominal somite 5 with deep, irregular, elongated longitudinal pits and grooves on posterior half. Telson with more 8–14 short spines on lateral margin *C. orientalis*
- Abdominal somite 5 with few small, shallow pits on posterior half 3
3. Telson with more 6–10 short spines on lateral margin *C. mehtae*
- Telson without spines on lateral margin 4

4. Telson dorsal surface densely setose; submedian boss without rounded boss proximally *C. tweediei*
 - Telson dorsal surface with low spinules; submedian boss with rounded boss proximally *C. trigibbosa*
5. Telson dorsal surface including bosses covered with numerous spines 6
 - Telson dorsal surface without numerous spines and spinules 9
6. Telson with sparsely distributed, short dorsal spines; lateral margin with 4–6 spines *C. brooksii*
 - Telson with densely distributed, long dorsal spines; lateral margin with 7–12 spines 7
7. Abdominal somite 6 anterior margin without spines *C. kroppi*
 - Abdominal somite 6 anterior margin with row of short anteriorly directed spines 8
8. Dorsum with uniform or slightly mottled colour pattern. Abdominal somite 5 with mid-dorsal surface smooth, or at most with shallow, transverse grooves along posterior margin *C. spinosissima*
 - Dorsum with irregularly banded colour pattern Abdominal somite 5 mid-dorsal surface with posterior half to one-third bearing distinct longitudinal carinae intervened by broad, deep excavations *C. hystrix*
9. Telson dorsal surface with numerous, closely set carinae extending to posterior margin *C. gyrosa*
 - Telson dorsal surface with 3 or 5 longitudinal bosses 10
10. Telson with submedian bosses each extending beyond base of submedian teeth 11
 - Telson with submedian bosses not extending beyond base of submedian teeth 12
11. Dactylus of the raptorial claw with inflated inner proximal margin and mesial tubercle *C. similis*
 - Dactylus of the raptorial claw without inflated inner proximal margin and mesial tubercle *C. quinquelobata*

12. Telson with submedian bosses not extending posteriorly beyond apex of median excavation in posterior margin; dorsal surface of all three bosses tuberculate *C. tuberculata*
- Telson with submedian bosses extending posteriorly beyond apex of median excavation in posterior margin; dorsal surface of all three bosses smooth 13
13. Abdominal somite 6 without posterolateral spine *C. andamanica*
- Abdominal somite 6 with posterolateral spine 14
14. Telson with median and submedian bosses with smooth regular margins *C. excavata*
- Telson with median and submedian bosses with strongly irregular, eroded margins 15
15. Telson with median and submedian bosses with strongly irregular, eroded margins; with 1 carina lateral to submedian boss, separated from submedian boss by deep groove *C. pococki*
- Telson with median and submedian bosses with deeply incised margins; with 2-3 carinae lateral to submedian boss; inner-most carina appressed to margin of each boss *C. convoluta*

3. *Chorisquilla orientalis* Hwang, Ah Yong & Kim, 2018 (Figs. 16–19)

Protosquilla brooksii: Fukuda, 1910: 140, pl. IV, figs. 1, 1a.

Gonodactylus spinosissimus: Komai, 1927: 342–343, tab. 1.

Chorisquilla spinosissima: Kim & Rho, 1972: 97.

Gonodactylus chiragra: Cho *et al.*, 2006: 78 [unnumbered fig.].

Chorisquilla sp. : Hamano, 2005: 32, fig. 2–7e; Ah Yong, 2012b: 247.

Chorisquilla orientalis Hwang, Ah Yong & Kim, 2018: 365–374, figs. 1–3.

Materials examined

Type materials

Holotype: Korea: NIBRIV0000160376, male (TL 36 mm), Geoje Island, Geoje-myeon, Geoje-si, Gyeongsangnam-do, 34°50'05.47"N, 128°42'35.32"E, 4 June 2009.

PARATYPES: Korea: Ulleung Island, Dodong-ri, Ulleung-eup, Ulleung-gun, Gyeongsangbuk-do, 37°31'27.69"N, 130°48'22.11"E: MADBK 600301_020, 1 female (TL 36 mm), 19 October 2001; MADBK 600301_018, 1 male (TL 35 mm), 28 November 1991; MADBK 600301_035, 1 male (TL 43 mm), 16 October 2001, coll. S.H. Kim; MADBK 600301_010, 3 females (TL 30–38 mm), 2 males (TL 32–38 mm), 22 June 2006.

Dokdo Island, Dokdo-ri, Ulleung-eup, Ulleung-gun, Gyeongsangbuk-do, 37°29'44.93"N, 130°55'51.38"E: MADBK 600301_005, 3 females (TL 20–37 mm), 1 male (TL 32 mm), 29 October 2014; MADBK 600301_012, 1 male (TL 31 mm), 3 June 2015; MADBK 600301_013, 1 male (TL 32 mm), 1 female (TL 30 mm), 2 males (TL 31–47 mm), 19 October 2014; MADBK 600301_015, 1 male (TL 32 mm), 10 June 2016; MADBK 600301_019, 2 females (TL 35–38 mm), 21 October 2014; MADBK 600301_025, 1 male (TL 37 mm), 1 female (TL 38 mm), 28 October 2014; MADBK 600301_033, 2 females (TL 40–47 mm), 1 male (TL 47 mm), 21 September 2015; AM P100683, 1 male (TL 32 mm), coll. H.S. Hwang, 29 October 2014; AM P100685, 1 male (TL 32 mm), coll. H.S. Hwang, 10 June 2016.

Geomundo Island, Geomun-ri, Sasam-myeon, Yeosu-si, Jeollanam-do, 34°2'54.77"N, 127°19'6.01"E: MADBK 600301_036, 1 female (TL 47 mm), 26 June 2006, Col. S.H Kim; MADBK 600301_017, 2 females (TL 31–34 mm), 11 March 2010, Col. S.H Kim.

Hakdong-ri, Dongbu-myeon, Geoje-si, Gyeongsangnam-do, 34°49'17.81"N, 128°36'29.30"E: MADBK 600301_002, 2 juvenile males (TL 12 mm), 9 October 2013.

Sangbaekdo Island, Geomun-ri, Sasam-myeon, Yeosu-si, Jeollanam-do, 34°1'37.57"N, 127°18'58.75"E: MADBK 600301_032, 1 female (TL 39 mm), 26 June 2002, Col. S.H Kim.

Chujado Island, Chuja-myeon, Jeju-si, Jeju-do, 33°56'49.25"N, 126°19'12.35"E: MADBK 600301_006, 1 male (TL 20 mm), 1 female (TL 38 mm), 31 March 2009; NIBRIV0000044633, 1 female (TL 35 mm), 30 June 2004.

Cha-gwido Island, Hangyeong-myeon, Jeju-si, Jeju-do, 33°18'45.01"N, 126°8'55.06"E: MADBK 600301_003, 1 female (TL 13 mm), 3 November 2000. Marado Island, Daejeong-eup, Segwipo-si, Jeju-do, 33°7'14.29"N, 126°16'1.63"E: MADBK 600301_001, 1 female (TL 10 mm), 4 November 2000. Hamo-ri, Daejeong-eup, Segwipo-si, Jeju-do, 33°12'39.86"N, 126°15'38.23"E: MADBK 600301_034, 1 male (TL 41 mm), 16 December 2013.

Non type materials

Japan: Banda, Tateyama City, Chiba Prefecture, Japan, 35°36'18.21"N, 140°07'23.90"E: AM P100676, 1 female (TL 49 mm), coll. C. Norman, on scuba, 29 Aug 1993; AM P100677, 1 female (TL 37 mm), coll. C. Norman, on scuba, 21 Mar 1994; AM P100678, 2 males (TL 20–39 mm), 1 female, (TL 39 mm), on scuba, coll. C. Norman, 6 Sep 1993.

Description. Eye (Figs. 17A, 18A) overreaching distal margin of antennular peduncle article 1, not reaching midlength of article 2. Cornea broadened, not bilobed, dorsoventrally flattened. Ocular scales separate, produced laterally, anterior margins approximately transverse; width together about three-fourths basal width of rostral plate.

Rostral plate (Figs. 17A, 18A) sharply trispinous; median spine not reaching to midlength of cornea.

Carapace (Figs. 17A, 18A) with anterior margin of lateral plates faintly concave, not extending laterally, anterolateral angle reaching to level of or slightly beyond level of base of rostral plate in specimens TL 32–40 mm or larger.

Antennular peduncle 0.50–0.74CL. Antennal protopod (Figs. 1A, 2C) mesial margin with blunt, fixed, anteriorly directed spine; short anteroventral spine below articulation with antennal scale. Antennal scale 0.32–0.48CL.

Mandibular palp 2-segmented. Maxilliped 1–5 with epipod.

Raptorial claw (Fig. 18B) stout; propodus occlusal margin minutely pectinated, with proximal movable spine. Dactylus outer margin with shallow basal notch; outer proximal margin strongly inflated, inner distal margin finely serrated, unarmed.

Thoracic somites 6–8 (Figs. 17A, 18D) lateral margin rounded to subtruncate, with low submarginal ridge; somite 8 lateral margin narrowly rounded. Male pleopod 1 endopod (Fig. 18E) posterior endite with lateral lobe.

Abdominal somites 1–3 (Figs. 17A, 18I) smooth medially, with low marginal carina; posterolateral angle rounded. Abdominal somite 4 (Figs. 17A, 18I) smooth medially, with shallow lateral corrugation above low marginal carina; with or without posterolateral spine. Abdominal somite 5 (Figs. 17A, 18G, I) smooth on anterior dorsal half, with deep, irregular, elongated longitudinal pits and grooves on posterior half; posteromedian margin strongly concave; lateral surface corrugated, with 2 or 3 longitudinal ridges; posterolateral spine. Abdominal somite 6 (Figs. 17A, 18G, I) with paired submedian, intermediate, and lateral bosses, each covered with short spinules, lateral boss with posterior spine; anterior margin adjacent to arthroal membrane and anterior sclerotized part of arthroal membrane between somites 5 and 6 each bearing row of minute spinules.

Telson (Figs. 17A, 18G, I) broader than long; submedian primary teeth spiniform, with curved, movable apices, articulating submarginally; 8–12 spiniform submedian denticles; 2 spiniform intermediate denticles; intermediate teeth triangular, apex blunt or with minute spinule; lateral teeth short, slender, directed posterolaterally, lateral denticle present or absent. Dorsal surface of bosses and marginal carina covered with minute spinules, those of marginal carina arranged in 2 or 3 uneven rows, with outermost spinules larger, inclined dorsolaterally, partially overhanging lateral margin. Median boss inverted triangular, not extending posteriorly to base of median fissure. Submedian bosses ovate to pyriform and longer than median boss, width distinctly greater than half their length, almost reaching posteriorly to base of intermediate denticles. Small round boss present anterior to each submedian boss. Lateral margin posterior one-third curved, unarmed; proximal two-thirds with 8–14 short spines in specimens >TL 20 mm, posteriormost spine set-off from preceding spines by short convex margin, corresponding to lateral primary tooth, sometimes with minute intermediate denticle at base. Ventral surface (Fig. 2F) smooth, without postanal carina.

Uropodal protopod (Figs. 17A, 18H) terminating in 2 flattened spines, outer longer; with small lobe between terminal spines; dorsal surface with spine above exopod articulation and a row of 1–3 (usually 2) slender spines proximally, adjacent to articulation with abdominal somite 6. Exopod proximal article with 6–12 (usually 10 or 11) movable spines and stout, fixed distal spine. Endopod slender, unarmed, with shallow median sulcus flanked laterally by low ridge; length 2.82–4.80 × width.

Coloration. Color-in-life mostly ivory to dark brown. Rostral plate, most of carapace, thoracic and abdominal somites, and telson largely brown. Antennular and antennal peduncle, ocular scale, antennal protopod, raptorial claw, pereopods, and uropod ivory. Distal article of antennular peduncle orange.

Measurements. Male (n = 20) TL 12–48 mm, female (n = 24) TL 10–49 mm. Other measurements of holotype: CL 7.43 mm, antennular peduncle length 5.00 mm, antennal scale length 3.40 mm. Komai (1927) recorded specimens to TL 59 mm (as *Gonodactylus spinosissimus*).

Habitat. In Korea, from preformed cavities or holes drilled by mollusks in rock walls; depth 10–25 m. Habitat in Japan not known.

Remarks. Of the known species of *Chorisquilla*, *C. orientalis* appears to be closely related to the following five species sharing the spinose lateral and dorsal surfaces of the telson and one or more dorsal spines on the proximal surface of the uropodal protopod adjacent to the articulation with abdominal somite 6: *C. brooksii* (De Man, 1887), *C. mehtae* Erdmann & Manning, 1998, *C. hystrix* (Nobili, 1906), *C. kroppi* Ah Yong & Erdmann, 1998, and *C. spinosissima* (Pfeffer, 1888). Of these *C. orientalis* n. sp. is most similar to *C. mehtae*, from Indonesia, sharing short lateral telson spines, numerous short, slender dorsal spinules that do not obscure the dorsal surface, and broad, pyriform submedian telson bosses. *Chorisquilla orientalis*, however, can be readily distinguished from *C. mehtae* by the features of abdominal somite 5, telson and ocular scales. In *C. orientalis*, the dorsal surface of abdominal

somite 5 is ornamented with deep longitudinal grooves and irregular pits (versus largely smooth with few small, shallow pits in *C. mehtae*). In *C. orientalis*, the anterior margin of abdominal somite 6 and the anterior sclerotized portion of the arthrodistal membrane between somites 5 and 6 each bear a transverse row of spinules; both rows of spinules are absent in *C. mehtae*. The median boss on the telson is more triangular in *C. orientalis*, with the anterior margin more weakly rounded than in *C. mehtae*, and a rounded boss present anterior to each submedian boss in *C. orientalis* (absent in *C. mehtae*). The ocular scales are more transversely oriented and proportionally wider in *C. orientalis* than in *C. mehtae*. Conversely, in *C. mehtae*, the anterior margins of the ocular scales are distinctly oblique to the body axis, and together, are about half the basal width of the rostral plate (versus about three-fourths). *Chorisquilla orientalis* also reaches a considerably larger size than *C. mehtae*, to TL 59 mm versus TL 17 mm, and males are mature by at least TL 20 mm (compared to *C. mehtae*, which are mature by at least TL 11 mm); *Chorisquilla orientalis* is presently the largest known species of the genus.

Like *C. orientalis*, *C. brooksii* also has short dorsal spines on the telson that do not obscure the surface, but can be separated by the much wider submedian telson bosses (length less than twice width versus less than twice width) and greater lateral marginal spination in adults (8–14 versus 4–6). The remaining species of the genus with a spinose telson, *C. hystrix*, *C. kroppi*, and *C. spinosissima*, all differ from *C. orientalis* in having long lateral and dorsal telson spines that obscure the surface and outline of the telson.

Chorisquilla orientalis shows allometric changes in the shape of the ocular scales and anterior margin of lateral plates of carapace, and in the spination of the telson. The ocular scales become wider with increasing body size, with the combined width 60% of the basal rostral width in juveniles increasing to 75% in adults. As in postlarvae and juveniles of other protosquillids, the dorsal bosses of abdominal somite 6 in the smallest juveniles of *C. orientalis* are posteriorly armed and slenderer than in adults. The number of lateral spines of the telson also increases with body size. Four lateral marginal spines are present on the telson by TL 11 mm (Fig. 19B), 8–13 spines by TL 20–48 mm (Fig. 18G), and 14 spines by TL 49 mm. Also, the

anterior margin of the lateral plate on carapace of *C. orientalis* slopes more posteriorly in smaller specimens. In specimens to about TL 32 mm, the anterolateral angle of the lateral plates of the carapace does not reach anteriorly to the level of the base of the rostral plate. By TL 32–40 mm, the anterolateral angle of the lateral plates of the carapace reach to or slightly anterior to the level of the base of the rostral plate.

Previous records of *C. brooksii* from Japan (Fukuda, 1910), reidentified as *C. spinosissima* by Komai (1927), are clearly referable to *C. orientalis* as shown by Fukuda (1910: pl. IV, fig. 1, 1a). Only one species of *Chorisquilla*, *C. spinosissima*, has been reported from Korea (Kim & Rho, 1972). This single report of *C. spinosissima* is not accompanied by figures or descriptive remarks, and the specimen on which the record is based is no longer extant. Extensive surveys in Korean waters over the past three decades, however, have only ever revealed a single species of *Chorisquilla*, that named here as *C. orientalis*. Given the broad morphological similarities between *C. orientalis* and *C. spinosissima*, especially in juveniles with lesser developed telson spination, and Komai's (1927) misidentification of *C. spinosissima* from Japan, we regard the record of Kim & Rho (1972) to be almost certainly based on *C. orientalis*. Similarly, the recent record of *Gonodactylus chiragra* from Korea figured by Cho *et al.* (2006) is clearly based on *C. orientalis*.

Distribution. Korea and central Japan (Tateyama, Chiba Prefecture, to Misaki, Osaka Prefecture).

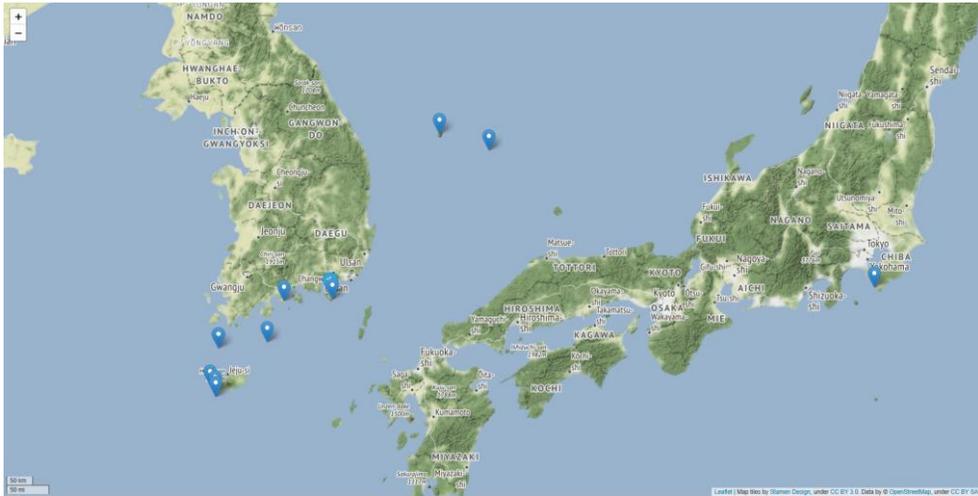


Fig. 16. Distribution of *Chorisquilla orientalis* Hwang, Ahnyong & Kim, 2018. Legend: star = type locality; circle = distribution in worldwide.

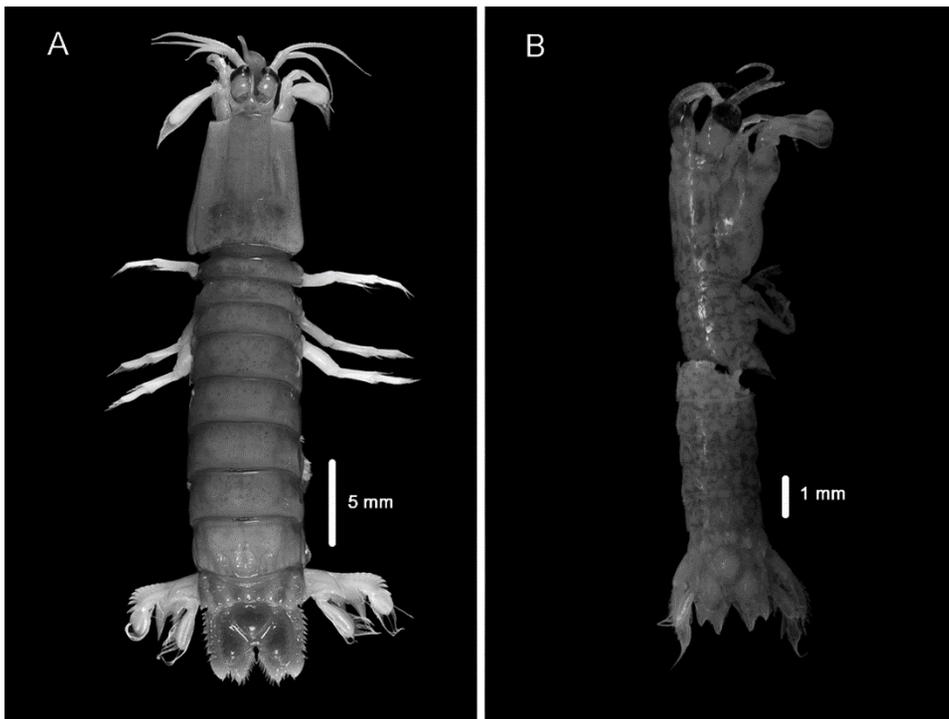


Fig. 17. *Chorisquilla orientalis*. A, male holotype, TL 36 mm, NIBRIV0000160376. B, female paratype, TL 13 mm, MADBK 600301_003. (Preserved coloration)

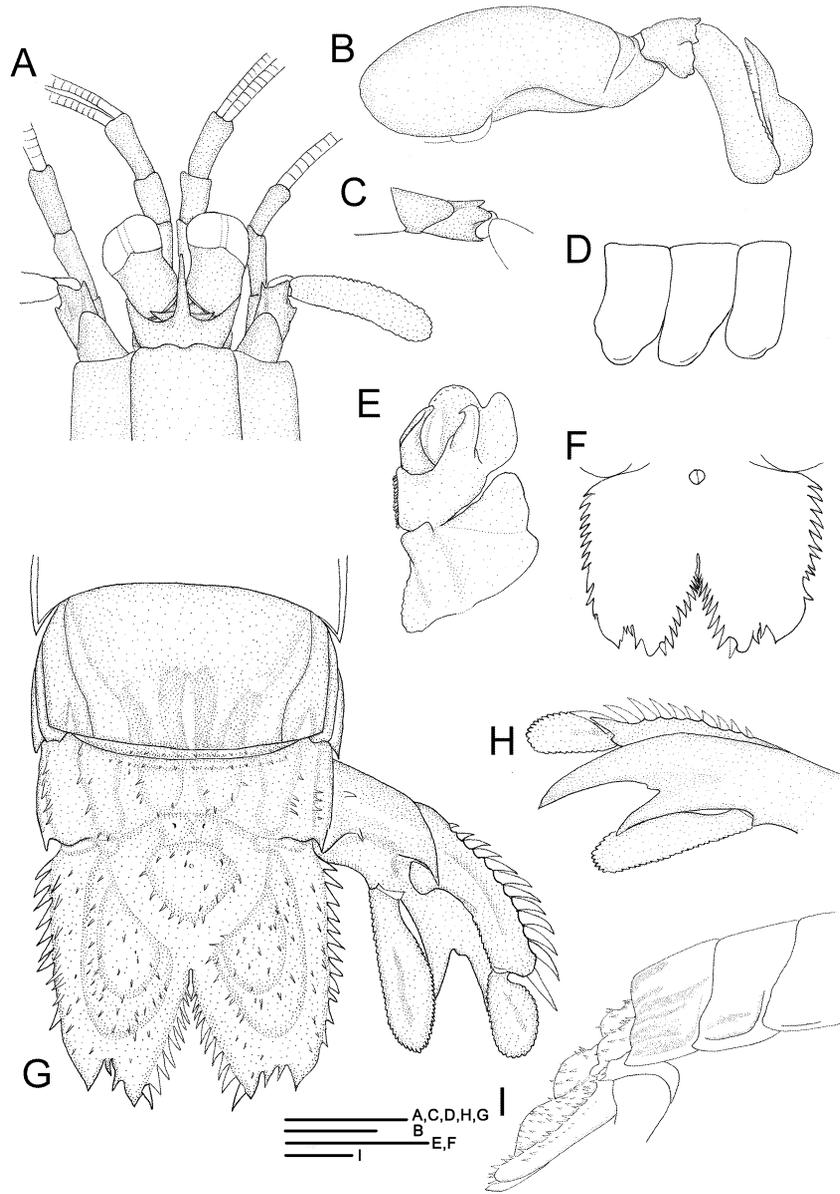


Fig. 18. *Chorisquilla orientalis*, male holotype, TL 36 mm, South Korea, NIBRIV0000160376. A, anterior cephalothorax; B, raptorial claw; C, antennal protopod; D, thoracic somites 6–8, right lateral view; E, right male pleopod 1 endopod; F, telson, ventral view; G, abdominal somites 4–6, telson, and uropod; H, right uropod, ventral; I, abdominal somites 3–5 and telson, right lateral view. Scale bars: A–I = 1.0 mm.

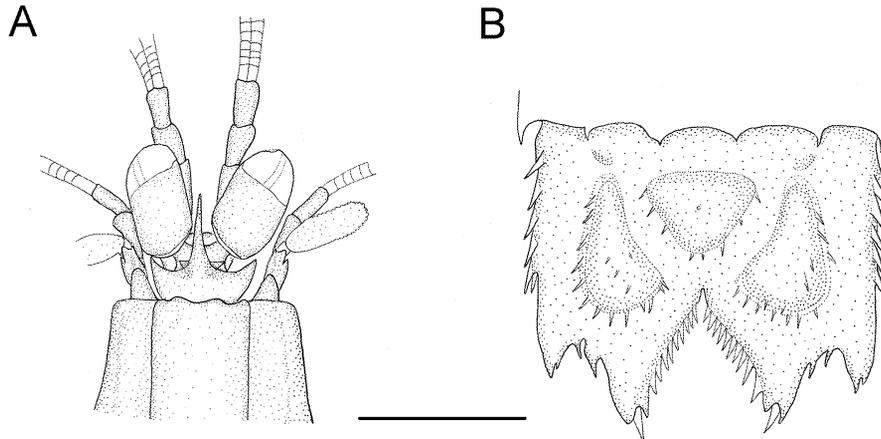


Fig. 19. *Chorisquilla orientalis*, juvenile male paratype, TL 12 mm, South Korea, MADBK 600301_002. A, anterior cephalothorax; B, telson. Scale bars = 1.0 mm.

4. *Chorisquilla mehtae* Erdmann & Manning, 1998 (Figs. 20–21)

Chorisquilla mehtae Erdmann & Manning, 1998: 616–617, fig. 1a; Ahyong, 2001: 87.

Materials examined

Type material

Holotype: USNM 260905, female (TL 16 mm), Gili Lawa Darat, Komodo, Indonesia, coll. M. Erdmann.

Paratype: USNM 260906, 3 males (TL 11–14 mm), Hoga, Tukang Besi Archipelago, Indonesia, coll. M. Erdmann. USNM 260907, 1 female (TL 17 mm), Taipi, Togian Islands, Indonesia, coll. M. Erdmann.

Non type material

Indonesia: AM P100681, 2 males (TL 15 mm), 1 female (TL 16 mm), Unauna, Togian Islands, Indonesia, 0°09.5'N, 121°39.5'E, coll. M. Erdmann, 28 Nov 1999.

Description. Eye (Fig. 21A) overreaching distal margin of antennular peduncle article 1. Cornea broadened but not bilobed, dorsoventrally flattened. Ocular scales narrow, sloping posteriorly, not produced laterally, anterior margins distinctly oblique to body axis, width together about three-fifths basal width of rostral plate.

Rostral plate (Fig. 21A) sharply trispinous; median spine reaching to proximal margin of cornea.

Carapace (Fig. 21A) with anterior margin of lateral plate concave, sloping posteriorly, anterolateral angles not extending anteriorly as far as level of base of rostral plate.

Antennular peduncle 0.70–0.88CL. Antennal protopod (Figs. 4A, B) mesial margin with blunt, fixed, anteriorly directed spine; short anteroventral spine below articulation with antennal scale. Antennal scale 0.43–0.52CL.

Mandibular palp 2-segmented. Maxilliped 1–5 with epipod.

Raptorial claw (Fig. 21C) robust; occlusal margin of propodus minutely pectinated, with movable spine proximally. Dactylus outer margin with shallow basal notch; inner distal margin finely serrated, unarmed.

Thoracic somites 6–7 (Fig. 21D) lateral margin rounded to subtruncate, width subequal, with low submarginal ridge; somite 8 lateral margin narrowly rounded.

Male pleopod 1 endopod (Fig. 21E) posterior endite with lateral lobe.

Abdominal somites 1–3 smooth medially, with low marginal carina; posterolateral angle rounded. Abdominal somite 4 (Figs. 21F, G) smooth medially, with shallow lateral corrugation above low marginal carina; posterolateral corner angular. Abdominal somite 5 (Figs. 21F, G) smooth dorsally, with few small, shallow pits; posteromedian margin strongly concave; lateral surface corrugated, with 3 longitudinal ridges; posterolateral spine blunt. Abdominal somite 6 (Figs. 4F, G) with paired submedian, intermediate, and lateral bosses, each covered with short spinules, lateral boss with posterior spine; anterior margin adjacent to arthrodistal membrane margin and anterior part of arthrodistal membrane between somites 5 and 6 unarmed.

Telson (Figs. 21F, G) broader than long submedian primary teeth with curved, movable apices, articulating submarginally; with 10–13 spiniform submedian denticles; 2 spiniform intermediate denticles; intermediate teeth triangular, apex

blunt or with minute spinule; lateral teeth short, slender, directed posterolaterally, lateral denticle present or absent. Dorsal surface of bosses and marginal carina covered with minute spinules, those of marginal carina arranged in 2 or 3 uneven rows, with outermost spinules larger, inclined dorsolaterally, partially overhanging lateral margin. Median boss ovate, not extending posteriorly to base of median fissure. Submedian bosses pyriform, longer than median boss, width distinctly greater than half-length, almost reaching posteriorly to base of intermediate denticles; without small boss anterior to each submedian boss. Lateral margin posterior one-third curved, unarmed; proximal two-thirds with 7–9 spines, posteriormost spine set-off from preceding spines by short convex margin, corresponding to lateral primary tooth (Figs. 21H, J), sometimes with minute lateral denticle at base (Fig. 21J); distal one-third curved, unarmed. Ventral surface of telson (Figs. 21H, J) smooth, without postanal carina.

Uropodal protopod (Figs. 21F, I) terminating in 2 flattened spines, outer longer; without lobe between terminal spines; dorsal surface with spine above exopod articulation and row of 2 or 3 (usually 2) slender spines proximally, adjacent to articulation of abdominal somite 6. Exopod proximal article with 8 or 9 movable spines and stout, fixed distal spine. Endopod slender, unarmed, with shallow median sulcus flanked laterally by low ridge; length $3.12\text{--}3.49 \times$ width.

Measurements. Male ($n = 5$) TL 11–15 mm, females ($n = 3$) 16–17 mm. Other measurements of holotype: CL 3.66 mm, antennular peduncle length 2.62 mm, antennal scale length 1.57 mm.

Habitat. Cavities in vertical reef surfaces and rock walls; 15 to at least 30 m depth.

Distribution. Eastern Indonesia, from Komodo, Tukang Besi and the Togian Islands.



Fig. 20. Distribution of *Chorisquilla mehtae* Erdmann & Manning, 1998.

Legend: star = type locality; circle = distribution in worldwide.

Remarks. Erdmann & Manning (1998) diagnosed and provided a brief figure of *C. mehtae*. To facilitate comparison with *C. orientalis*, *C. mehtae* is redescribed and figured herein based on type and other material. Features distinguishing *C. mehtae* and *C. orientalis* are discussed under the account of the latter. All specimens examined are sexually mature.

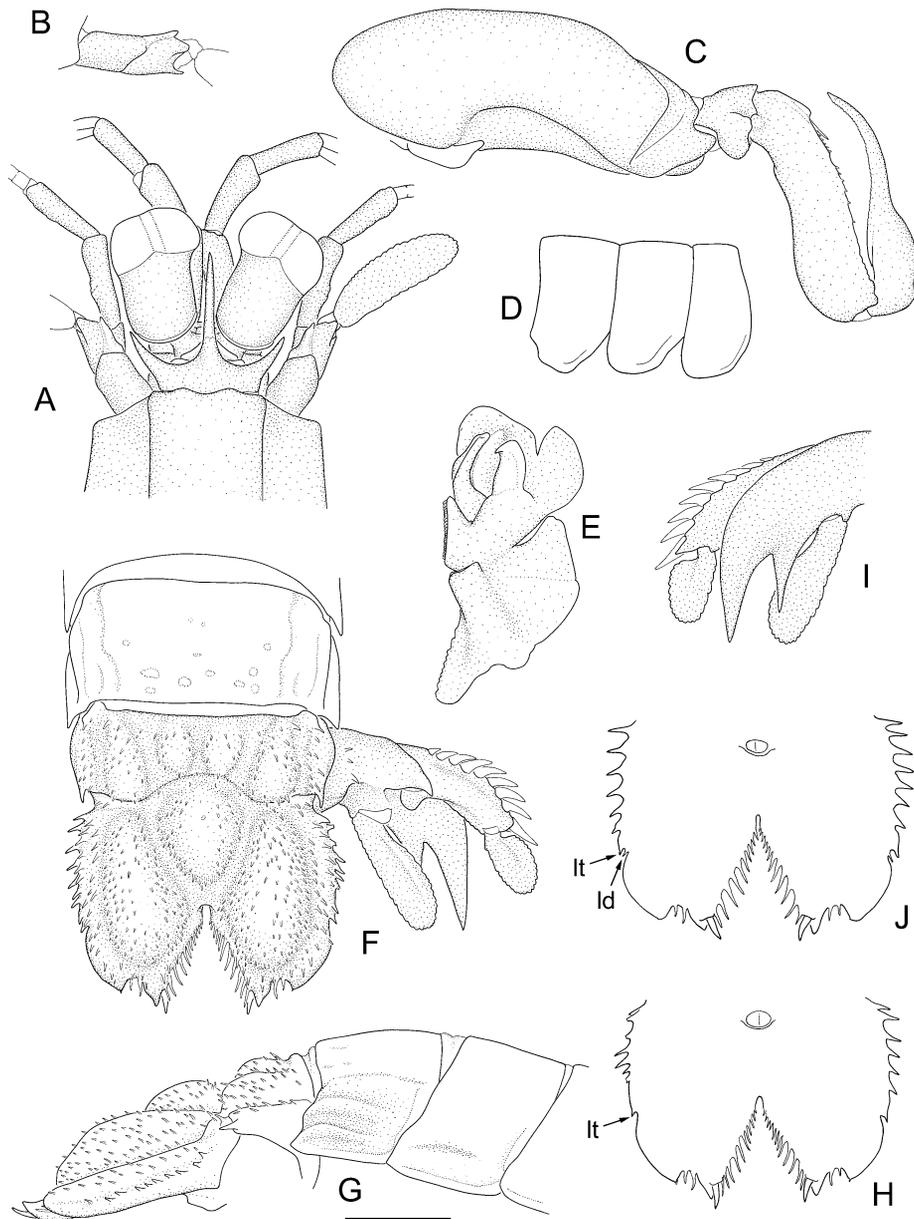


Fig. 21. *Chorisquilla mehtae* Erdmann & Manning, 1998. A–I, male, TL 15 mm, Indonesia, AM P100681. J, female, TL 16 mm, Indonesia, AM P100681. A, anterior cephalothorax; B, right antennal protopod; C, right raptorial claw; D, thoracic somites 6–8; E, right male pleopod 1 endopod; F, abdominal somites 5–6, telson, and uropod; G, abdominal somites 4–6 and telson; H, telson, ventral view; I, right uropod, ventral; J, telson, ventral view. (lt = lateral tooth; ld = lateral denticle). Scale bars: A–D, F–I = 1.0 mm, E = 0.5 mm.

5. *Chorisquilla brooksii* (de Man, 1888) (Figs. 22–23)

Protosquilla brooksii de Man, 1888, in de Man, 1887–1888: 579, pl. 22a, fig. 8.

Gonodactylus brooksi: Kemp, 1913: 4, 11, 149, 189–190.

Gonodactylus brooksii: Holthuis, 1941: 290–292.

Chorisquilla brooksii: Manning, 1969: 159; Moosa, 1974: 73; Sun & Yang, 1998: 145–146, 152, fig. 2; Manning, 1995: 94–97, pl. 16, figs. 9n, 43a, 44–47.

Materials examined

Type materials

Lectotype: ZMG 966, male (TL 28 mm), Edam Island, Jakarta Bay, Indonesia.

Paralectotype: ZMG 966, female (TL 24 mm), type locality.

Non type material

Vietnam: AM P12157, female (TL 21 mm), Station Cauda, French Indo-China, coll. R. Serene, 10 July 1947.

Diagnosis. Telson (Fig. 23) with two pairs of primary teeth (submedian, intermediate); dorsal surface with pyriform median and submedian bosses, bearing short spines around margin. Submedian bosses longer than median boss, extending beyond midlength of telson; with 5–7 submedian denticles and 2 spiniform intermediate denticles; lateral margin with 4–6 spines; ventral surface without postanal carina. Posterior margin of telson divided by deep V-shaped median emargination. Uropodal protopod (Fig. 23) with small dorsal spine proximally and with dorsal spine above proximal exopod articulation; proximal segment of exopod with 9–10 movable spine. Cornea (Fig. 23) broadened laterally, flattened dorsally. Rostral plate tri-spinous. Mandibular palp 2-segmented. Maxilliped 1–5 with epipod. Abdominal somite 1 with pleural plate. Abdominal somite 5 (Fig. 23) with posterior spine; dorsal surface smooth proximomedially, distomedially with deep longitudinal pits and corrugated laterally. Abdominal somite 6 (Fig. 23) fused with telson, demarcated by dorsal groove.

Habitat. Coral reef flats among rubble (Ahyong, 2001)

Distribution. Australia, Indonesia, the South China Sea, and Vietnam (Ahyong, 2001).



Fig. 22. Distribution of *Chorisquilla brooksii* (de Man, 1888). Legend: star = type locality; circle = distribution in worldwide.

Remarks. Among *Chorisquilla* species, *C. brooksii* is morphologically similar to *C. spinosissima* in having 2 pairs of telson primary teeth, numerous spines on the dorsal surface of telson. Especially, telson primary teeth of *C. brooksii* are well developed. *C. brooksii*, however, is easily distinguished from congeners including *C. spinosissima* by the presence of relatively short spine on the dorsal surface of telson, and 4-6 lateral spine on the lateral margin of telson. The specimens examined here agree well with these characteristics.



Fig. 23. *Chorisquilla brooskii*, female, TL 21 mm, AM P12157.

6. *Chorisquilla andamanica* Manning, 1975 (Fig. 24)

Chorisquilla andamanica Manning, 1975: 258–260, fig. 3; Ahyong, 2001: 88.

Type material

Paratype: USNM 143562, male, no further information.

Diagnosis. Telson with two pairs of primary teeth (submedian, intermediate); dorsal surface with 3 or 5 broad, smooth longitudinal bosses; submedian bosses extending posteriorly beyond apex of median excavation in posterior margin. Mandibular palp 2-segmented. Maxilliped 1–5 with epipod. Abdominal somite 1 with pleural plate. Abdominal somite 6 fused with telson but usually demarcated by dorsal groove, without posterolateral spine. Uropodal endopod without dorsal spines.

Habitat. Information is not available.

Distribution. Andaman Islands (Schram & Müller, 2004).



Fig. 24. Distribution of *Chorisquilla andamanica* Manning, 1975. Legend: star = type locality.

Remarks. Among *Chorisquilla* species, *C. andamanica* is morphologically similar

to *C. tuberculata* by the following characteristics: 1) the presence of 2 pairs of telson primary teeth, 2) the absence of numerous spines on the dorsal surface of telson, 3) the presence of submedian bosses of telson not extending to the base of submedian teeth. *C. andamanica*, however, is easily distinguished from congeners including *C. tuberculata* in having submedian bosses extending posteriorly beyond the apex of median excavation in the posterior margin and smooth surface of three bosses on the telson. *C. tuberculata* has submedian bosses not extending posteriorly beyond the apex of median excavation and tuberculate bosses surface. The specimens examined here agree well with these characteristics.

7. *Chorisquilla convoluta* Ahyong, 2001 (Fig. 25)

Chorisquilla convoluta Ahyong, 2001: 89–91, fig. 43.

Type material

Holotype: WAM C7828, 1 female (TL 29 mm), 3.2 km SW of Peek Island, Honolulu dredge, 18.3 m, coll. B. Wilson, 18 June 1960.

Diagnosis. Telson with two pairs of primary teeth (submedian, intermediate); dorsal surface with 3 or 5 broad, smooth longitudinal bosses; median and submedian bosses with strongly irregular, eroded or convoluted margins; submedian bosses extending posteriorly beyond apex of median excavation in posterior margin; with 2 or 3 carinae lateral to submedian bosses, with inner-most carina appressed to margin of boss. Mandibular palp 2-segmented. Maxilliped 1–5 with epipod. Abdominal somite 1 with pleural plate. Abdominal somite 6 fused with telson but usually demarcated by dorsal groove, with posterolateral spine. Uropodal endopod without dorsal spines.

Habitat. Shallow coral reefs to silty sand (Schram & Müller, 2004).

Distribution. Australia (Ahyong, 2001; Schram & Müller, 2004).



Fig. 25. Distribution of *Chorisquilla convoluta* Ahyong, 2001. Legend: star = type locality; circle = distribution in worldwide.

Remarks. *Chorisquilla convoluta* is morphologically similar to *C. pococki* in having posterolateral spines on abdominal somite 6 and irregular telson bosses but differs in the following characteristics: 1) the dorsal bosses of abdominal somite 6 and the telson, instead of being strongly eroded, bear deeply convoluted and fissured margins, 2) there are two or three carinae lateral to the submedian bosses extending the full length of the telson instead of a single marginal carina and a short distal carina originating from the apices of the intermediate teeth 3) the distomedial surface of abdominal somite 5, instead of being entirely smooth, bears a series of deep pits, and 4) the inner most carina lateral to the submedian telson boss is appressed to the margin of the boss in contrast to other species belonging to *C. excavata* complex species in which the carina is separated from the submedian boss by a deep, broad groove. The specimens examined here agree well with these characteristics.

8. *Chorisquilla excavata* (Miers, 1880) (Figs. 26–27)

Gonodactylus excavata Miers, 1880: 123, pl. 3, figs 11–12.

Chorisquilla excavata; Ahyong, 2001: 91; 2002: 369.

Material examined

Type material

BMNH 75.14, male, no further information

Non type material

French Polynesia: AM P64480, male, TL 16.5 mm, Society Islands, Tahiti, Baie de Matavai, Point Venus, coll. J.K. Lowry & M. Arakino, 27 August 1991.

Diagnosis. Telson (Fig. 26) with two pairs of primary teeth (submedian, intermediate); dorsal surface with 3 or 5 broad, smooth longitudinal bosses; median and submedian bosses with smooth regular margins; submedian bosses extending posteriorly beyond apex of median excavation in posterior margin. Mandibular palp 2-segmented. Maxilliped 1–5 with epipod. Abdominal somite 1 with pleural plate. Abdominal somite 6 (Fig. 26) fused with telson but usually demarcated by dorsal groove, with posterolateral spine. Uropodal endopod (Fig. 26) without dorsal spines.

Habitat. Shallow coral reef habitats amongst rubble to a depth of 108 m on silty sand (Ahyong, 2001).

Distribution. French Polynesia (Ahyong, 2001).



Fig. 26. Distribution of *Chorisquilla excavata* (Miers, 1880). Legend: star = type locality.

Remarks. *C. excavata* has most strongly irregular and eroded margins of the telson bosses in the smallest specimens. With increasing size, the margins of the telson bosses become less irregular than the smaller specimens but are still distinctly eroded in the largest specimens. Additionally, the lateral and marginal carinae are distinct in the smallest specimens becoming fused in the largest specimens.

Although the type locality of *C. excavata* is unknown, *C. excavata* is presently known with certainty only from French Polynesia. Because the fact that the only other record of its occurrence is from French Polynesia, suggests that the holotype was collected from a central Pacific locality visited by the HMS Herald, probably Fiji (Ahyong, 2001).



Fig. 27. *Chorisquilla excavata*, male, TL 16.5 mm, AM P64480.

9. *Chorisquilla gyrosa* (Odhner, 1923) (Figs. 28–29)

Gonodactylus gyrosus Odhner, 1923: 11–13, figs. 4–5; Tiwari & Biswas, 1952: 349–363, fig. 5.

Chorisquilla gyrosa: Manning, 1969: 158.

Material examined.

Type material

Holotype: SMNH 2538, male, Aranuka, Gilbert Island, no further information.

Non Type material

Mauritius: AM P88131, male, TL 32.5 mm, coll. M. Ward, no further information.

Diagnosis. Telson (Fig. 29) with two pairs of primary teeth (submedian, intermediate); dorsal surface with numerous, closely set carinae extending to posterior margin. Cornea (Fig. 29) broadened laterally, flattened dorsally. Rostral plate (Fig. 29) tri-spinous. Mandibular palp 2-segmented. Maxilliped 1-5 with epipod. Abdominal somite 1 with pleural plate. Abdominal somite 5 (Fig. 29) laterally carinate and corrugated; smooth proximomedially, distomedially with short, shallow pits. Abdominal somite 6 fused with telson, demarcated by dorsal groove. Uropodal protopod (Fig. 29) with small dorsal spine proximally and without dorsal spine above proximal exopod articulation; proximal segment of exopod with 9–10 movable spine.

Habitat. Information is not available.

Distribution. Seychelles, Andaman Islands, Diego Garcia, Gilbert Islands, and Marshall Islands.



Fig. 28. Distribution of *Chorisquilla gyrosa* (Odhner, 1923). Legend: star = type locality; circle = distribution in worldwide.

Remarks. Among *Chorisquilla* species, *C. gyrosa* is morphologically similar to *C. quinquelobata* by the following characteristics: 1) the presence of 2 pairs of telson primary teeth, 2) the absence of numerous spines on the dorsal surface of telson. *C. gyrosa*, however, is easily distinguished from congeners including *C. quinquelobata* in having numerous, closely set carinae extending to posterior margin of telson. *C. quinquelobata* has three bosses on the dorsal surface of telson. The specimens examined here agree well with these characteristics.



Fig. 29. *Chorisquilla gyrosa*, male, TL 32.5 mm, AM P88131.

10. *Chorisquilla kroppi* Ahyong & Erdmann, 2003 (Fig. 30)

Chorisquilla kroppi Ahyong & Erdmann, 2003: 326–329, fig. 1.

Type material

Holotype: USNM 304499, 1 male, TL 19 mm, Tumon Bay, Guam, 10.5 m, RK, 3–8 November 1984.

Diagnosis. Telson with 2 pairs of primary teeth (submedian, intermediate); dorsal surface entirely covered with long spines, obscuring median and submedian bosses; median boss circular to ovate, submedian bosses extending posteriorly beyond apex of median excavation. Cornea broadened laterally, flattened dorsally. Rostral plate tri-spinous. Mandibular palp 2-segmented. Maxilliped 1-5 with epipod. Abdominal somite 1 with pleural plate. Abdominal somite 5 laterally carinate and corrugated; smooth proximomedially, distomedially with shallow pits. Abdominal somite 6 anterior margin without transverse row of short posteriorly directed spines; dorsally ornamented with numerous spines in three transverse rows. Uropodal protopod dorsally with a short proximal spine and shorter spine above proximal exopod articulation.

Habitat. Information is not available.

Distribution. Guam and Pohnpei in the northwestern Pacific Ocean (Ahyong & Erdmann, 2003).

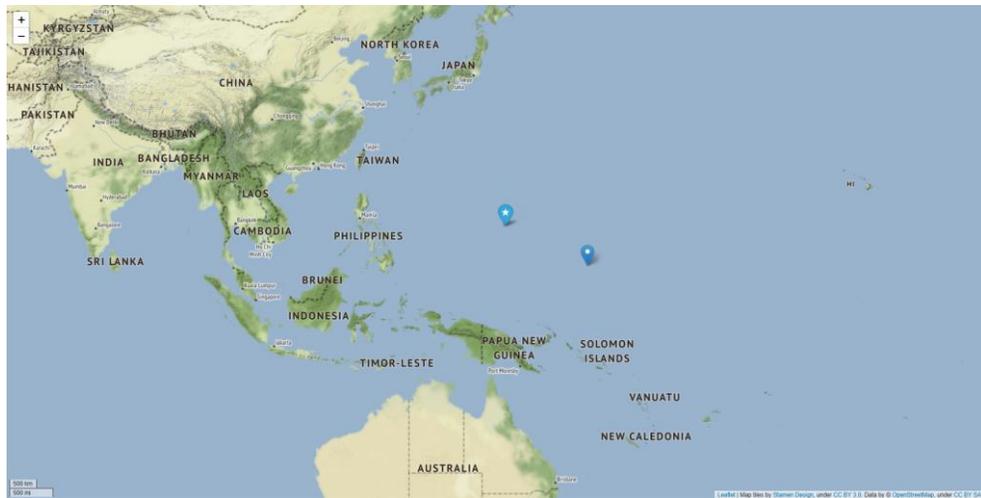


Fig. 30. Distribution of *Chorisquilla kroppi* Ahyong & Erdmann, 2003. Legend: star = type locality; circle = distribution in worldwide.

Remarks. Among these characteristics, *C. kroppi* is most similar to *C. hystrix* in having the following characteristics: 1) a similar color pattern, 2) the similar number

of rows of dorsal spines on abdominal somite 6, 3) a dorsal spine on the proximal margin of the uropodal protopod. This species differs from *C. hystrix* and resembles *C. spinosissima* in having short shallow pits of abdominal somite 5 instead of the distinct broad pits intervened by carinae. *C. kroppi* differs from both *C. hystrix* and *C. spinosissima* in lacking the row of short anteriorly directed spines along the anterior margin of abdominal somite 6. Ahyong (2001) removed *C. hystrix* (Nobili 1899) from the synonymy of *C. spinosissima* (Pfeffer 1888) by the presence of differences in the following characteristics: 1) color pattern (whether banded or uniformly mottled), 2) the morphology of the mid-dorsal surface of abdominal somite 5 (whether with carinae or shallow pits, 3) the density of dorsal spines on abdominal somite 6. In the same case, *C. kroppi* can be easily distinguished from both species.

11. *Chorisquilla pococki* Manning, 1975 (Figs. 31–32)

Chorisquilla pococki Manning, 1975b: 256–258, figs. 1b, 2; Moosa, 1991: 163; Ahyong, 2001: 91.

Material examined

Type material

Holotype: BMNH 92.8-28.9-10, male, South China Sea, no further information.

Non type material

Japan: AM P87568, male, TL 20.6 mm, Okinawa Prefecture, Ryukyu Islands, off the coast of Kume Island, near Gima, 16 November 2009.

Diagnosis. Telson (Fig. 32) with two pairs of primary teeth (submedian, intermediate); dorsal surface with 3 or 5 broad, smooth longitudinal bosses; median and submedian bosses with strongly irregular, eroded margins, with one carina lateral to submedian boss, separated from submedian boss by deep, broad, groove; submedian bosses extending posteriorly beyond apex of median excavation in

posterior margin; with 2 or 3 carinae lateral to submedian bosses, with inner-most carina appressed to margin of boss. Mandibular palp 2-segmented. Maxilliped 1–5 with epipod. Abdominal somite 1 with pleural plate. Abdominal somite 6 (Fig. 32) fused with telson but usually demarcated by dorsal groove, with posterolateral spine. Uropodal endopod (Fig. 32) without dorsal spines.

Habitat. Mud and hard sand, coral sand, and sand bottom with algae (Manning, 1975; Moosa, 1991).

Distribution. Japan, South China Sea, Philippines, Ogasawara Islands, Indonesia, and East Timor (Schram & Müller, 2004).

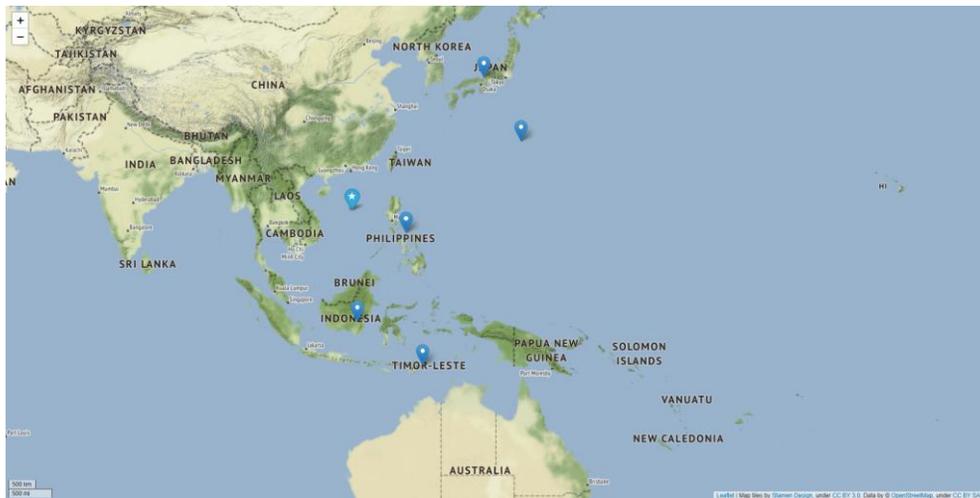


Fig. 31. Distribution of *Chorisquilla pococki* Manning, 1975. Legend: star = type locality; circle = distribution in worldwide.

Remarks. *Chorisquilla pococki* is morphologically similar to *C. convoluta* in having posterolateral spines on abdominal somite 6 and irregular telson bosses but differs by the presence of the following characteristics: 1) the presence of strongly eroded margins of the dorsal bosses of abdominal somite 6 and the telson, instead of being deeply convoluted and fissured, 2) the presence of a single marginal carina and a short distal carina originating from the apices of the intermediate teeth instead of two

or three, 3) the presence of entirely smooth on the distomedial surface of abdominal somite 5, instead of a series of deep pits, and 4) the lateral to the submedian telson boss which is separated from the submedian boss by a deep, broad groove. The specimens examined here agree well with these characteristics.



Fig. 32. *Chorissquilla pococki*, male, TL 20.6 mm, AM P87568.

12. *Chorisquilla quinquelobata* (Gordon, 1935) (Figs. 33–34)

Gonodactylus quinquelobatus Gordon, 1935: 635–637, fig. 3 (type locality: Flying Fish Cove, Christmas Island, Indian Ocean).

Chorisquilla quinquelobata: Manning, 1969: 159; 1995: 20, 94.

Material examined.

Type material

HOLOTYPE: NHM 1935.8.10.1, 1 femlae, TL 18 mm, Flying Fish Cove, Christmas Island, Indian Ocean, in pilings of pier, coll. Prof. Harms, no further information.

Non type material

Australia: AM P91059, male, TL 16 mm, Christmas Island, Thundercliff Cave, coll. L.E. Hughes, 19 October 2008

Diagnosis. Telson (Fig. 34) with two pairs of primary teeth (submedian, intermediate); dorsal surface with 5 broad longitudinal bosses; surface of all five bosses smooth, without setae, tubercles or spinules; submedian bosses extending beyond base of submedian teeth. Mandibular palp 2-segmented. Maxilliped 1–5 with epipod. Abdominal somite 1 with pleural plate. Abdominal somite 6 (Fig. 34) fused with telson but demarcated by dorsal groove, without posterolateral spine. Uropodal endopod without dorsal spines. Raptorial claw propodus with movable spine proximally.

Habitat. found on pilings of a pier (Schram & Müller, 2004).

Distribution. Australia (Christmas Island) (Ahyong, 2001).



Fig. 33. Distribution of *Chorisquilla quinquelobata* (Gordon, 1935). Legend: star = type locality.

Remarks. Among *Chorisquilla* species, *C. quinquelobata* is easily distinguished from congeners by the presence of the submedian bosses overreaching the bases of the submedian teeth on the telson. The specimens examined here agree well with these characteristics.



Fig. 34. *Chorisquilla quinquelobata*, male, TL 16 mm, AM P91059.

13. *Chorisquilla similis* Ahyong, 2002 (Fig. 35)

Chorisquilla similis Ahyong, 2002: 737–740, fig. 1.

Material examined

Type material

Holotype: USNM 306086, 1 female, TL 20 mm, Society Islands, French Polynesia,

17°30' 45"5, 149°55' 34"N, 9.1–12.2 m, RW89–25, rotenone, R. Winterbottom, 11 Decemeber 1989.

Diagnosis. Telson with 2 pairs of primary teeth (submedian, intermediate); dorsal surface with 5 strongly inflated longitudinal bosses; surface of all 5 bosses smooth, without setae, tubercles or spines; median boss extending to anterior extent of posterior median emargination; movable apices of primary submedian teeth articulating submarginally; submedian and intermediate denticles absent. Mandibular palp 2-segmentend. Maxilliped 1–5 with epipod. Abdominal somite 1 with pleural plate. Abdominal somite 6 with submedian bosses separated by deep, narrow fissure. Uropodal endopod without dorsal spines. Raptorial claw dactylus with inner proximal margin convex, inflated, and with anteriorly directed tubercle; propodus without movable spine proximally.

Habitat. Information is not available.

Distribution. Known only from the Sociefy Islands, French Polynesia (type locality) in depth of 9.1–12.2 m (Ahyong, 2002).

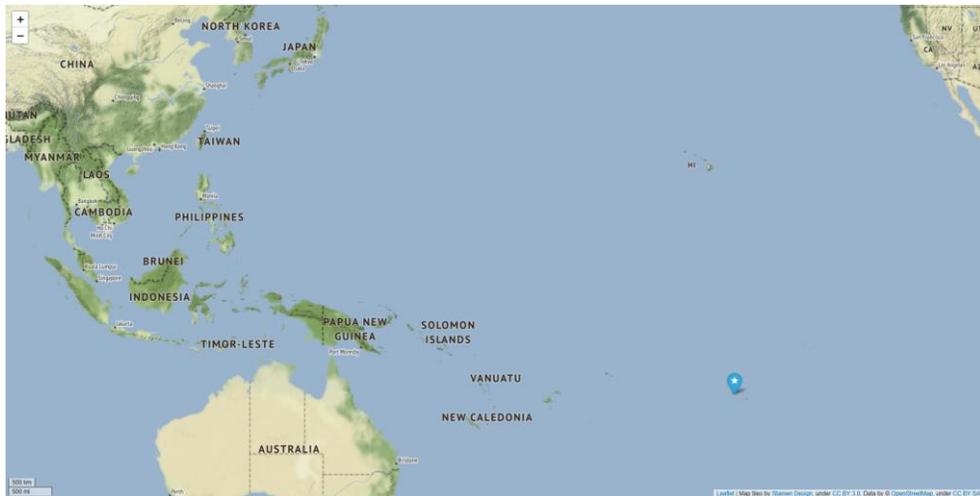


Fig. 35. Distribution of *Chorisquilla similis* Ahyong, 2002. Legend: star = type locality.

Remarks. Among *Chorisquilla* species, *C. similis* is morphologically *C. quinquelobata* from Christmas Island, Indian Ocean, and together differ from all other congeners by the combination of the following characteristics: 1) the presence of smooth, strongly inflated telson bosses which are separated dorsally by deep fissure, 2) submarginally articulating movable apices of the primary submedian teeth. *C. similis*, however, differs from *C. quinquelobata* in the following features of raptorial claw: 1) the presence of the inflated inner proximal margin and a distinct mesial tubercle of the dactylus of the raptorial claw 2) the absence of the proximal movable spine of the propodus, 3) the deeper and more strongly inflated outer basal portion of the dactylus. Also, this species has the distinctly more elongated median boss of the telson and the boss reaches the anterior margin of the posterior median emargination and the submedian bosses of abdominal somite 6 are separated by a deep fissure instead of a shallow groove and the basal portion of the rostral plate is distinctly more elongate than the basal width of the median spine. The specimens examined here agree well with these characteristics.

14. *Chorisquilla spinosissima* (Pfeffer, 1888) (Figs. 36–37)

Gonodactylus spinosissimus Pfeffer, 1888: 35 [type locality: Mombasa, Kenya, 4°05'S 39°41'E]; Nobili, 1906: 326–327; Kemp, 1913: 150, 191, pl. 10: figs. 124, 125; Hansen, 1926: 38; Holthuis, 1941: 291–293, fig. 9c.

Protosquilla spinosissima: Manning, 1968: 55–56.

Chorisquilla spinosissima: Manning, 1969: 158, 159; Manning, 1991: 5; Ahyong, 2001: 95–97, fig. 46.

Material examined

Type material

Neotype: ZMUC CRU 3671, 1 male, TL 22 mm, Mombasa, Kenya, 4°05'S 39°41'E, 1–2 m, corals, Galathea stn 256, 22 March 1951.

Non type material

Sri Lanka: AM P3971, female, TL 23.5 mm, Indian Museum Marine Survey, no

further information.

Diagnosis. Telson (Fig. 37) with 2 pairs of primary teeth (submedian, intermediate); dorsal surface covered with long spines, obscuring median and submedian bosses; median boss circular to ovate; submedian bosses ovate, extending posteriorly beyond apex of median excavation; lateral margin with 7–12 spines; ventral surface with low postanal carina; with 7–10 spiniform submedian denticles and 2 spiniform intermediate denticles. Abdominal somite 4 (Fig. 37) smooth medially; laterally corrugated. Abdominal somite 5 (Fig. 37) smooth medially, with row of short, transverse grooves on posterior margin; laterally corrugated; posterior margin unarmed. Abdominal somite 6 (Fig. 37) anterior margin with row of short posteriorly directed spines; dorsally ornamented with numerous long spines. Uropodal protopod (Fig. 37) dorsally with 1–2 short proximal spines and shorter spine above proximal exopod articulation. Uropodal exopod proximal segment outer margin with 10–11 movable spines. Raptorial claw propodus with movable spine proximally.

Habitat. Rock or coral crevices on coral reefs, from the reef flat, reef slope, and vertical drop-offs down to in depth of 14 m (Ahyong, 2001).

Distribution. Zanzibar, Ceylon, northwestern Australia and the Nansha Islands, and South China Sea (Ahyong, 2001).



Fig. 36. Distribution of *Chorisquilla spinosissima* (Pfeffer, 1888). Legend: star = type locality; circle = distribution in worldwide.

Remarks. *Chorisquilla spinosissima* is most similar to *C. hystrix* (Nobili 1899) in all respect and they were synonymized by Manning (1995). After that, Ahyong (2001) removed *C. hystrix* (Nobili 1899) from the synonymy of *C. spinosissima* (Pfeffer 1888) by the presence of differences in the following characteristics: 1) color pattern (whether banded or uniformly mottled), 2) the morphology of the mid-dorsal surface of abdominal somite 5 (whether with carinae or shallow pits), 3) the density of dorsal spines on abdominal somite 6, and 4) the density of dorsal spines on abdominal somite 6. The two species are clearly distinguished as follows: 1) The color pattern of *C. spinosissima* is uniformly dark green-brown, while *C. hystrix* has irregular, mottled, brown transverse bands. 2) The morphology of the mid-dorsal surface of abdominal somite 5 of *C. spinosissima*, the mid-posterior margin of abdominal somite 5 is smooth or has short, shallow, transverse grooves, abdominal somite 4 lacks a posterolateral spine, two spines are usually present on the dorsal proximal margin of the uropodal protopod. In *C. spinosissima*, the posterior half or one-third of the mid-dorsal surface of abdominal somite 5 bears several deep, broad depressions forming distinct carinae. 3) The density of dorsal spines on abdominal somite 6 is as follows: In *C. hystrix*, three rows of dorsal spines are present medially on the abdominal somite 6, with additional spines interspersed between the rows

laterally. In *C. spinosissima*, four or five rows of dorsal spines are present medially on the abdominal somite 6, again with additional spines interspersed between the rows laterally. Both species bear a transverse row of short, posteriorly directed spines along the anterior margin of abdominal somite 6. Additionally, this row of spines can be concealed by the posterior margin of abdominal somite 5 and is best observed by flexure of the posterior abdominal segments. The specimens examined here agree well with differences comparing two species.



Fig. 37. *Chorisquilla spinosissima*, female, TL 23.5 mm, AM P3971.

15. *Chorisquilla hystrix* (Nobili, 1899) (Figs. 38–39)

Protosquilla hystrix Nobili, 1899: 276 [type locality: Wongat Island, Madang, Papua New Guinea]; 1906: 327.

Gonodactylus spinosissimus: Hansen, 1926: 38; Holthuis, 1941: 291–293, fig. 9c (not *Gonodactylus spinosissimus* Pfeffer, 1888).

Protosquilla spinosissima: McNeill, 1968: 89–90 [not *Protosquilla spinosissima* (Pfeffer, 1888)].

Chorisquilla spinosissima: Moosa, 1991: 164; Manning, 1995: 97–98, fig. 48; Debelius, 1999: 284 [not *Chorisquilla spinosissima* (Pfeffer, 1888)].

Mesacturoides spinosocarinatus: Gosliner et al., 1996: 197 [not *M. spinosocarinatus* (Fukuda)].

Materials examined

Type material

Lectotype: AM P58557, male, TL 19 mm, Wongat Island, Madang, Papua New Guinea, P. Hutchings, 29 Jun 1987.

Non type material

Australia: AM P67858, two females, TL 24–25 mm, Queensland, lagoon drop off, Lizard Island, coll. P.A. Hutchings & P.B. Weate, 6 November 1976.

Diagnosis. Telson (Fig. 39) with two pairs of primary teeth (submedian, intermediate); dorsal surface entirely covered with long spines, obscuring median and submedian bosses; median boss circular to ovate; submedian bosses ovate, extending posteriorly beyond apex of median excavation; lateral margin with 7–10 spines; with low, short, postanal carina; with 9–13 spiniform submedian denticles, 2 spiniform intermediate denticles. Posterior margin of telson divided by deep V-shaped median emargination. Abdominal somites 4–5 (Fig. 39) with posterolateral spine. Abdominal somite 4 smooth medially; laterally corrugated. Abdominal somite 5 (Fig. 39) corrugated laterally; smooth proximomedially, distomedially with 4–6

carinae intervened by deep cavities; posterior margin unarmed. Abdominal somite 6 (Fig. 39) anterior margin with row of short posteriorly directed spines; dorsally ornamented with numerous long spines. Uropodal protopod (Fig. 39) dorsally with slender proximal spine and shorter spine above proximal exopod articulation. Uropodal exopod proximal segment outer margin with 9–11 movable spines.

Habitat. Coral reef flats among rubble (Ahyong, 2001)

Distribution. Australia, Papua New Guinea, eastern Indonesia and New Caledonia. (Ahyong, 2001).



Fig. 38. Distribution of *Chorisquilla hystrix* (Nobili, 1899). Legend: star = type locality; circle = distribution in worldwide.

Remarks. Features distinguishing *C. hystrix* and *C. spinosissima* are discussed under the account of the former. *C. spinosissima* can be easily distinguished from *C. hystrix* by the presence of differences comparing two species. The specimens examined here agree well with these characteristics.



Fig. 39. *Chorisquilla hystrix*, female, TL 25 mm, AM P67858.

16. *Chorisquilla tweediei* (Serène, 1950) (Figs. 40–41)

Gonodactylus tweediei Serène, 1950: 571–572.

Chorisquilla tweediei: Ahyong, 2001: 92, 97–99, fig. 47; 2002: 65–66.

Material examined

Type material

Lectotype: AM P10805, Elizabeth Reef, North Lord Howe Island, no further

information.

Non type material

Australia: AM P60071, 15 males (TL 20–30 mm), 18 females (TL 18–25 mm), Queensland, Capricorn Group, One Tree Island, no further information.

Diagnosis. Telson (Fig. 41) with 3 pairs of primary teeth; outermost primary teeth indicated by short notch; dorsal surface with median and submedian bosses; median boss circular; submedian bosses ovate to pyriform, extending posteriorly beyond apex of median excavation; dorsal surface and lateral margins densely covered with fine setae; with 10–14 submedian setae and 2 intermediate setae; ventral surface without postanal carina. Abdominal somite 4 (Fig. 41) with rounded posterolateral angle. Abdominal somite 5 (Fig. 41) smooth medially, laterally with 2 low carinae above marginal carina. Abdominal somite 6 (Fig. 41) densely covered with short, fine setae; submedian and intermediate bosses unarmed, lateral boss with posterior spine. Uropodal protopod (Fig. 41) unarmed dorsally excepting dorsal spine above proximal exopod articulation; exopod proximal segment outer margin with 9–10 movable spines. Raptorial claw propodus with movable spine proximally.

Habitat. Coral reefs in depth of 1–16 m (Schram & Müller, 2004).

Distribution. Australia and New Caledonia (Schram & Müller, 2004).



Fig. 40. Distribution of *Chorisquilla tweediei* (Serène, 1950). Legend: star = type locality; circle = distribution in worldwide.

Remarks. Among *Chorisquilla* species, *C. tweediei* is morphologically similar to *C. trigibbosa* in that both species have three pairs of telson primary teeth and no spine in the telson lateral margin. *C. trigibbosa*, however, differ from *C. tweediei* in having the following characteristics: (1) the presence of a small, round boss anterior to each submedian boss on the telson, (2) the dorsal surface of the telson including the bosses which are covered with low, sparse spines instead of a momentum of long, fine setae, and (3) the ovate median and submedian telson bosses. The specimens examined here agree well with these characteristics.



Fig. 41. *Chorissquilla tweediei*, male, TL 25 mm, AM P60071.

17. *Chorissquilla trigibbosa* (Hansen, 1926) (Fig. 42)

Gonodactylus trigibbosus Hansen, 1926: 36–38, pl. 2, fig. 5a–b.

Chorissquilla trigibbosa: Manning, 1969: 159.

Type material

Holotype: ZMA De 103021, Saleyer anchorage (Station 213), Indonesia, no further information.

Diagnosis. Telson with 3 pairs of primary teeth; outermost primary teeth indicated by short notch; dorsal surface with median and submedian bosses; median boss and submedian bosses ovate; submedian bosses with small, rounded boss proximally; dorsal surface with low, sparse setae; ventral surface without postanal carina. Abdominal somite 4 with rounded posterolateral angle. Abdominal somite 5 smooth medially, laterally with 2 low carinae above marginal carina. Uropodal protopod unarmed dorsally excepting dorsal spine above proximal exopod articulation; exopod proximal segment outer margin with 9–10 movable spines. Raptorial claw propodus with movable spine proximally.

Habitat. The information is not available.

Distribution. Indonesia (Saleyer) (Schram & Müller, 2004).



Fig. 42. Distribution of *Chorisquilla trigibbosa* (Hansen, 1926). Legend: star = type locality.

Remarks. Features distinguishing *C. tweediei* and *C. trigibbosa* are discussed under the account of the former. *C. trigibbosa* can be easily distinguished from *C. tweediei* by the presence of differences comparing two species. The specimens examined here agree well with these characteristics.

18. *Chorisquilla tuberculata* (Borradaile, 1907) (Fig. 43)

Protosquilla tuberculata Borradaile, 1907: 209–210, pl. 22, fig. 1.

Gonodactylus tuberculatus: Kemp & Chopra, 1921: 311.

Chorisquilla tuberculata: Ahyong, 2001: 88; 2002: 369.

Type material

Holotype: Madagascar: MZC I.50, 2645, Providence Island, no further information.

Diagnosis. Telson with two pairs of primary teeth (submedian, intermediate); dorsal surface with 3 broad, tuberculate longitudinal bosses; submedian bosses not extending posteriorly beyond apex of median excavation in posterior margin. Mandibular palp 2-segmented. Maxilliped 1–5 with epipod. Abdominal somite 1 with pleural plate. Abdominal somite 6 fused with telson but usually demarcated by dorsal groove, without posterolateral spine. Uropodal endopod without dorsal spines.

Habitat. The information is not available.

Distribution. Madagascar (Providence Island), Japan, New Caledonia, Marquesas (Schram & Müller, 2004).



Fig. 43. Distribution of *Chorisquilla tuberculata* (Borradaile, 1907). Legend: star = type locality; circle = distribution in worldwide.

Remarks. Among *Chorisquilla* species, *C. tuberculata* is most similar to *C. andamanica* by the following features: 1) the presence of 2 pairs of telson primary teeth, 2) the absence of numerous spines on the dorsal surface of telson, 3) the presence of submedian bosses of telson not extending to the base of submedian teeth. *C. tuberculata* however, is easily distinguished from congeners including *C. andamanica*, by the presence of submedian bosses not extending posteriorly beyond the apex of median excavation in the posterior margin and tuberculate surface of three bosses on the telson. *C. andamanica* has submedian bosses extending posteriorly beyond the apex of median excavation and smooth surface of bosses.

CHAPTER 2.

TAXONOMIC REVISION OF THE SELECTED STOMATOPOD GROUP RELATED TO ROSTRAL PLATE

2-1. Taxonomic review of the genus *Gonodactylaceus* (Gonodactyloidea: Gonodactylidae)

INTRODUCTION

Gonodactylaceus Manning, 1995, is one of nine genera of Gonodactylidae Giesbrecht, 1910, distinguished from other gonodactylids by the presence of a subglobular cornea, five longitudinal dorsal carinae on telson, and the absence of a movable proximal spine on the propodus of the raptorial claw. Among *Gonodactylaceus* species, characteristics of rostral plate, abdominal somite 6 and telson are used as the main identification keys and the identification of the stomatopods can be changed according to the different interpretation of these characteristics. Among them, *G. falcatus* (Forskål, 1775) was originally described from the Red Sea and is a widespread species, ranging from the Eastern Africa the Red Sea, to Indonesia, Australia, New Caledonia, Japan, Fiji, Hawaii, French Polynesia, New Zealand (Ahyong, 2012) and Korea (Hwang et al., 2018), with six nominal species in its synonymy. In this part, these characteristics of the all species of the genus *Gonodactylaceus* including *G. falcatus*, were examined.

MATERIALS AND METHODS

MATERIAL

The study area spans all localities within the known distribution of *Gonodactylaceus falcatus* and its nominal species, ranging from the Eastern Africa and the Red Sea, Maldives, Vietnam, to Indonesia, Vietnam, Australia, New Caledonia, Japan, Hawaii, Papua New Guinea, New Zealand and Korea. Specimens of each nominal species were examined based on those collected from respective type locality. Specimens examined are deposited in the Australian Museum, Sydney, Australia (AM);

Queensland Museum, Brisbane, Australia (QM); Tasmanian Museum, Hobart, Australia (TM); Western Australian Museum, Perth, Australia (WAM); Museum Victoria, Melbourne, Australia (NMV); South Australia Museum, Adelaide, Australia (SAM); National Institute of Water and Atmospheric Research, New Zealand (NIWA); Marine Arthropod Depository Bank of Korea, Seoul National University, Seoul, Korea (MADBK); National Institute of Biological Resources, Incheon, Korea (NIBRIV); National Museum of Natural History, Smithsonian Institution, Washington D.C. (USNM); Natur-Museum und Forschungsinstitut Senckenberg, Frankfurt am Main (SMF); the Zoological Reference Collection of the Lee Kong Chian Museum of Natural History (ZRC); Leiden Nationaal Natuurhistorische Museum, National Museum of Natural History Naturalis, Darwinweg 2, Leiden, Netherlands (RMNH); National Science Museum, Tokyo, Japan (NSMT); University Museum of Zoology, Cambridge, England (MZC); Florida Museum of Natural History, USA (FLMNH).

METHODS

The barcoding region of the mitochondrial cytochrome oxidase subunit 1 gene were sequenced. Thirty sequences from the specimens of *Gonodactylaceus falcatus* from throughout its range for comparison with published sequences from each nominal species, previously identified as *Gonodactylaceus falcatus* (GenBank accession numbers: KM 982433.1, HM 138786.1, AF205230.1, KM 982437.1, AF205251.1, AF205232.1, KY 263447.1) (BOLD accession numbers: DSMYS124-07, DSMYS125-07). Additionally, two published sequences from *Gonodactylellus affinis* were selected as the outgroup owing to the close relationship between *Gonodactylaceus* and *Gonodactylellus* (Ahyong & Harling 2000; Ahyong & Jarman 2009; Porter et al. 2010). Their GenBank Accession numbers of *Gonodactylellus affinis* are KM982426.1 and KM982428.1.

Key to species of *Gonodactylaceus* ≥ TL 20 mm

1. Abdominal somite 6 with median carinule. Telson ventral surface with postanal carina 2
 - Abdominal somite 6 without median carinule. Telson ventral surface with or without postanal carina 4
2. Abdominal somites 1–5 ornamented dorsally with fine transverse grooves. Rostral plate with sharp anterolateral angles *G. graphurus*
 - Abdominal somites 1–5 smooth, without fine transverse grooves 3
3. Margin of uropodal endopod with multiple row of setae, some deflected dorsally. Uropodal protopod with two lobes between terminal spines *G. randalli*
 - Margin of uropodal endopod with single row of setae, some deflected dorsally. Uropodal protopod with one lobes between terminal spines.5
4. Rostral plate with angular anterolateral corners. Telson ventral surface with sharp postanal carina *G. glabrous*
 - Rostral plate with blunt, rounded anterolateral corners. Telson ventral surface with or without postanal carina 6
5. Telson ventral surface with sharp, distinctively inflated postanal carina *G. falcatus*
 - Telson ventral surface with low, shallow postanal carina *G. siamensis*
6. Telson with knob undivided. Telson ventral surface with shallow postanal carina *G. ternatensis*
 - Telson with knob bilobed (occasionally indistinctly bilobed). Telson ventral surface with or without postanal carina 7
7. Anterior margin of basal portion of rostral plate “distinctively transvers” and rostral plate “slender”. Telson ventral surface without postanal carina *G. mutatus*
 - Anterior margin of basal portion of rostral plate “posteriorly sloping” and rostral plate “thicker” Telson ventral surface with shallow postanal carina (occasionally indistinct) *G. insularis*

SYSTEMATIC ACCOUNTS

Order Stomatopoda Latreille, 1817

Superfamily Gonodactyloidea Giesbrecht, 1910

Family Gonodactylidae Giesbrecht, 1910

Genus *Gonodactylaceus* Manning, 1995

Gonodactylaceus Manning, 1995: 42–43. (type species *Gonodactylus ternatensis* de Man, 1902, by original designation. Gender masculine).

Diagnosis. Eye subcylindrical; cornea narrower than stalk dorsally. Ocular scales small, narrower than basal width of median spine of rostral plate. Rostral plate with slender median spine and short trapezoid basal portion. Mandibular palp 3-segmented. Anterolateral margins of carapace convex, extending anteriorly beyond base of rostral plate. Opposable margin of propodus of raptorial claw without proximal movable spine. Telson with 5 mid-dorsal carinae; intermediate carina without accessory longitudinal carina on mesial margin; anus located ventrally. Uropodal protopod with one or two proximal lobes between terminal spines; endopod without spines on inner margin.

Composition. *G. falcatus* (Forskål, 1775); *G. glabrous* (Brooks, 1886); *G. graphurus* (Miers, 1875); *G. insularis* Manning & Reaka, 1982; *G. mutatus* Lanchester, 1903; *G. randalli* (Manning, 1978); *G. siamensis* Manning & Reaka, 1981; and *G. ternatensis* (de Man, 1902).

Remarks. Among Gonodactyloids, Gonodactylids can be easily distinguished from other families by the combination of the following characteristics: (1) the presence

of subterminal ischiomerall articulation and strongly inflated base of dactylus of raptorial claw, (2) the presence of subterminal uropodal exopod segment articulation, and (3) the presence of straight distal spines on outer margin of uropodal exopod. Among them, *Gonodactylaceus* differs from other gonodactylids by the combination of the following characteristics: (1) the presence of a subglobular cornea, (2) the presence of five longitudinal dorsal carinae on the telson, and (3) the absence of a movable proximal spine on the propodus of the raptorial claw. Among *Gonodactylaceus* species, the presence of fine transverse grooves of abdominal somite 1–5, the median carinule on abdominal somite 6, the bilobed knob of telson, and angular anterolateral corner of the rostral plate, are used as identification keys. *Gonodactylaceus* species, however, have an allometric variation on these characteristics. In this part, a taxonomic review for *Gonodactylaceus* species was conducted. As a result of, the rostral plate characteristics, median carinule on abdominal somite 6, and postanal carina on ventral surface were described in detail, recognizing as four separate species within synonyms of *Gonodactylaceus falcatus*.

Taxonomic key characters to classify *Gonodactylaceus* species newly

ROSTRAL PLATE

In some gonodactylids that Gonodactylids belongs to, the rostral plate has a “trispinous” form consisting of slender median spine and a short, broad basal portion in which the anterolateral margins are variable (Schram et al., 2013) and it is used as key characters in identification of the species according to its character states. In general, the characters of the rostral plate can be changed according to allometric growth in the relative length of the rostral plate and anterior margins of the basal portion. The rostral spine is proportionally longest in small specimens and becomes shorter with increasing body size and can become proportionally thicker. Also, the anterior margin of the basal portion of the rostral plate slopes more posteriorly in smaller specimens and become transverse or even slightly concave with increasing body size. We divided a large series of specimens including those collected from the respective type locality of nominal species, into similar size and re-examined this

morphological trait. In case of *Gonodactylaceus falcatus*, it evidently matures at a small size, with the penes and modified pleopod 1 endopod well developed even in the smallest males examined (TL 9 mm; Ah Yong, 2001) and reaches a considerably larger size (TL 80 mm; Ah Yong, 2001). Accordingly, the specimens including type specimens collected from throughout its range of *G. falcatus* were divided by following total length (TL): relatively small size (TL less than 20 mm), small size (TL 20 mm or more and 30 mm or less), middle size (TL 30 mm or more and 40 mm or less), large size (TL 40 mm or more and 50 mm or less), relatively large size (50 mm or more). After that, we examined the morphological character states of the rostral plate.

As a result, two forms in the species *G. falcatus* are recognized at each similar size: One form, anterior margin of the basal portion of the rostral plate is distinctively posteriorly sloping, corresponding to *Gonodactylus insularis* and *Gonodactylus takedai*. The other form, however, the shape is transverse (or even concave), corresponding to the rest of nominal species of *G. falcatus*. At any given size in the respective forms, we recognize the character of the rostral plate as a constant morphological character in *G. falcatus* nominal species.

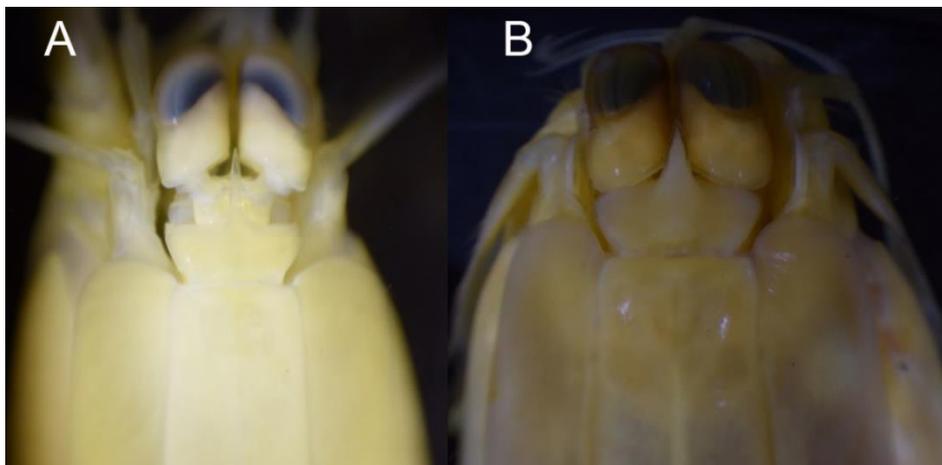


Fig. 44. A, *Gonodactylaceus falcatus* (Forskål, 1775), male, TL 55 mm, Red Sea, USNM 119278; B, *Gonodactylaceus insularis* Manning & Reaka, 1982, male, TL 56 mm, Japan, USNM120731.

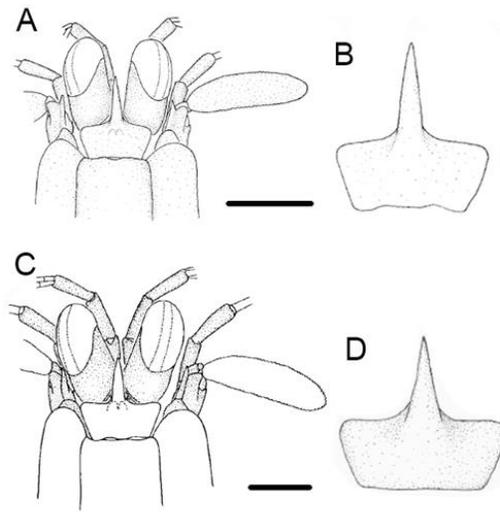


Fig. 45. A–B: *Gonodactylaceus insularis* Manning & Reaka, 1982 (NIWA 23968, female, TL 30 mm). A, anterior cephalon; B, rostral plate. C–D: *Gonodactylaceus siamensis* Manning & Reaka (AM P54457, male, TL 37 mm). A, anterior cephalon; B, rostral plate. Scale bars: A = 2.5 mm, B= 1.2 mm. C–D =1.25 mm. Modified from Ahyong (2001, 2012).

Postanal carina on telson ventral surface

On the ventral surface of the telson, the anus is placed proximo-medially, and various other carinae may be present (Schram et al., 2013) and these ventral telson carinae used as key characters in identification of the species according to its characteristics state (presence or absence, shallow or sharp, number of carinae). In case of the nominal species of *G. falcatus*, it exists in three forms following groups: One group has sharp and distinctively inflated postanal carina, corresponding to *G. falcatus* sensu stricto. It is clearly evident even at a relatively small size (female, TL 18 mm, UF37177). The second group has low and shallow postanal carina, corresponding to *G. siamensis* and *G. gravieri*. Most typical specimens have this characteristics state, but occasionally it is very shallow and can be difficult to distinguish. The Third group has no postanal carina, corresponding to *G. mutatus*, *G. insularis* and *G. takedai*. Most typical specimens have this characteristics state, but occasionally it remains indistinct traces. According to the result of the re-examination of morphological character based on a large series of specimens of *G. falcatus* as well as respective

original description and published accounts, we recognize the character of the postanal carina on telson ventral surface as a constant morphological character in the nominal species of *G. falcatus*.

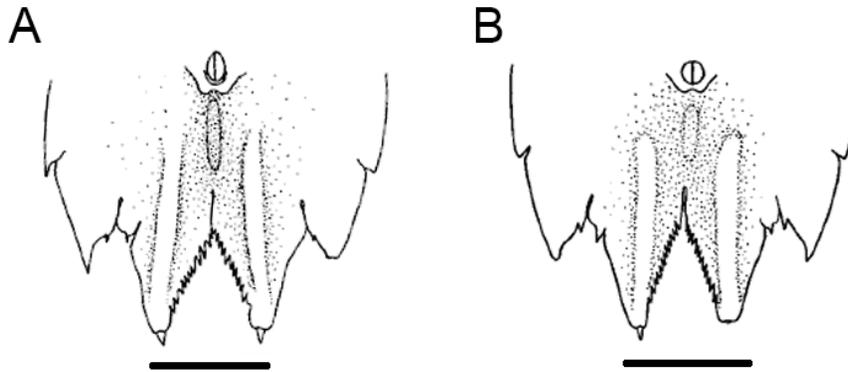


Fig. 46. Telson, ventral. A, *Gonodactylaceus siamensis* Manning & Reaka (AM P54457, male, TL 37 mm); B, *Gonodactylaceus insularis* Manning & Reaka, 1982 (NIWA 23968, female, TL 30 mm). Modified from Ahyong (2001, 2012).

Median carinule on the sixth abdominal somite

The median carinule is a shallow groove between the submedian carina of the sixth abdominal somite. Within *Gonodactylaceus* species, *G. graphurus* and *G. randalli* have median carinule, while *G. ternatensis* and *G. glabrous* doesn't have it is used as key characters in the identification of the species. In the case of *G. falcatus*, some studies had been conducted on whether the presence of the median carinule on AS6 is a constant morphological trait in *G. falcatus* (Manning, 1978; Ahyong, 2001). We re-examined this morphological trait based on a large series of specimens of *G. falcatus* as well as those collected from the respective type locality of nominal species. As a result, we distinctively recognized three forms in the nominal species of *G. falcatus* following groups: One group has a median carinule, corresponding to *G. falcatus* sensu stricto. Except for relatively small size (female, TL 18 mm, UF37177), the specimens examined here have it. The second group, most typical specimens have a median carinule, corresponding to *G. siamensis* and *G. gravieri*. However, some specimens occasionally have faint carinule exist as difficult to

distinguish. Of the specimens examined here, 80% of specimens examined bear distinct median carinule on AS6. The third group doesn't have a median carinule corresponding to *G. mutatus*, *G. insularis* and *G. takedai*. In the case of *G. mutatus*, this species doesn't have a median carinule based on specimens as well as original description and published accounts.

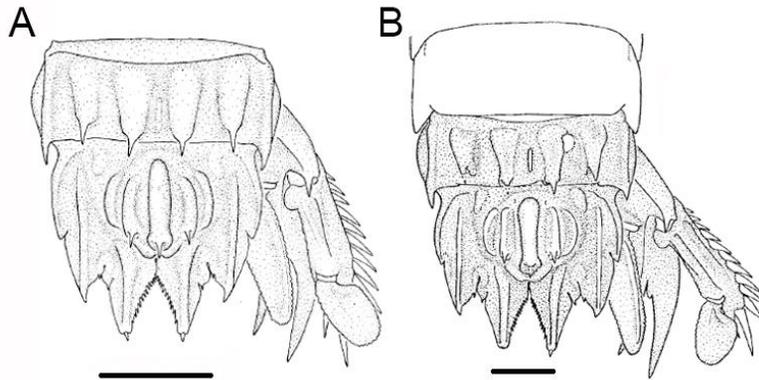


Fig. 47. Abdominal somites 5–6, telson and uropod. A, *Gonodactylaceus insularis* Manning & Reaka, 1982 (NIWA 23968, female, TL 30 mm). B, *Gonodactylaceus siamensis* Manning & Reaka (AM P54457, male, TL 37 mm). Scale bars: A = 2.5 mm, B= 1.25 mm. Modified from Ahyong (2001, 2012).

RESULTS

Molecular data

Within nominal species of *Gonodactylaceus falcatus*, four separate forms are recognized based on molecular data following as (Fig. 48): a primarily Indian Ocean population corresponding to *G. siamensis* and *G. gravieri*, a western Indian Ocean population corresponding to *G. falcatus* sensu stricto, a Maldive population corresponding to *G. mutatus*, a Pacific population corresponding to *G. insularis* and *G. takedai*. Mean divergence among the respective clades was following as, corresponding to separate species: the difference between it and a Western Indian

Ocean population and a Maldivian population is 8%, and difference from a Pacific form is 15%. In addition, the difference between a Maldivian population and a Pacific population is 16%, the difference between a Pacific population and a western Indian Ocean population is 13%. Internal divergence in COI of a primarily Indian Ocean population was 0.0–5.0 %. In case of the rest three forms, internal divergence in COI was 0.0–2.0 %. Observed intra-specific and inter-specific divergences among the four forms within nominal species of *G. falcatus* are consistent with those observed for other species of Stomatopoda at <2.4%, >3.0%, respectively (Tang et al., 2010). The comparative analysis of genetic distances shows that respective species of nominal species of *G. falcatus* are distinct and separate species, so their synonymy of *G. falcatus* can be removed.

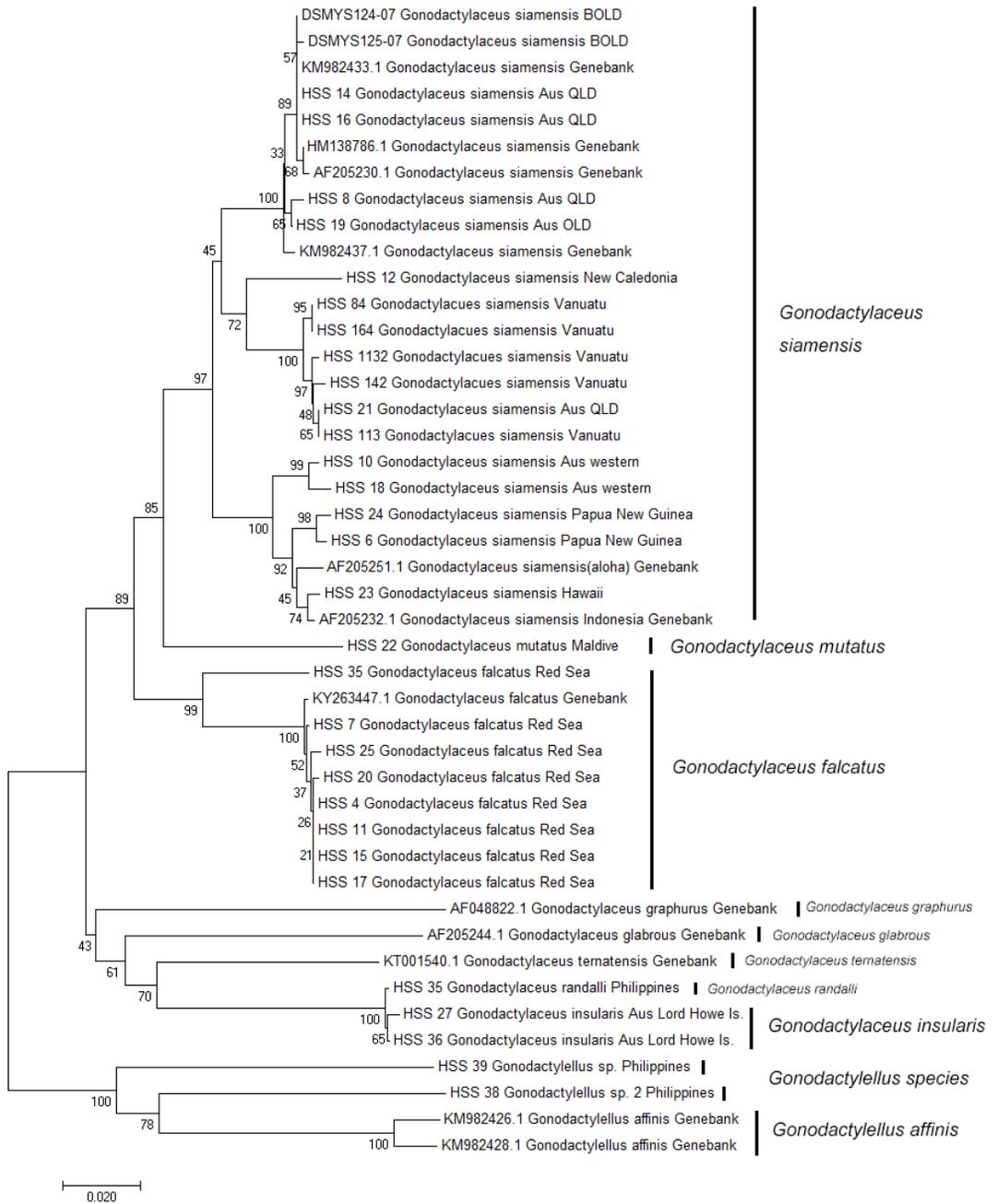


Fig. 48. Neighbor-joining (NJ) tree of COI sequences from four nominal species of *Gonodactylaceus falcatus*, four *Gonodactylaceus* species, and *Gonodactylellus* species as outgroup.

19. *Gonodactylaceus falcatus* (Forskål, 1775) (Figs. 49–50)

Cancer falcatus Forskål, 1775: 96.

Gonodactylus falcatus: Manning & Lewinsohn, 1981: 314–316, fig. 1.

Gonodactylaceus falcatus: Manning, 1995: 19, 42; Ahyong, 2001: 35–38 [part, not *G. falcatus*, (Forskål, 1775)].

Material examined

Non type material

Saudi Arabia: RMNH S874, female (TL 63 mm) (Neotype of *G. falcatus*, (Forskål, 1775); SMF-RSS1-2012-36, 2 males (TL 41–42 mm), 5 females (TL 19–47 mm), Zuluf Island, 28°22'30.0"N 49°17'30.0"E, 0.5–1m, under stones, coll. Biosing, 26 Feb 2012; SMF-RSS1-2012, St. 1, 3–4m, from pocillopora colony, coll. V. spiridonov, 19 Feb 2012; SMF, 1 female (TL 31 mm), north of Jeddah, coll. Biosing, 26 April 2011; SMF-RSS1-54, 1 female (TL 37 mm), Al Lith, 20°10'01.9"N 40°13'23.9"E, Pier, 0.5 m, by Handdredging, coll. Biosing, 5 March 2012; UF 37205, 1 male (TL 45 mm), off thuwal, Abu Shosha Reef, 22°12'10.4"N 39°02'54.2"E, 5 m (Shelter side), coll. Jenna Moore and Jessica Bouwmeester, 24 March 2013; UF 37162, 1 male (TL 31 mm), Al Lith, 1–2m mangroves, 20°10'01.9"N 40°13'23.9"E, coll. Arthur Anker, Patrick Norby, Jenna Moore, 21 March 2013; UF 37163, 1 male (TL 31 mm), Al Lith, 1–2m mangroves, 20°10'01.9"N 40°13'23.9"E, coll. Arthur Anker, Patrick Norby, Jenna Moore, 21 March 2013; UF 37177, 1 female (TL 17.5 mm), off thuwal, Abu shosha Reef, 22°12'10.4"N 39°02'54.2"E, 5 m (Shelter side), coll. Jenna Moore and Jessica Bouwmeester, 24 March 2013.

Madagascar: UF 14011, 1 female (TL 28 mm), Nosy Be. W of Heilville, 13°24'56.2"N 48°14'44.2"E, sandflat, sea grass, patch reefs, in rubble, 0–3 m, coll. Arthur Anker, G. Bakary, F. Michonneanu, G. paulay, T. Werner, 25 May 2008; UF 14353, 1 female (TL 28 mm), Nosy Be, across bay from CNRO complex, off Lokobe Reserve, 13°24'50.0"N 48°18'20.2"E, seagrass flat and adjacent sand/reef slope, under rocks, 1–3 m, coll. G. Bakary, H. Bruggemann, F. Michonneau, G. Paulay, T. Werner, 16 May 2008; UF 14331, 1 male (TL 23.3 mm), Nosy Be, across bay from

CNRO complex, off Lokobe Reserve, 13°24'50.0"N 48°18'20.2"E, seagrass flat and adjacent sand/reef slope, under rocks, 1–3 m, coll. G. Bakary, H. Bruggemann, F. Michonneau, G. Paulay, T. Werner, 16 May 2008;

Eritrea: USNM 119280, 1 male (TL 67 mm), 4 females (TL 20–56 mm), Dahlak Archipelago, 0.5–1.5 m, 25 Oct 1962.

Description. Eye subcylindrical, reaching midlength of antennular peduncle article 3. Cornea subconical, narrower than stalk dorsally. Ocular scales small, separate; apics rounded.

Rostral plate (Fig. 50A) not sharply tri-spinuous, longer than wider; median spine longer than base, not reaching to proximal margin of cornea; basal portion with distinctively transverse anterior margin; anterolateral angle rounded; lateral margin divergent anteriorly.

Raptorial claw not sharply tri-spinuous; dorsal margin of carpus unarmed; opposable margin of propodus sparsely pectinate proximally, without movable spine. Dactylus without proximal notch; outer proximal margin strongly inflated; inner distal margin without tooth.

Mandibular palp 3-segmented. Maxillipeds 1–5 with epipod.

Lateral processes of thoracic somites 6–7 width subequal; lower margin rounded, slightly flattened. Anterolateral margin of thoracic somite 8 broadly rounded; sternal keel obsolete.

Endopod of pereopod slender, 2-segmented; basal segment unarmed.

Male Pleopod 1 endopod posterior endite with distinct lateral lobe.

Abdominal somites 1–5 smooth; dorsal surfaces without transverse grooves; posterolateral angles unarmed. AWCLI 729–832. Abdominal somite 6 (Fig. 50B) with posteriorly armed submedian, intermediate and lateral carinae; with distinct median carinule.

Telson (Fig. 50B) wider than long, bearing a couple of three pairs of primary teeth; with 8–12 spiniform submedian denticles and 2 intermediate denticles. Submedian primary teeth (Fig. 50B) unarmed dorsally. Intermedian primary teeth (Fig. 50B) distinct, apex sharp, extending posteriorly well beyond apics of intermediate

denticles. Lateral primary teeth (Fig. 50B) demarcated by short notch, apex angular, not projecting well off margin of telson. Dorsal surface (Fig. 50B) bearing median carina and four pairs of longitudinal carinae. Median carina more strongly inflated in males than in females, bearing posterior spine. Accessory median carina uninterrupted, extending anteriorly beyond dorsal pit but not as far as anterior end of median carina; bearing posterior spine. Submedian carina interrupted; anterior submedian carina smooth, unarmed, arcuate, as long as accessory median carina. Intermediate carina uninterrupted, slender, extending anteriorly as far as accessory median and anterior submedian carinae. Marginal carina uninterrupted, relatively slender, extending to posterior margin of lateral primary tooth. Knob (Fig. 50B) usually medially bilobed (occasionally indistinctly bilobed). Ventral surface with a pair of low carinae on submedian teeth; with distinct, sharp post-anal carina.

Uropodal protopod terminating in 2 flattened spines, outer longer; with small lobe on inner proximal margin of outer proximal margin of inner spine. Uropodal exopod having 10–12 (usually 11) movable spines (distalmost extending to or exceeding apex of distal segment) on proximal segment; margin fully setose; distal margin with ventral spine; distal segment rounded, entire margin setose. Uropodal endopod narrow, bearing low dorsolateral carina; outer margin with a row of marginal setae; length about 4 times width.

Life coloration: Highly variable. The body colouration varies from yellow, orange, blue to green. According to Forskal (1775)'s description, color of the specimens from Red Sea was green, yellowish ventrally. Also, Holthuis (1977: 31, 32) noted that in females the background color was green and that "the other thoracopods are yellow as are often also the pleopods". Males frequently have red intersegmental bands on the body as well as blue antennal scales, the meral spot of the raptorial claw is orange (Manning & Reaka, 1981).

Habitat: Intertidal and shallow subtidal coral and rocky reefs: According to Forskal (1775)'s description, this species occurred in branched coral (*corallia fruitcosa*).

Also, Holthuis (1977) reported numerous lots of this species from corals, which may be its preferred habitat.

Remarks: When Forskal (1775) first established *Gonodactylaceus falcatus* (as *Cancer*), it was originally described from “Djeddah, Red Sea”. According to previous studies of Manning (1968), it belongs to the *Falcatus* group among the three groups comprising Indo-West Pacific species and distinguished by narrow ocular scales and five mid-dorsal carinae on the telson. At that time, it actually was known as a complex of species sharing many morphological features as well as habitat preference, six species were established from the species which belong to the *Falcatus* group. Because each of these species was established based on few specimens and was distinguished by morphological characters which are variable and belong to allometric variation and sex dimorphism in *G. falcatus*. Accordingly, the study of Ahyong (2001) shows that six nominal species are regarded as synonyms of *G. falcatus* and it is a widespread species by those synonyms.

Through the present study, a relatively large number of samples of various sizes are re-examined for considering allometric variation and sex dimorphism. As a result, *G. falcatus* is clearly distinguished from the nominal species and respective nominal species are valid by the morphological traits used in this study. *G. falcatus* sensu stricto is uniquely recognized by the combination of the following character states: 1) anterior margin of the basal portion of the rostral plate is a presence of transverse, which is posteriorly sloping in *G. insularis*, 2) the anterior margin of the basal portion of the rostral plate is more round. And the anterolateral angle is blunter, and 3) the species has both postanal carina on telson ventral surface and median carinule on sixth abdominal somite. Especially, postanal carina on telson ventral surface is more inflated and distinctively sharp when compared to the nominal species of *G. falcatus*. In the case of *G. siamensis* and *G. insularis*, the species have low or shallow carina and *G. mutatus* doesn't have it.

Accordingly, the distribution of *G. falcatus* sensu stricto is the Red Sea and the Persian Gulf as the distribution of widely distributed this species is revised through the present study.

Distribution. Saudi Arabia, Madagascar, and Eritrea.



Fig. 49. Distribution of *Gonodactylaceus falcatus* (Forskål, 1775). Legend: star = type locality; circle = distribution in worldwide.

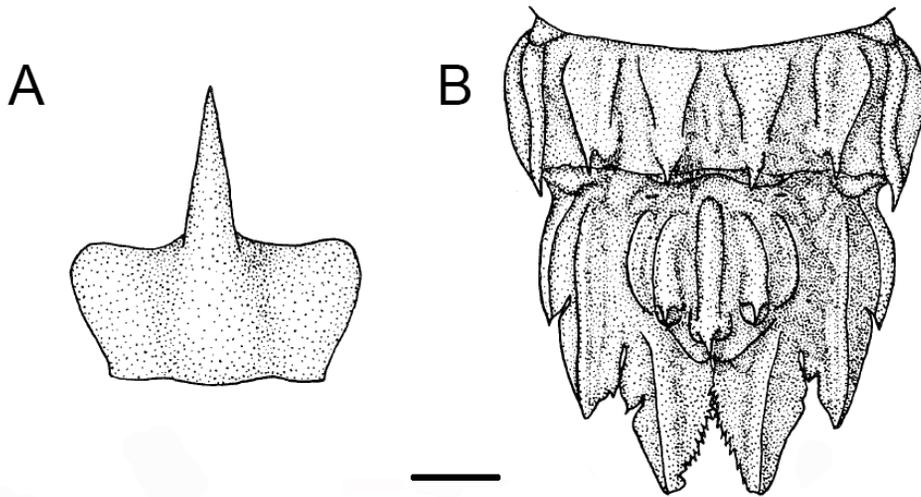


Fig. 50. *Gonodactylaceus falcatus* (Forskål, 1775), female, TL 47 mm, Red Sea. A, rostral plate; B, telson. Scale bars: A–B = 2 mm. Modified from Manning & Lewinsohn (1981).

20. *Gonodactylaceus siamensis* (Manning & Reaka, 1981b) comb. nov.

(Figs. 51–53)

Gonodactylus siamensis Manning & Reaka, 1981b: 479–482, fig. 1

Gonodactylus aloha Manning & Reaka, 1981a: 190–200, figs. 1–3.

Gonodactylaceus gravieri Manning, 1995: 42, 43, 46–48, fig. 13.

Gonodactylaceus falcatus: Manning, 1995: 19, 42–43; Ahyong, 2001: 35–38, fig. 17A–K [part, not *G. falcatus*, (Forskål, 1775)].

Material examined.

Type material

Thailand: USNM 181673, 1 female (TL 36 mm), Sattahip, Gulf of Thailand, 12°40'00.0"N 100°52'00.0"E, coral rubble, intertidal reef flat, coll. M. Reaka & R. Caldwell, Jul 1974 (holotype of *Gonodactylus siamensis* Manning & Reaka).

Non type materials

Australia: Queensland: UF 16800, 1 male (TL 36 mm), Lizard Island, 14°39'46.4"S 145°27'48.6"E, Larger mangrove Bay, shallow sand flat, rocks, burrows, under large rocks or on mounds, 0–1 m, by dip netting, coll. Arthur Anker, Robert Lasley, 11 Feb 2009. AM P84080, 1 female (TL 22 mm), Lizard Island, Coconut Beach reef crest, 14°40'00.0"S 145°27'00.0"E, coll. M. Porter, R.L. Caldwell, T.W. Cronin, J. Marshall, T. Chiou, M. How, M.J. Bok & K.D. Feller, 02 Jun 2010. AM P45588, 1 male (TL 43 mm), 2 females (TL 36–40 mm), Thursday Island, 10°34'42.6"S 142°13'19.4"E, coll. M. Ward. AM P84081, 1 female (TL 26 mm), Lizard Island, Coconut Beach reef crest, 14°40'00.0"S 145°27'00.0"E, coll. M. Porter, R.L. Caldwell, T.W. Cronin, J. Marshall, T. Chiou, M. How, M.J. Bok & K.D. Feller, 02 Jun 2010. AM P84079, 1 male (TL 22 mm), Lizard Island, Coconut Beach reef crest, 14°40'00.0"S 145°27'00.0"E, coll. M. Porter, R.L. Caldwell, T.W. Cronin, J. Marshall, T. Chiou, M. How, M.J. Bok & K.D. Feller, 02 Jun 2010. AM P72227, 1 female (TL 28 mm), Moreton Bay, North Stradbroke Island, Dunwich, 27°30'00.9"S 153°11'07.9"E, coll. S.T. Ahyong & R. Ahyong, Jul 1977. AM P56067, 1 female (TL 32 mm), Capricorn Group, One Tree Island, 23°24'32.7"S

151°57'30.7"E, coll. J.C. Yaldwyn, 19 Nov 1966. AM P56180, 1 male (TL 32 mm), Capricorn Group, North West Island, 23°18'00.0"S 151°42'00.0"E, coll. M. Ward & W. Boardman, Jul 1929. AM P56067, 1 female (TL 32 mm), Capricorn Group, One Tree Island, 23°30'00.0"S 152°05'00.0"E, coll. J.C. Yaldwyn, 19 Nov 1966. AM P56971, 1 male (TL 65 mm), Moreton Bay, North Stradbroke Island, Dunwich, 27°30'00.0"S 153°24'00.0"E, coll. S. Ahyong, P.J. Davie & J. Short, Sep 1998. AM P1759, 1 female (TL 20 mm), Capricorn Group, Mast Head Island, 23°32'20.0"S 151°43'32.0"E. AM P67827, 1 femlae (TL 46 mm), Heron Island, 23°26'00.0"S 151°55'00.0"E, coll. University of Queensland Biology Dept excursion, 30 May 1947. USNM, 3 males (TL 26–35 mm), 1 female (TL 31 mm), Lizard I., coll. N. Marshall, 7 Apr 1994. USNM, 1 male (CL 5.9 mm, broken), Great Barrier Reef, N. Marshall *et al.*, 1991. UF 21512, 1 male (TL 32 mm), Ningaloo Reef, 18°08'52.5"S 112°45'47.8"E, S shallow bommies, back reef, patchy corals on sand, in rubble, 2–3m, coll. Robert Lasly, 15 May 2009. UF 21808, 1 male (TL 31mm), Ningaloo Reef, 18°08'52.5"S 112°45'47.8"E, channel, high energy, 25 m, May 2009. UF 22502, 1 female (TL 31 mm), Ningaloo Reef, Norwegian Bommies, 22°37'23.5"S 113°39'11.5"E, back reef, patches of live corals and rubble on sand, in rubble 6–7 meters, coll. Francois Michonneau, May 2009. AM P92622, 1 female (TL 32 mm), Ningaloo Reef, 22° 42' S, 113° 38' 35" E, coll. P.A. Hutchings, M. Capa, R.S. Wilson & L. Avery, 14 May 2009. AM 21796, 2 females (TL 17–22 mm), Warroora, 23°29'00.0"S 113°48'00.0"E, coll. N. Coleman, 28 Jun 1972. AM P72095, 1 female (TL 47 mm), Houtman Abrolhos, Rat Island, 28°44'00.0"S 113°48'00.0"E, coll. P.A. Hutchings, 25 Aug 1981. AM P54457, 1 male (TL 37 mm), NSW, Shelly Beach, Manly, 33°49'54.0"S 151°17'48.0"E, coll. M. Ward, 26 May 1926.

Vietnam: MNHN St 68, 1 male (TL 52 mm), Poulo Condore, Vietnam, Dawydoff, 8 Feb 1930 (holotype of *Gonodactylaceus gravieri* Manning).

Hawaiian Island, USA: USNM 113724, 1 female (TL 48 mm), Oahu, Hawaii, coral heads, R. Kinzie III (holotype of *Gonodactylus aloha* Manning & Reaka).

Indonesia: SMF 25780, 1 female (TL 51 mm), Ternate, Indonesia, coll. W. Kenthal, 1894 (paralectotype of *Gonodactylus ternatensis* de Man).

New Caledonia: UF 38907, 1 female (TL 23 mm), Ile des Pins, 22°40'05.2"N 167°25'29.3"E, coral rubble, corline algae, 1-2 m, coll. Nathaniel Evans, 2 Nov 2013. AM G1832, 1 female, (TL 46 mm), Oubatche, 20°25'00.0"S 164°38'00.0"E, coll. C. Hedley.

Papua New Guinea: AM P64497, 1 male (TL 18 mm), 2 females (TL 8.2–29 mm), Bootless Bay, west side of Motupore Island, 9°31'30.0"S 147°17'00.0"E, coll. S.P. Arnam & J.K. Lowry, 30 Oct 1980.

Description. Eye (Figs. 52, 53A) subcylindrical, overreaching distal margin of antennular peduncle article 2. Cornea subconical, narrower than stalk dorsally. Ocular scales separate; apics rounded.

Rostral plate (Figs. 52, 53A) about as long as wide; median spine longer than base, not reaching to proximal margin of cornea; basal portion with distinctively transverse anterior margin; anterolateral angle blunt, rounded; lateral margin divergent anteriorly.

Raptorial claw (Fig. 53B) not sharply tri-spinuous; dorsal margin of carpus unarmed; opposable margin of propodus infinitesimally pectinated, without movable spine. Dactylus without proximal notch; outer proximal margin strongly inflated; inner distal margin without tooth.

Mandibular palp 3-segmented. Maxillipeds 1–5 with epipod.

Lateral processes of thoracic somites 6–7 (Figs. 52, 53F) width subequal; lower margin rounded, slightly flattened. Anterolateral margin of thoracic somite 8 broadly rounded; sternal keel obsolete.

Endopod of pereopod slender, 2-segmented; basal segment unarmed.

Male pleopod 1 endopod (Fig. 53C) poseterior endite with distinct lateral lobe.

Abdominal somites 1–5 (Fig. 52) smooth; dorsal surfaces without transverse grooves; posterolateral angles unarmed. AWCLI 719–843. Abdominal somite 6 (Fig. 53E) with posteriorly armed submedian, intermediate and lateral carinae; with short median carinule.

Telson (Figs. 52, 53E) wider than long, bearing a couple of three pairs of primary teeth; with 9–15 spiniform submedian denticles and 2 intermediate denticles.

Submedian primary teeth unarmed dorsally. Intermedian primary teeth distinct, apex sharp, extending posteriorly well beyond apics of intermediate denticles. Lateral primary teeth demarcated by short notch, apex angular, not projecting well off margin of telson. Dorsal surface (Figs. 52, 53E) bearing median carina and four pairs of longitudinal carinae. Median carina more strongly inflated in males than in females, bearing posterior spine. Accessory median carina uninterrupted, extending anteriorly beyond dorsal pit but not as far as anterior end of median carina; bearing posterior spine. Submedian carina interrupted; anterior submedian carina smooth, unarmed, arcuate, as long as accessory median carina. Intermediate carina uninterrupted, slender, extending anteriorly as far as accessory median and anterior submedian carinae. Marginal carina uninterrupted, relatively slender, extending to posterior margin of lateral primary tooth. Knob (Figs. 52, 53E) medially bilobed (occasionally indistinctly bilobed). Ventral surface (Fig. 53I) with a pair of low carinae on submedian teeth; usually with low post-anal carina (occasionally with indistinct carina).

Uropodal protopod (Fig. 52, 53E) terminating in 2 flattened spines, outer longer; with 1–2 (usually 1) lobe on inner proximal margin of outer proximal margin of inner spine. Uropodal exopod having 11–12 (usually 11) movable spines (distalmost extending to or exceeding apex of distal segment) on proximal segment; margin fully setose; distal margin with ventral spine; distal segment rounded, entire margin setose. Uropodal endopod narrow, bearing low dorsolateral carina; outer margin with a row of marginal setae; length about 4 times width.

Life coloration: Highly variable. The body colouration varies from yellow, orange, blue to green. According to Forskal (1775)'s description, color of the specimens from Red Sea was green, yellowish ventrally. Also, Holthuis (1977: 31, 32) noted that in females the background color was green and that “the other thoracopods are yellow as are often also the pleopods”. Males frequently have red intersegmental bands on the body as well as blue antennal scales, the meral spot of the raptorial claw is orange (Manning & Reaka, 1981).

Habitat: Intertidal and shallow subtidal coral and rocky reefs. Usually under boulders and coral rubble or in crevices in rock and sponge (Ahyong, 2001).

Remarks: *Gonodactylaceus siamensis* (as *Gonodactylus*) was originally described from “Gulf of Thailand, Sattahip”, Thailand, based on 10 males (TL 21–39.5 mm), 13 females (TL 16–38 mm) and distinguished from other congeners by the presence of the relatively long spine of rostral plate, slender and sharp carinae on the telson, and undivided knob. In addition, the color pattern (antennal scale and meral spot) was used for a major morphological trait (Manning & Reaka, 1981). As mentioned, however, the relative length of the rostral spine, the sharpness of telson teeth, spines and carinae decreases with increasing size and the distinctness of bilobation of the knob on the telson and color pattern are variable in nominal species of *G. falcatius* (Ahyong, 2001). On the other hand, this species is easily distinguished by the results of the re-examination through the morphological traits used in this study. *Gonodactylaceus siamensis* is readily recognized by the combination of the following character states: 1) anterior margin of the basal portion of the rostral plate is a presence of transverse, which are posteriorly sloping in *G. insularis*, Smaller specimens of *G. siamensis*, having undifferentiated rostral plate, may be difficult to distinguish from size-matched *G. insularis*. From the smallest specimens (TL 9 mm) which have well-developed the penes and well developed male pleopod 1 endopod, however, *G. siamensis* has constantly transverse shape of anterior margin of the basal portion of the rostral plate with increasing size, 2) postanal carina on telson ventral surface generally exists and is shallow. It does not exist in the case of *G. mutatus* and *G. insularis* but exists in the inflated state in case of *G. falcatius* sensu stricto, and 3) a median carinule on sixth abdominal somite generally exists.

In conclusion, *G. siamensis* is clearly distinguished from the nominal species of *G. falcatius* by the presence of a transverse anterior margin of the basal portion of the rostral plate, a median carinule on sixth abdominal somite, and shallow postanal carina on telson surface.

With the present recognition of *G. siamensis* as distinct species, this species now ranges from Sri Lanka, Thailand, Vietnam, Philippines, mainland Australia (Queensland and Western region), to Indonesia and Hawaii.

Distribution. Thailand (type locality), Vietnam, Philippines, mainland Australia (Queensland and Western region), to Indonesia and Hawaii.



Fig. 51. Distribution of *Gonodactylaceus siamensis* Manning & Reaka, 1981. Legend: star = type locality; circle = distribution in worldwide.



Fig. 52. *Gonodactylaceus falcatus*, male, TL 36 mm, AM 64265.

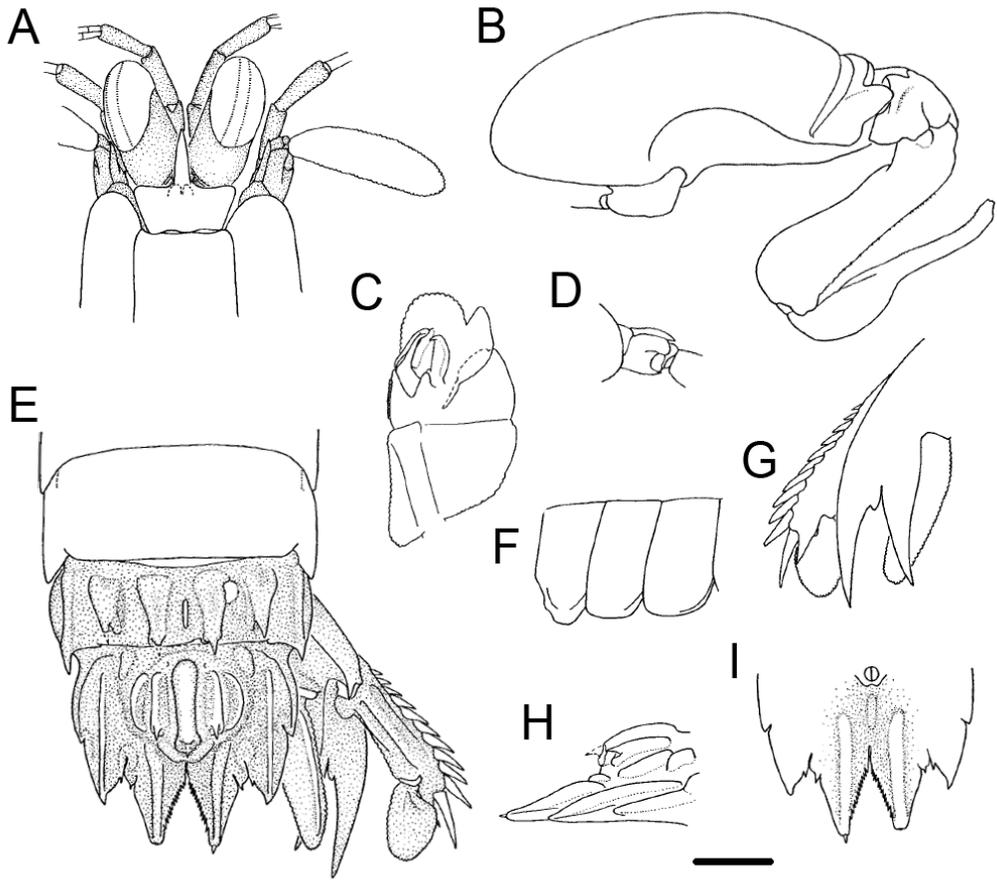


Fig. 53. *Gonodactylaceus siamensis* Manning & Reaka, 1981b comb. nov., Australia, Queensland. A–I: male, TL 37 mm (AM P54457). A, anterior cephalon; B, raptorial claw; C, right pleopod 1 endopod; D, antennal protopod; E, abdominal somites 5–6, telson and uropod; F, thoracic somites 6–8, right lateral; G, uropod, right ventral; H, telson, right lateral; I, telson, ventral. Scale bars: A–B, D–I = 1.25 mm, C = 0.6 mm. Modified from Ahyong (2001).

21. *Gonodactylaceus insularis* (Manning & Reaka, 1982) comb. nov.

(Figs. 54–56)

Gonodactylus insularis Manning & Reaka, 1982: 347–351, figs. 1, 2

Gonodactylaceus falcatus: Ahyong, 2001: 35–38, fig. 17L [part, not *G. falcatus*, (Forskål, 1775)].

Gonodactylus takedai Moosa, 1989: 223–226, fig. 1.

Material examined

Type materials

Enewetak: USNM 135632, 1 female (TL 33 mm), Kidrenen Island, 11°22'50"N 162°10'30"E, 23 m, scattered coral heads on coral sand, C.A. Child, 23 Sep 1969 (holotype of *Gonodactylus insularis* Manning & Reaka); NSMT-Cr9332, holotype male (TL 27 mm), Miyano-hama, Chichi-jima, Ogasawara Is, M. Takeda, 1 Jul 1976 (holotype of *Gonodactylus takedai* Moosa, 1989).

Non type materials

Australia: Lord Howe Island: AM G2450, 1 male (TL 61 mm), 4 females (TL 40–59 mm), coll. J.B. Waterhouse; AM P100916, 1 female (TL 57 mm), Lord Howe Island, Signal Point, 31°31'30.0"S 159°03'35.0"E, coll. A.D. Hegedus, A.C. Miller & S.J. Keable, 04 Apr 2017; AM G2500, 3 males (TL 49–66 mm), 3 females (TL 46–80 mm), coll. Mrs Nicholls; AM G2631, 1 male (TL 61 mm), coll. Mr Thompson; AM G3861, 2 males (TL 57–61 mm), 2 females (TL 52–54 mm), coll. Mrs Nicholls; AM G3953, 1 male (TL 65 mm), coll. F. Farnell; AM P1173–1174, 2 females (TL 54–68 mm), coll. Mrs Nicholls, Jan 1907; AM P1176–1180, 1 male (TL 46 mm), 5 females (TL 52–63 mm), coll. Mrs Nicholls, Jan 1907; AM P1638, 2 females (TL 44–51 mm), coll. E. Waite, 1898; AM P5712, 2 males (TL 32–65 mm), coll. McCulloch & Troughton; AM P5272, 1 female (TL 57 mm), coll. A.R. McCulloch; AM P15364, 2 females (TL 65–73 mm), coll. Ms Langley; AM P16291, 1 male (TL 56 mm), lagoon, 14 Feb 1934; AM P53615, 4 males (TL 26–67 mm), 9 females (TL 27–65 mm), coll. J. Booth, 18 Sep 1962; NMV J13827, 1 male (TL 32 mm), Jan 1959; NMV J13828, 2 males (TL 36–46 mm), 1 female (TL 43 mm), Lord Howe &

Norfolk Island, coll. Giesbrecht; TM G3835, 1 female (TL 37 mm), North Reef, Lord Howe Island, near low tide level, coll. J. Penprase, 30 Jun 1977; TM G3836, 1 female (TL 30 mm), Ned's Beach, , in pools on rocky shelf, near low tide level, coll. J. Penprase, 28 Jun 1977; TM G3837, 1 female (TL 46 mm), off Dawson Point, , subtidal, coll. J. Penprase, 11 Nov 1977; TM G3838, 1 male (TL 65 mm), Dawson Point,, J. Penprase, Nov 1977; TM G3839, 1 male (TL 19 mm), 1 female (TL 17 mm), Dawson Point, under subtidal basalt rocks, Mr & Mrs Penprase, Nov 1977.

Korea, Jeju Island (33°13'37.3"N 126°33'57.2"E): MADBK600103001, 1 male (TL 32 mm), Seogwipo-si, Seogwipo-dong, near Munseom Island, by SCUBA diving, 21 Jul 1993; NIBRIV0000316631, 1 male (TL 61.5 mm), Seogwipo-si, Seogwipo-dong, near Munseom Island, by SCUBA diving, coll. Park T, Kil HJ, 11 Mar 2009.

Japan: AM P87561, 1 male (TL 33 mm), 1 female (TL 25 mm), Okinawa Prefecture, Ryukyu Islands, west coast of Oh-jima Islet near Kume Island, near Ou, 26°20'18.0"N 126°49'22.0"E, 18 Nov 2009.

Description. Eye (Figs. 55, 56A) elongate, reaching midlength of antennular peduncle article 3. Cornea subconical, narrower than stalk dorsally. Ocular scales separate; apics rounded. Antennular peduncle length 0.46–0.65CL. Antennal scale length 0.45–0.59CL.

Rostral plate (Figs. 55, 56A) about as long as wide; median spine longer than base, not reaching to proximal margin of cornea; basal portion with posteriorly sloping anterior margin; anterolateral angle rounded; lateral margin divergent anteriorly.

Raptorial claw (Fig. 56B) not sharply tri-spinuous; dorsal margin of carpus unarmed; opposable margin of propodus sparsely pectinate proximally, without movable spine. Dactylus without proximal notch; outer proximal margin strongly inflated; inner distal margin without tooth.

Mandibular palp 3-segmented. Maxillipeds 1–5 with epipod.

Lateral processes of thoracic somites 6–7 (Fig. 56G) width subequal; lower margin rounded, slightly flattened. Anterolateral margin of thoracic somite 8 broadly rounded; sternal keel obsolete.

Endopod of pereopod slender, 2-segmented; basal segment unarmed.

Male Pleopod 1 endopod posterior endite with distinct lateral lobe.

Abdominal somites 1–5 smooth; dorsal surfaces without transverse grooves; posterolateral angles unarmed. AWCLI 741–838. Abdominal somite 6 (Figs. 55, 56G) with posteriorly armed submedian, intermediate and lateral carinae; with shallow median carinule (occasionally with faint or indistinct carinule).

Telson (Figs. 55, 56D) wider than long, bearing a couple of three pairs of primary teeth; with 8–14 spiniform submedian denticles and 2 intermediate denticles. Submedian primary teeth unarmed dorsally. Intermedian primary teeth distinct, apex sharp, extending posteriorly well beyond apices of intermediate denticles. Lateral primary teeth demarcated by short notch, apex angular, not projecting well off margin of telson. Dorsal surface (Figs. 55, 56D) bearing median carina and four pairs of longitudinal carinae. Median carina more strongly inflated in males than in females, bearing posterior spine. Accessory median carina uninterrupted, extending anteriorly beyond dorsal pit but not as far as anterior end of median carina; bearing posterior spine. Submedian carina interrupted; anterior submedian carina smooth, unarmed, arcuate, as long as accessory median carina. Intermediate carina uninterrupted, slender, extending anteriorly as far as accessory median and anterior submedian carinae. Marginal carina uninterrupted, relatively slender, extending to posterior margin of lateral primary tooth. Knob (Figs. 55, 56D) medially bilobed (occasionally indistinctly bilobed). Ventral surface with a pair of low carinae on submedian teeth; usually without post-anal carina (occasionally with faint or indistinct carina).

Uropodal protopod (Figs. 55, 56E) terminating in 2 flattened spines, outer longer; with small lobe on inner proximal margin of outer proximal margin of inner spine. Uropodal exopod (Fig. 55, 56E) having 11–16 (usually 11) movable spines (distalmost extending to or exceeding apex of distal segment) on proximal segment; margin fully setose; distal margin with ventral spine; distal segment rounded, entire

margin setose. Uropodal endopod narrow, bearing low dorsolateral carina; outer margin with a row of marginal setae; length about 4 times width.

Life coloration: Highly variable. The body colouration varies from uniform or mottled ivory, yellow to orange red to black green, purple. The meral spot of the raptorial claw is always yellow. Males frequently have transverse rows of dark spots on thoracic and abdominal somites together giving impression of about eight dark longitudinal stripes along the body (Ahyong, 2012).

Habitat: Crevices in or under rocks, rubble, boulders, corals, mussels, sponge and fouling on rocky and coral reefs and associated seagrass beds. Usually from intertidal or shallow subtidal habitats but possibly to 400 m depth from New Zealand (Ahyong, 2012).

Remarks: *Gonodactylaceus insularis* (as *Gonodactylus*) was originally described from “Kidrenen Island, Enewetak”, Republic of the Marshall Islands, based on 9 males (TL 13 to 30 mm) and 18 females (TL 10 to 31.5 mm) and distinguished by colour pattern in life, differences in the degree of inflation of the telson carina (Manning and Reaka, 1982). In this study, the species was established based on few specimens which are a relatively small size. Also, these morphological traits are variable in the nominal species of *Gonodactylaceus falcatus*. Because color pattern can change dramatically between moults and differs according to habitat, the overall body coloration of *G. falcatus* is highly variable but also sexually dimorphic. In males, each somite usually has a transverse row of 4.6 dark spots or patches that become proportionally larger with increasing size; females lack these dark patches; the meral spot of a raptorial claw in both sexes is yellow (Ahyong, 2012). Thus, previous studies show that living specimens from Australia and Japan displayed the full range of color variations (Ahyong, 2001; Ahyong, 2012). The degree of inflation of the telson carina as another morphological trait also can be changed according to sex. In case of *G. falcatus*, it is generally more strongly inflated median carina in males than in females. In addition, Manning & Reaka (1982) commented that the

specimens which were tentatively identified as *G. insularis* (as *Gonodactylus*), the specimens have narrower carinae with relatively long posterior spines on the median and accessory carinae on the telson, and much sharper, more-slender intermediate marginal teeth on the telson. This morphological trait, however, also can be changed according to size: In general, the relative length of the spine, the sharpness of telson teeth, spines and carinae decreases with increasing size (Ahyong, 2001).

Through the present study, a large number of specimens of various size, including type materials, for other morphological traits (the characteristics of the rostral plate, postanal carina on telson ventral surface, and median carinule on sixth abdominal somite) were reviewed. *G. insularis* can be easily distinguished from the nominal species of *G. falcatus* by the presence of the distinctively posteriorly sloping anterior margin of rostral plate, which are transverse in the rest nominal species of *G. falcatus*. At any given size, we confirmed this morphological trait as constant, regardless of the development of rostral plate.

In the case of *Gonodactylaceus takedai*, the species was distinguished by the presence of fused ocular scales, an undivided knob on the telson, and a faint trace of a median carinule on AS6 (Moosa, 1989). In case of the presence of ocular scales, it appears to be based on an aberrant specimen and an undivided knob on the telson is variable in *G. falcatus* (Ahyong, 2001). By the other morphological traits examined in this study, *Gonodactylaceus takedai* is re-examined and is regarded herein as a junior synonym of *G. insularis* with the same morphological characters. As such, the revised distribution of *G. insularis*, now ranges from the oceanic margins of the western Pacific to the central-western Pacific.

Distribution. Marshall Islands (type locality), Korea, Japan, Lord Howe Island from Australia and New Zealand).



Fig. 54. Distribution of *Gonodactylaceus insularis* Manning & Reaka, 1982. Legend: star = type locality; circle = distribution in worldwide.



Fig. 55. *Gonodactylaceus insularis*, male, TL 61.5mm, NIBRIV0000316631.

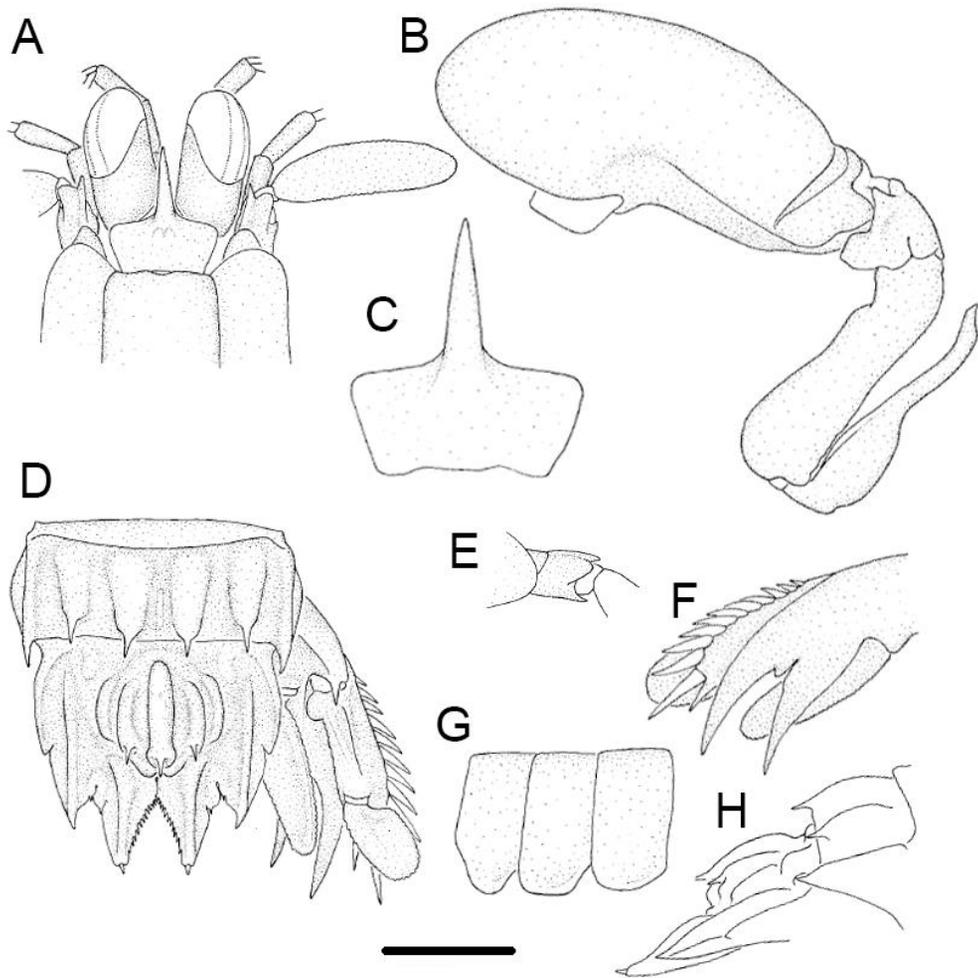


Fig. 56. *Gonodactylaceus insularis* Manning & Reaka, 1982 comb. nov., New Zealand, Three Kings Islands (NIWA 23968, female, TL 30 mm). A, anterior cephalon; B, raptorial claw; C, rostral plate; D, abdominal somites 5-6, telson and uropod; E, right antennal protopod, lateral view; F, right uropod, lateral view; G, thoracic somites 6-8, right lateral; H, telson, right lateral view. Scale bars: A–B, D–H= 2.5 mm, C = 1.2 mm. Modified from Ahyong (2012).

22. *Gonodactylaceus mutatus* (Lanchester, 1903) comb. nov. (Figs. 57–58)

Gonodactylus chiragra var. *mutates* Lanchester, 1903: 450.

Gonodactylus mutatus: Manning, 1995: 48–51, figs. 9G, H, 15, 16.

Material examined

Type material

Maldives: MZC 20.06.1900, 1 female (TL 44 mm), Furnadu Velu, Miladumadulu Atoll, coll. J.S. Gardiner (lectotype of *Gonodactylus mutatus* Lanchester).

Non type materials

Maldives: UF 39600, 1 female (TL 24.3 mm), Magoodhoo Island, Bicocca Field Station, 8°04'50.2"N 72°57'56.5"E, lagoon, sand, seagrass, 0-1 m, coll. Jenna Moore, 8 May 2014.

India: AM P3165, 1 male (TL 50 mm), Rameswaram, coll. British Museum.

Srilanka: AM P7717, 3 males (TL 45–50 mm), 1 female (TL 40 mm), coll. Colombo Museum, Ceylon.

Description. Eye elongated, reaching midlength of antennular peduncle article 3. Cornea subconical, narrower than stalk dorsally. Ocular scales small, separate; apices rounded.

Rostral plate (Fig. 58A) not sharply tri-spinuous, longer than wider; median spine relatively short, not reaching to proximal margin of cornea; basal portion with distinctively transverse anterior margin; anterolateral angle blunt, rounded; lateral margin divergent anteriorly.

Raptorial claw not sharply tri-spinuous; dorsal margin of carpus unarmed; opposable margin of propodus sparsely pectinate proximally, without movable spine. Dactylus without proximal notch; outer proximal margin strongly inflated; inner distal margin without tooth.

Mandibular palp 3-segmented. Maxillipeds 1–5 with epipod.

Lateral processes of thoracic somites 6–7 width subequal; lower margin rounded, slightly flattened. Anterolateral margin of thoracic somite 8 broadly rounded; sternal keel obsolete.

Endopod of pereopod slender, 2-segmented; basal segment unarmed.

Male Pleopod 1 endopod posterior endite with distinct lateral lobe.

Abdominal somites 1–5 smooth; dorsal surfaces without transverse grooves; posterolateral angles unarmed. Abdominal somite 6 with posteriorly armed submedian, intermediate and lateral carinae; without median carinule.

Telson (Fig. 58B) as long as wide, bearing a couple of three pairs of primary teeth; with 10–12 spiniform submedian denticles and 2 intermediate denticles. Submedian primary teeth unarmed dorsally. Intermedian primary teeth distinct, apex sharp, extending posteriorly well beyond apices of intermediate denticles. Lateral primary teeth demarcated by short notch, apex angular, not projecting well off margin of telson. Dorsal surface (Fig. 58B) bearing median carina and four pairs of longitudinal carinae. Median carina more strongly inflated in males than in females, bearing posterior spine. Accessory median carina uninterrupted, extending anteriorly beyond dorsal pit but not as far as anterior end of median carina; bearing posterior spine. Submedian carina interrupted; anterior submedian carina smooth, unarmed, arcuate, as long as accessory median carina. Intermediate carina uninterrupted, slender, extending anteriorly as far as accessory median and anterior submedian carinae. Marginal carina uninterrupted, relatively slender, extending to posterior margin of lateral primary tooth. Knob (Fig. 58B) medially bilobed. Ventral surface with a pair of low carinae on submedian teeth; without post-anal carina.

Uropodal protopod terminating in 2 flattened spines, outer longer; with small lobe on inner proximal margin of outer proximal margin of inner spine. Uropodal exopod having 10–11 (usually 11) movable spines (distalmost extending to or exceeding apex of distal segment) on proximal segment; margin fully setose; distal margin with ventral spine; distal segment rounded, entire margin setose. Uropodal endopod narrow, bearing low dorsolateral carina; outer margin with a row of marginal setae; length about 4 times width.

Life coloration: The meral spot of the raptorial claw is yellow (Ahyong, 2001).

Habitat: Intertidal and shallow subtidal coral and rocky reefs: According to Serene, he commented that this species taken in Cauda Bay were collected by breaking up blocks of coral. (Manning, 1995).

Remarks: When Lanchester (1903) first established *Gonodactylaceus mutatus* (as *Gonodactylus*), he mentioned that this species can be easily distinguished from other congeners by the presence of the relatively shorter spine of the rostral plate, tumid carinae on the telson, and a bilobed knob. In addition, the color pattern was used for major morphological trait. As mentioned, however, the relative length of the rostral spine, the sharpness of spines and carinae decreases with increasing size and the distinctness of bilobation of the knob on the telson and color pattern are variable in nominal species of *G. falactus* (Ahyong, 2001). On the other hand, this species is easily distinguished by the results of the re-examination through the morphological traits used in this study. *Gonodactylaceus mutatus* is readily recognized by the combination of the following character states: 1) anterior margin of the basal portion of the rostral plate is a presence of transverse, which are posteriorly sloping in *G. insularis*, 2) the species doesn't have both postanal carina on telson ventral surface and median carinule on sixth abdominal somite. Based on the specimens examined here and original description and published accounts, this species did not have both.

On the other hand, it was confirmed that *Gonodactylaceus aloha* from Hawaii and *Gonodactylaceus mutatus* collected from Indonesia and Australia are conspecific species through the mitochondrial DNA studies. However, according to the result of the study, specimens collected from the Maldives is distinguished from other groups of nominal species of *G. falactus* and we recognize it as separate species.

With the present recognition of *G. mutatus* from the Maldives as distinct species, the distribution of *G. mutatus* now is the Maldives, the type locality. However, this species was a common species in Thailand (Manning, 1995) and other countries, so specimens that were identified as *Gonodactylus mutatus*, which was obtained in areas

other than the Maldives, will require further study for confirmation of morphological and molecular character.

Distribution. Maldives (type locality), India, and Sri Lanka,



Fig. 57. Distribution of *Gonodactylaceus mutatus* Lanchester, 1903. Legend: star = type locality; circle = distribution in worldwide.

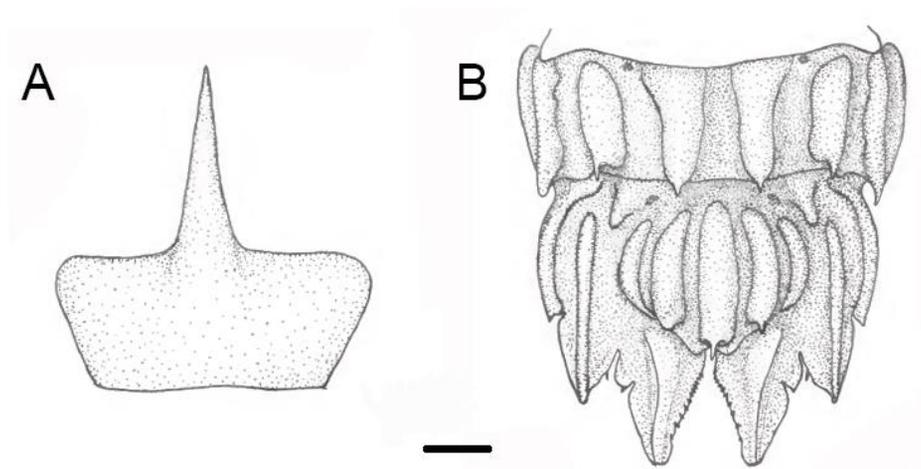


Fig. 58. *Gonodactylaceus mutatus* Lanchester, 1903 comb. nov., female, TL 44 mm, MZC. A, rostral plate; B, telson. Scale bars: A–B = 1.25 mm, C = 1.2 mm. Modified from Manning (1978).

23. *Gonodactylaceus glabrous* (Brooks, 1886) (Figs. 59–60)

Gonodactylus glabrous Brooks, 1886: 22, 64, pl. 14: fig. 5, pl. 15: figs. 7, 9 [type locality: Samboangan reefs, Philippines]; Manning, 1978: 5–7, figs. 3, 10 [part, holotype only].

Gonodactylus bossorotundus Roxas & Estampador, 1930: 94, 122, pl. 6, figs. 1, 2

Gonodactylus chiragra var. *crescentus* Roxas & Estampador, 1930: 94, 120, pl. 5: fig. 3.

Gonodactylaceus glabrous: Manning, 1995: 19, 42–46, fig. 12; Ahyong & Norrington, 1997: 99; Debelius, 1999: 275.

Gonodactylaceus gravieri: Manning, 1995: 46, fig. 14 [paratype only, not *G. gravieri* Manning, 1995].

Material examined

Non type material

Japan: AM P87562, female (TL 32 mm), Station Cauda, Ryukyu Islands, west coast of Oh-jima Islet near Kume Island, near Ou, 18 November 2009.

Diagnosis. Rostral plate (Fig. 60) with distinctly angular anteorlatereal corners; anterior margin transverse, not posteriorly sloping. Abdominal somites 1–5 (Fig. 60) without fine transverse grooves. Abdominal somite 6 (Fig. 60) without median carinule. Telson (Fig. 60) with 5 carinae, with 11–13 sumedian denticles; mid-dorsal carinae relatively uninflated; median and accessory median carinae each with short posterior spine; knob bilobed. Ventral surface with sharp postanal carina and distinct carina on each submedian tooth. Uropod (Fig. 60) with exopod having 10–11 movable spines on proximal segment. Protopod with one proximal lobe between terminal spines. Endopod outer margin with single row of marginal setae, directed dorsally.

Habitat. Coral reefs; intertidal to shallow subtidal; amongst dead coral rubble (Ahoyn, 2001).

Distribution. Australia, Philippines, Indonesia, Japan and Vietnam (Ahoyn, 2001).



Fig. 59. Distribution of *Gonodactylaceus glabrous* (Brooks, 1886). Legend: star = type locality; circle = distribution in worldwide.

Remarks. Among the known species of *Gonodactylaceus*, *G. glabrous* is morphologically similar to *G. falcatus* (Forskal, 1775) in having following characteristics: (1) the absence of transverse grooves from the first to the fifth abdominal somites, (2) the presence of a lobe between terminal spines of uropodal protopod, and (3) the presence of bilobed knob on the telson. However, *G. glabrous* can be easily distinguished from its congeners by the shape of the anterolateral corner of the rostral plate. The shape is rounded and blunt in *G. falcatus*, whereas it is distinctively angular in *G. glabrous*. In addition, it turned out through this study that *G. glabrous* and *G. falcatus* are clearly distinguished by the following characteristics. In the case of median carinule, *G. glabrous* doesn't have it, *G. falcatus* usually has it. In the case of the postanal carina, *G. glabrous* has sharp postanal carina and distinct carina on each submedian tooth exists whereas *G. falcatus* has shallow ones. As with *G. falcatus* and *G. graphurus*, the number of lobes between the terminal

spines of the uropodal protopod is variable in *G. glabrous*. About this characteristics, further study is necessary.



Fig. 60. *Gonodactylaceus glabrous*, female, TL 32 mm, AMP87562.

24. *Gonodactylaceus ternatensis* (de Man, 1902) (Figs. 61–62)

Gonodactylus glabrous var. *ternatensis* de Man, 1902: 914 [part, type locality: Ternate, Indonesia, 0°48'N 127°20'E)].

Gonodactylus falcatus: Tweedie, 1950: 140; Serène, 1954: 6, 7, 10, 11, 31, 41, 42, 45, 47, 54, 74, 78, 79, 80, 81, 87, figs. 8, 13–16, pl. 9 [not *G. falcatus* (Forskål, 1775)].

Gonodactylus ternatensis: Manning, 1978a: 10, figs. 7, 8, 13.

Gonodactylaceus ternatensis: Manning, 1995: 19, 42, 43, 51–55, pls. 1, 2, figs. 8a–b, 9f, 10d, 11e, 17–19.

Material examined

Non type material

Australia: AM P58574, male (TL 16 mm), Queensland, GBRMPA Reef 11-102, 14 January 1993.

Diagnosis. Rostral plate (Fig. 62) with distinctly angular anteorlatereal corners; anterior margin transverse, not posteriorly sloping. Abdominal somites 1–5 without fine transverse grooves. Abdominal somite 6 (Fig. 62) without short median carinule. Telson (Fig. 62) with 5 carinae, with 9–15 sumedian denticles; mid-dorsal carinae sometimes inflated in adult males; median and accessory median carinae each with short posterior spine; knob bilobed. Ventral surface with sharp postanal carina and distinct carina on each submedian tooth. Uropod (Fig. 62) with exopod having 10–14 movable spines on proximal segment. Protopod with one proximal lobe between terminal spines. Endopod outer margin with single row of marginal setae, directed dorsally.

Habitat. This species usually occurs amongst live coral (Dingle *et al.*, 1977) from the intertidal to shallow subtidal zone. Ahyong (2001) noted that single Australian specimen studied live in this study was collected from a crevice in live *Goniopora*

coral.

Distribution. Eastern Australia and the Cocos-Keeling Islands, southern China, Indonesia, Thailand, and Vietnam (Ahyong, 2001).



Fig. 61. Distribution of *Gonodactylaceus ternatensis* (de Man, 1902). Legend: star = type locality; circle = distribution in worldwide.

Remarks. Considering characteristics of the rostral plate, anterior margin of *G. ternatensis* is transverse, not posteriorly sloping. Among *Gonodactylaceus* species, *G. ternatensis* is similar to *G. falcatus* (Forskål, 1775), *G. glabrous* (Brooks, 1886), *G. mutatus* Lanchester, 1903, *G. siamensis* Manning & Reaka, 1981, and *G. ternatensis* (de Man, 1902). *G. ternatensis* differs from its congeners in having the following characteristics: (1) the presence of undivided knob on the telson, (2) the presence of slender dorsal carinae, a lower median carina and longer carinal spines on the telson, and (3) the presence of the lateral tooth more widely set off from the telson margin and its longer apex, than in other species of *Gonodactylaceus*.



Fig. 62. *Gonodactylaceus ternatensis*, male, TL 16 mm, AM P58574.

25. *Gonodactylaceus graphurus* (Miers, 1875) (Figs. 63–64)

Gonodactylus graphurus Miers, 1875: 344 [part, White's material only] [type locality: Torres Strait, Queensland, Australia]; Kemp, 1913: 169–170; Balss, 1921:

5; Alexander, 1916: 9; Stephenson, 1952: 12; 1953: 47; Stephenson & McNeill, 1955: 250; Stephenson, 1962: 35; Manning, 1966: 108–109; 1978: 5, fig. 2b; Cannon et al., 1987: 63.

Gonodactylaceus graphurus: Manning, 1995: 19, 42–43; Ahyong & Norrington, 1997: 99–100.

Gonodactylus sp. : Jones & Morgan, 1994: 43.

Material examined

Non type material

Australia: AM P56810, male (TL 75 mm), Queensland, Rat Island, Port Curtis, July 1929, coll. M. Ward & W. Boardman.

Diagnosis. Rostral plate (Fig. 64) with distinctly angular anteorlatereal corners; anterior margin transverse, not posteriorly sloping. Abdominal somites 1–5 (Fig. 64) with fine transverse grooves. Abdominal somite 6 (Fig. 64) with short median carinule. Telson (Fig. 64) with 5 carinae, with 11–13 sumedian denticles; mid-dorsal carinae relatively inflated; median and accessory median carinae each with short posterior spine; knob bilobed. Ventral surface with sharp postanal carina and distinct carina on each submedian tooth. Uropod (Fig. 64) with exopod having 10–14 movable spines on proximal segment. Protopod with one proximal lobe between terminal spines. Endopod outer margin with single row of marginal setae, directed dorsally.

Habitat. Intertidal amongst coral rubble, under boulders and in sponges on nearshore tidal and coral reef flats, or in sponge on seagrass beds in depth of about 70 m (Ahyong, 2001).

Distribution. Aru, Australia, southern Indonesia, and Anaiteum, New Hebrides. (Ahyong, 2001).



Fig. 63. Distribution of *Gonodactylaceus graphurus* (Miers, 1875) (Legend: star = type locality; circle = distribution in worldwide).

Remarks. Considering characteristics of the rostral plate, anterolateral corner of *G. ternatensis* is angular, not rounded, so *G. ternatensis* is most similar to *G. glabrous*. But it differs from other *Gonodactylaceus* species in having the transverse grooves on abdominal somites 1–5.



Fig. 64. *Gonodactylaceus graphurus*, male, TL 75 mm, AM P56810

26. *Gonodactylaceus randalli* (Manning, 1978) (Figs. 65–66)

Gonodactylus randalli Manning, 1978: 9–10, figs. 6, 12.

Gonodactylaceus randalli: Ahyong, 2001: 34.

Material examined

Non type material

Vanuatu: AM P72148, female (TL 21 mm), Namyalala Reef, Sulua Bay, Emae Island, 7 June 1996, coll. D. Bray, M. Westneat, J. Williams, and D.J. Smith.

Diagnosis. Rostral plate (Fig. 66) with distinctly rounded anteorlatereal corners; anterior margin transverse, not posteriorly sloping. Abdominal somites 1–5 (Fig. 66) without fine transverse grooves. Abdominal somite 6 (Fig. 66) with median carinule. Telson with 5 carinae, with 12–13 sumedian denticles; mid-dorsal carinae slender; median and accessory median carinae each with short posterior spine; knob (Fig. 66) undivided. Ventral surface with sharp postanal carina and distinct carina on each submedian tooth. Uropodal protopod (Fig. 66) with two proximal lobes between terminal spines. Uropodal endopod outer margin with multiple row of setae, deflected dorsally.

Habitat. Coral reefs (Manning, 1978)

Distribution. Pacific Ocean, from the Marshall Islands, the Phoenix Islands, and the Society Islands, at depths between 12–21 m (Manning, 1978).



Fig. 65. Distribution of *Gonodactylaceus randalli* (Manning, 1978). Legend: star = type locality; circle = distribution in worldwide.

Remarks. Among *Gonodactylaceus*, *G. randalli* is morphologically similar to other *Gonodactylaceus* species except for *G. graphurus* in lacking fine transverse grooves on abdominal somites 1–5. *G. randalli*, however, *G. randalli* can be easily distinguished from other *Gonodactylaceus* species in having combination of following characteristics: (1) the presence of multiple rows of setae on the margin of uropodal endopod, (2) a median carinule on abdominal somite 6, and (3) two lobes between terminal spines of uropodal protopod.



Fig. 66. *Gonodactylaceus randalli*, male, TL 21 mm, AM P72148

DISCUSSION

Previous geographical studies of *Gonodactylaceus* suggested that many species of this genus have narrow, restricted distributions (Manning & Lewinsohn, 1986). While, the study of Ah Yong (2001) show that six nominal species are regarded as synonyms of *G. falcatus*, and thus *G. falcatus* is known to be one of the most widespread gonodactylids. Through this study, however, we reexamined a large series of specimens of *G. falcatus* based on three morphological characters to classify *G. falcatus* newly and molecular data and it is revealed the presence of four geographically discrete species: a western Indian Ocean population ranging from the Red Sea and Persian Gulf (Saudi Arabia, Madagascar, and Eritrea) corresponding to *Gonodactylaceus falcatus* sensu stricto, a primarily Indian Ocean population ranging from Thailand, Vietnam, Philippines, mainland Australia (Queensland and Western region), to Indonesia and Hawaii, corresponding to *Gonodactylaceus siamensis*, a Maldivian population from Maldivian Islands, India, and Sri Lanka, corresponding to *Gonodactylus mutatus*, a Pacific population ranging from the oceanic margins of the western Pacific to the central-western Pacific (Korea, Japan, Marshall Islands, Lord Howe Island from Australia and New Zealand), corresponding to *Gonodactylaceus insularis* and *Gonodactylaceus takedai*, herein removed from synonymy, respectively. *G. aloha* and *G. gravieri* is retained in the synonymy of *G. falcatus*. Except for *G. aloha* (as *Gonodactylus*) which was accidentally introduced after the Second World War (Kinzi, 1968), this present study shows that most species of *Gonodactylaceus* have a narrow distribution. Further study, however, will be needed for species whose distribution is overlapped in this study. According to Manning (1995), *G. mutatus* were abundant at Poulo Condore, Vietnam and a common species in living near the low tide line at Phuket and Laem Pan Wa, Thailand. Through the present study, we re-examined the specimens collected from Vietnam and Thailand, so that from Vietnam (USNM 266611) belongs to *G. siamensis* and recognize *G. mutatus* from the Maldives as valid species. Additional field studies including further sampling will help us again a much better understanding of the distribution patterns

of the species in this group and better determine the distribution of these species in Indo-West Pacific. We re-examined morphological traits on a relatively large number of samples from fifteen countries known as its distribution. The examined characters and the key to species of *Gonodactylaceus* through the present study could identify nominal species of *G. falcatus* at a very high rate. However, morphological traits except for the anterior margin of the rostral plate have variations for female or smaller than TL 20 mm specimens. In the case of *G. siamensis*, postanal carina on telson surface generally exists and is shallow. *G. siamensis* is clearly distinguished from its congeners because it does not exist in the case of *G. mutatus* and *G. insularis*, but exists in the inflated state in case of *G. falcatus*. However, four female specimens (AM P92622 (TL 32 mm, Western region of Australia), AM P72095 (TL 47 mm, Western region of Australia), AM P1759 (TL 20 mm), AM P7717 (TL 40 mm, Queensland of Australia), are atypical in having too shallow that it is difficult to distinguish. A median carinule on sixth abdominal somite also generally exists. Seven female specimens (AM P92622 (TL 32 mm, Western region of Australia), AM P 21796 (TL 17, 22mm, Western region of Australia), UF 22502 (TL 30 mm, Western region of Australia), AM P7227 (TL 28 mm, Queensland of Australia), JDT LIZ-17 (TL 16 mm, Queensland of Australia), AM P100916 (TL 57 mm, New South Wales of Australia), however, are atypical in having too shallow that it is difficult to distinguish. In case of *G. falcatus* sensu stricto, a median carinule on sixth abdominal somite exists. One female specimen, UF 37177 (TL 17.5 mm, Saudi Arabia) don't have a carinule.

Finally, a further study including additional sampling and examination will be required for species which has overlapped distribution and has morphological variations. In addition, these re-examination including new taxonomic key characters in the present study is required for other Gonodactylid species. If such a study is carried out, it can help understand genus *Gonodactylaceus*, which is known as a monophyletic group in the family known to be polyphyletic and then it can make clear the phylogenetic structure of this relatively old stomatopod lineage.

2-2. Taxonomic review of the genus *Gonodactylus* (Gonodactyloidea: Gonodactylidae)

INTRODUCTION

The genus *Gonodactylus* is easily distinguished from other genera by the presence of large ocular scales that are truncate and broader than the base of the rostral spine. *Gonodactylus* species, mostly *G. chiragra*, *G. platysoma* and *G. smithii*, are among the most frequently reported coral reef stomatopods. Conversely, species that are not commonly found, there are no additional studies on *Gonodactylus acutirostris*, *G. botti* and *G. childi*. *Gonodactylus acutirostris*, originally reported from the Mergui Archipelago and the Red Sea, is referable to *G. smithii*. Also, *G. botti* was originally described from Jakarta, Indonesia and it has only been reliably reported from the western Indian Ocean. The single record of *G. botti* from the Pacific is that of Moosa (1991) female specimens (TL 23 mm) from New Caledonia specimen. According to description of Moosa's (1991), this species has a strongly inflated median carina on the telson and doesn't have accessory median carinae, that author suggests that it is may be *Gonodactylellus annularis*, a species which was misidentified as *G. botti* by Moosa & Erdmann (1994). Moreover, *G. botti* doesn't have strongly inflated telson carinae at size TL 23 mm. Accordingly, the type material *G. botti* may have originated in the western Indian Ocean rather than the published type locality, Jakarta, Indonesia. The type material *G. botti* may have originated in the western Indian Ocean rather than the published type locality, Jakarta, Indonesia. Like *Gonodactylaceus* group that has been reviewed in the previous chapter, additional reexamination is required for morphological characteristics for the *Gonodactylus* species.

MATERIALS AND METHODS

Morphological terminology largely follows Ahyong (2001, 2012). All specimen measurements are given in millimeters (mm). Total length (TL) was measured along the dorsal midline from the apex of the rostral plate to the apex of the submedian tooth of the telson, and carapace length (CL) along the dorsal midline and the rostral plate are excluded. The abdominal-width-carapace-length index (AWCLI) is given as $100 \times$ abdominal somite 5 width/carapace length.

Key to the species of *Gonodactylus* Berthold 1827

1. Telson without lateral tooth. Ocular scales extending to anterolateral angle of rostral plate *G. platysoma*
 - Telson with lateral tooth, indicated by shallow notch. Ocular scales not extending to anterolateral angle of rostral plate 2
2. Lateral margins of rostral plate strongly divergent 3
 - Lateral margins of rostral plate subparallel 4
3. Apices of anterolateral angles blunt *G. smithii*
 - Apices of anterolateral angles spiniform *G. acutirostris*
4. Rostral plate with anterior margins distinctly concave *G. chiragra*
 - Rostral plate with anterior margins transverse 5
5. Ocular scales with anterior margins sloping posteriorly. Telson with sharp intermediate teeth *G. childi*
 - Ocular scales with relatively transverse anterior margins. Telson with blunt intermediate teeth *G. botti*

SYSTEMATICS ACCOUNTS

Superfamily Gonodactyloidea Giesbrecht, 1910

Family Gonodactylidae Giesbrecht, 1910

Genus *Gonodactylus* Berthold 1827

Gonodactylus Berthold, 1827: 271 (type species *Squilla chiragra* Fabricius, 1781, by subsequent designation by the International Commission of Zoological Nomenclature under its plenary powers in Opinion 785. Name on *Official List* of International Commission on Zoological Nomenclature. Gender masculine).

Diagnosis. Eye subcylindrical; cornea not broader than stalk dorsally. Ocular scales broader than basal width of median spine of rostral plate, distinctly wider than high, anteriorly truncate. Rostral plate with slender median spine and trapezoid basal portion. Mandibular palp present. Carapace anterolateral margin convex, extending anteriorly beyond base of rostral plate. Telson with 3 mid-dorsal carinae; intermediate carina of telson without accessory longitudinal carina on mesial margin. Opposable margin of propodus of raptorial claw with proximal movable spine. Uropodal protopod without lobes between terminal; endopod without spines on inner margin.

Composition. *G. acutirostris rostris* de Man, 1898; *G. botti* Manning, 1975; *G. chiragra* (Fabricius, 1781); *G. childi* Manning, 1971; *G. platysoma* Wood-Mason, 1875; and *G. smithii* Pocock, 1893.

Remarks. Among Gonodactylids, *Gonodactylus* species can be easily distinguished from other genera by the combination of following characteristics: (1) the presence of mandibular palp, (2) slender median spine and trapezoid basal portion of rostral plate, and 3) large ocular scales that are truncate and broader than the base of the

rostral spine. In *Gonodactylus* species, characteristics of telson lateral tooth, anterior margin, lateral margin of the rostral plate, and ocular scale are used as main identification keys. As in the *Gonodactylaceus* group, these morphological character can be changed according to allometric growth. In the case of the rostral plate, the rostral spine is proportionally longest in small specimens and becomes shorter with increasing body size and can become proportionally thicker. Also, the anterior margin of the basal portion of the rostral plate slopes more posteriorly in smaller specimens and become transverse or even slightly concave with increasing body size. Since this allometric variation has not been considered and morphological traits have been interpreted, a taxonomic review of *gonodactylus* species has been carried out in this chapter.

Morphological characteristics variation in *Gonodactylus*

The genus *Gonodactylus* includes the largest members of the Gonodactylidae, with some species exceeding TL 100 mm. In *Gonodactylus* species, characteristics of telson lateral tooth, anterior margin, lateral margin of the rostral plate, and ocular scale are used as main identification keys. Especially, the identification of the stomatopods can be changed according to the different interpretation of these morphological characters. According to Ahyong's comment (2012), the morphological traits were not well developed before the stomatopod grew to a certain size. Also, it can be changed according to allometric growth. Among *Gonodactylus chiragra*, *G. botti*, and *G. childi*, anterior margin of the rostral plate is a main key character in identification of species: *Gonodactylus chiragra* has a distinctively concave anterior margin of the rostral plate, whereas *G. botti*, and *G. childi* have a transverse or slightly concave anterior margin. In general, the rostral spine is proportionally longest in small specimens and becomes shorter with increasing body size and can become proportionally thicker. Also, the anterior margin of the basal portion of the rostral plate slopes more posteriorly in smaller specimens and become transverse or even slightly concave with increasing body size. Identification of *Gonodactylus* species should be interpreted synthetically with other morphological traits, together with the total length of the corresponding individuals.

27. *Gonodactylus childi* Manning, 1971 (Figs. 67–68)

Gonodactylus childi Manning, 1971: 75–77 [type locality: Runit (Yvonne) Island, Eniwetak Atoll]; Ahyong, 2001: 67, Fig. 33.

Material examined

Type material

Australia: AM P60070, male (TL 38 mm), 2 females (TL 33–34 mm), Capricorn Group, One Tree Island, no further information.

Diagnosis. Rostral plate (Fig. 68) with distinctly rounded anteorlatereal corners; anterior margin straight or slightly concave; apical spine longer than base. Ocular scales flattened, separate, broader than half of rostral plate width; anterior margin sloping posteriorly. Lateral margin of thoracic somite 6 (Fig. 68) broader than thoracic somite 7. Telson (Fig. 68) short, with 3 carinae; lateral tooth indicated by shallow notch in margin of telson between anterolateral angle and apex of intermediate tooth; mid-dorsal carinae blunt; median carina without posterior spine; accessory median carinae forming anchor shape; with 12–18 submedian denticles. Uropod (Fig. 68) with exopod having 10–11 movable spines on proximal segment; Protopod without proximal lobe between terminal spines. Endopod inner margin without spines.

Habitat. Coral reef flats in tide pools and amongst coral rubble (Ahyong, 2001)

Distribution. Australia, Eniwetak Atoll, respectively Pacific Ocean, French Polynesia, and Indonesia (Ahyong, 2001).



Fig. 67. Distribution of *Gonodactylus childi* Manning, 1971. Legend: star = type locality; circle = distribution in worldwide.

Remarks. In the case of *Gonodactylus childi*, anterior margin of the rostral plate is transverse or slightly concave. So this species is morphologically similar with *G. falcatus*, *G. siamensis*, and *G. mutatus* in *Gonodactylaceus* group that has been reviewed in the previous chapter.

By this characteristics, it can be easily distinguished from other congeners. Within *Gonodactylus* species, *G. childi* is the smallest species of the genus and most closely resembles *G. botti*. In *G. childi* and *G. botti*, the anterior margin of the rostral plate is transverse or slightly concave, instead of distinctly concave. However, *Gonodactylus childi* differs from *G. botti* in having posteriorly sloping instead of transverse anterior margins of the ocular scales, and a relatively shorter telson with sharper intermediate telson teeth. The intermediate teeth of the telson are blunt in case of *G. botti*. *Gonodactylus botti* occurs principally in the Indian Ocean, *G. childi* occurs principally in the central to western Pacific Ocean, and the two species apparently overlap in Indonesia.

Gonodactylaceus group that has been reviewed in the previous chapter, additional reexamination is required for morphological characteristics for the *Gonodactylus* species.



Fig. 68. *Gonodactylus childi*, female, TL 33 mm, AM 60070.

28. *Gonodactylus chiragra* (Fabricius, 1781) (Figs. 69–70)

Squilla chiragra Fabricius, 1781: 515 [type locality: restricted to Ambon, Indonesia, 3°43'S 128°12'E].

Gonodactylus chiragra): Moosa, 1986: 381; 1991: 155–156); Manning, 1991: 2; 1995: 71–75, pls. 5–8, figs. 8e, f, 9a, b, 10a, 11a, 27a, 28–30); Gosliner *et al.*, 1996: 195); Ahyong & Norrington, 1997: 100–101.

Material examined

Type material

Australia: AMP 70023, female (TL 75 mm), Darwin, East Point, coll. O.J. Cameron, 2 January 1972.

Diagnosis. Rostral plate (Fig. 70) with distinctly rounded anteorlatereal corners; anterior margin strongly concave; apical spine shorter of longer than base. Ocular scales (Fig. 70) flattened, separate, broader than half of rostral plate width. Lateral margin of thoracic somite 6 and thoracic somite 7 subequal. Telson (Fig. 70) short, with 3 carinae; lateral tooth indicated by shallow notch in margin of telson between anterolateral angle and apex of intermediate tooth; mid-dorsal carinae blunt; median carina without posterior spine; accessory median carinae forming anchor shape; with 8–17 submedian denticles. Uropod (Fig. 70) with exopod having 10–14 movable spines on proximal segment; protopod without proximal lobe between terminal spines; endopod inner margin without spines.

Habitat. Common on coral reef flats under boulders or among coral rubble, especially in the upper intertidal zone, but is also common on nearshore or onshore rocky reefs (Ahyong, 2001).

Distribution. French Polynesia to Japan, Australia, and the Indo-Malayan region to the western Indian Ocean (Ahyong, 2001).



Fig. 69. Distribution of *Gonodactylus chiragra* (Fabricius, 1781). Legend: star = type locality; circle = distribution in worldwide.

Remarks. The recent record of *Gonodactylus chiragra* from Korea figured by Cho *et al.* (2006) is clearly based on *Chorisquilla orientalis*. Given the broad morphological similarities between *C. orientalis* and *G. chiragra*, especially in juveniles with lesser developed telson spination, the record of Cho *et al.* (2006) is almost certainly considered to be based on *C. orientalis*.

Comparing the characteristics of the rostral plate, *G. chiragra* has a strongly concave anterior margin of the rostral plate and can be distinguished from *G. falcatus*, *G. siamensis*, and *G. mutatus* in *Gonodactylaceus* group that has been reviewed in the previous chapter.

Juvenile of *G. chiragra*, however, has occasionally only slightly concave as in *G. childi* and *G. botti*. It is necessary to re-examine the morphological characteristics based on a large number of specimens.



Fig. 70. *Gonodactylus chiragra*, female, TL 75 mm, AMP 70023.

29. *Gonodactylus platysoma* Wood-Mason, 1895 (Figs. 71–72)

Gonodactylus platysoma Wood-Mason, 1895: 11, pl. 3, figs. 3–9 [type locality: restricted to Society Island, French Polynesia].

Gonodactylus chiragra var. *platysoma*: Ghosh & Manning, 1988: 654.

Material examined

Type material

Australia: AMP 45589, female (TL 37.5 mm), Queensland, Thursday Island, coll. M. Ward, no information.

Diagnosis. Rostral plate (Fig. 72) with distinctly rounded anteorlateral corners; anterior margin strongly concave; apical spine shorter of longer than base. Ocular scales (Fig. 72) flattened, separate, almost as broad as rostral plate. Lateral margin of thoracic somite 6 and thoracic somite 7 subequal. Telson (Fig. 72) short, with 3 carinae; without lateral tooth; margin unbroken between anterolateral angle and apex of intermediate tooth; mid-dorsal carinae blunt; median carina without posterior spine; accessory median carinae indistinct; with 14–21 submedian denticles. Uropod (Fig. 72) with exopod having 9–13 movable spines on proximal segment; protopod without proximal lobe between terminal spines; endopod inner margin without spines.

Habitat. Coral reef flats under coral boulders or live coral heads. (Ahyong, 2001).

Distribution. Australia, French Polynesia to Japan, Indo-Malayan region to the western Indian Ocean. (Ahyong, 2001).



Fig. 71. Distribution of *Gonodactylus platysoma* Wood-Mason, 1895. Legend: star = type locality; circle = distribution in worldwide.

Remarks. Comparing the characteristics of the rostral plate, *G. platysoma* has rounded anterolateral corners, strongly concave anterior margin and is morphologically similar with *G. falcatus*, *G. siamensis*, and *G. mutatus* in *Gonodactylaceus* group that has been reviewed in the previous chapter. Among the known species of *Gonodactylus*, *Gonodactylus platysoma* has a unique characteristics so can be easily distinguished from its congeners in having following characteristics: 1) the presence of the widest ocular scales. It almost reaches the anterolateral corners of the rostral plate, 2) the absence of lateral telson tooth, 3) relatively broader body.



Fig. 72. *Gonodactylus platysoma*, female, TL 37.5 mm, AMP 45589.

30. *Gonodactylus smithii* Pocock, 1893 (Figs. 73–74)

Gonodactylus smithii Pocock, 1893: 475, pl. 20B [type locality: Arafura Sea].

Gonodactylus chiragra var. *anancyrus* Borradaile, 1900: 395, 397, 401.

Gonodactylus smithii: Manning, 1966: 112–113; Moosa, 1974: 6; Manning, 1991: 4; 1995: 20, 76–80, pls. 11, 12, figs. 9e, 10c, 11d, 27c, 32–35; Gosliner et al., 1996: 195; Ahyong & Norrington, 1997: 101–102; Debelius, 1999: 272.

Gonodactylus chiragra: Stephenson & McNeill, 1955: 250–252 [part, not *G. chiragra* (Fabricius, 1781)].

Gonodactylus minikoiensis Ghosh, 1990: 201, 202, fig. 1.

Gonodactylus arabica Ghosh, 1990: 201, 205, figs. 2, 3e.

Material examined

Non type material

Australia: AMP 43215, male (TL 37.5 mm), Queensland, Bird Island, Moreton Bay, January 1938.

Diagnosis. Rostral plate (Fig. 74) with distinctly concave anterior margin; anteorlateral angle acute but not spiniform; lateral margins strongly divergent anteriorly; apical spine shorter or longer than base. Ocular scales (Fig. 74) flattened, separate, half of rostral plate width. Telson (Fig. 74) short, with 3 carinae; with lateral tooth indicated by shallow notch in margin of telson between anterolateral angle and apex of intermediate tooth; mid-dorsal carinae blunt; median carina with posterior spine; accessory median carinae forming anchor shape, with 11–21 submedian denticles. Uropod (Fig. 74) with exopod having 10–13 movable spines on proximal segment; protopod without proximal lobe between terminal spines; endopod inner margin without spines.

Habitat. Common on intertidal or shallow subtidal coral reef flats amongst dead coral rubble and live coral, at depth of 62 m (Ahyong, 2001).

Distribution. Western Indian Ocean to Australia, New Caledonia, Japan (Okinawa) and Vietnam (Ahyong, 2001).

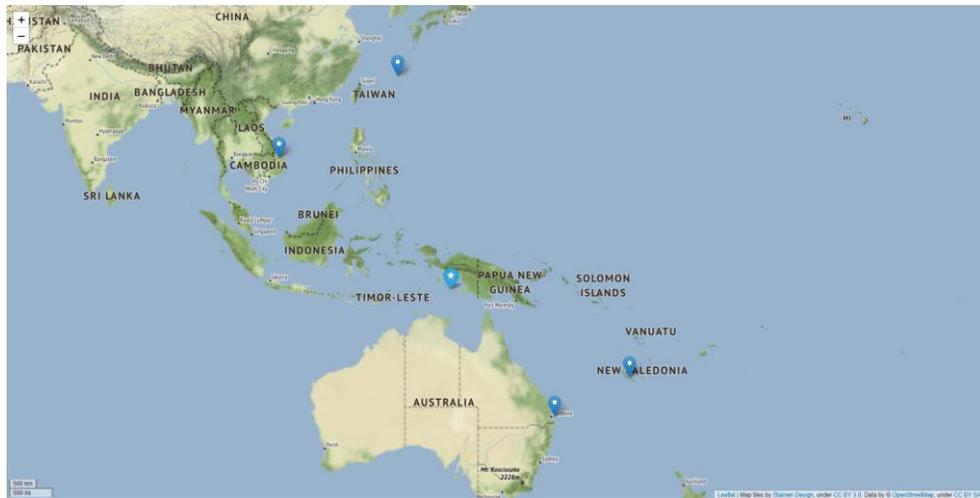


Fig. 73. Distribution of *Gonodactylus smithii* Pocock, 1893 (Legend: star = type locality; circle = distribution in worldwide).

Remarks. Comparing the characteristics of the rostral plate, *Gonodactylus smithii* has strongly divergent lateral margins of the rostral plate. Including this characteristics and the slender telson carinae, this species can be easily distinguished from other congeners by these characteristics. However, the sharpness of the anterolateral corners of the rostral plate in larger specimens varies and may approach that figured for the holotype of *G. acutirostris*. *G. acutirostris* is distinguished based on differences in telson ornamentation as well as the sharper rostral plate angles, the former difference is based on deformity (Holthuis, 1967; Manning & Lewinsohn, 1986). Therefore, the only difference between *G. acutirostris* and *G. smithii* is the degree of acuteness of the anterolateral angles of the rostral plate. The acuteness of the anterolateral angles of the rostral plate generally increases with increasing size. It is necessary to re-examine the morphological characteristics based on a large number of specimens. As *Gonodactylus* species group in the previous chapter, *Gonodactylus* species has some unknown species, indicating a possibility of new species differing from the congeneric species.



Fig. 74. *Gonodactylus smithii*, male, 55.5 mm, AM P43215

31. *Gonodactylus acutirostris* de Man, 1898 (Fig. 75)

Gonodactylus acutirostris de Man, 1898: 695, pl. 38, fig. 77b, c [Type locality: Mergui Archipelago]; Ahyong, 2001: 75.

Material examined

Type material

Information is not available.

Diagnosis. Rostral plate with distinctly concave anterior margin; anteorlateroal angle acute, spiniform; lateral margins strongly divergent anteriorly; apical spine longer than base. Ocular scales flattened, separate, not extending laterally to anterolateral angle of rostral plate. Telson short, with 3 carinae; with lateral tooth indicated by shallow notch in margin of telson between anterolateral angle and apex of intermediate tooth; mid-dorsal carinae blunt; median carina without posterior spine; accessory median carinae forming anchor shape, with 7–10 submedian denticles. Protopod without proximal lobe between terminal spines. Endopod inner margin without spines.

Habitat. Reef flat, from dead coral (Manning & Lewinsohn, 1986)

Distribution. Red Sea (Gulf of Aqaba; southern tip of Sinai Peninsula), Persian Gulf (Iran), Saudi Arabia, Sri Lanka, and Merqui Archipelago.



Fig. 75. Distribution of *Gonodactylus acutirostris* de Man, 1898. Legend: star = type locality; circle = distribution in worldwide.

Remarks. Comparing the characteristics of the rostral plate, *Gonodactylus smithii* has an acute and spiniform anterolateral angle of the rostral plate. Among *Gonodactylus* species, this species is morphologically similar to *G. acutirostris*. As mentioned earlier, the only difference between *G. acutirostris* and *G. smithii* is the degree of acuteness of the anterolateral angles of the rostral plate. However, the acuteness of the anterolateral angles of the rostral plate increases with increasing size. In addition, the length (TL 19–28 mm) of holotype type specimen of *G. acutirostris* is about twice that (TL 56 mm) of the type specimen of *G. smithii*. It is necessary to re-examine the morphological characteristics based on a large number of specimens. As *Gonodactylus* species group in the previous chapter, *Gonodactylus* species has some unknown species, indicating a possibility of new species differing from the congeneric species.

32. *Gonodactylus botti* Manning, 1975 (Fig. 76)

Gonodactylus chiragra: Holthuis, 1967: 26, 41, fig. 7a; Hughes, 1977:90. [Not *G. chiragra* (Fabricius, 1787)].

Gonodactylus botti Manning, 1975: 289–291 [Type locality: Indonesia]; Manning,

1990: 97–98; 1995: 68.

Type material

Holotype: SMF 6356, male, Batavia Sea, near Jakarta, Indonesia.

Diagnosis. Rostral plate with transverse anterior margin; lateral margins strongly subparallel or slightly divergent; apical spine longer than base. Ocular scales flattened, separate, not extending laterally to anterolateral angle of rostral plate. Telson short, with 3 carinae; with lateral tooth indicated by shallow notch in margin of telson between anterolateral angle and apex of intermediate tooth; mid-dorsal carinae blunt; median carina without posterior spine, with 14–15 submedian denticles. Protopod without proximal lobe between terminal spines. Endopod inner margin without spines.

Habitat. Sandy reef flat with algae (Manning & Lewinsohn, 1986), rocky tide pools and surrounding rocky sandy tidal flats (Manning, 1990).

Distribution. Red Sea (Gulf of Aqaba; southern tip of Sinai Peninsula; Gulf of Suez), Somalia, Persian Gulf (Iran), Saudi Arabia, Sri Lanka, and Indonesia (Schram & Müller, 2004)



Fig. 76. Distribution of *Gonodactylus botti* Manning, 1975. Legend: star = type locality; circle = distribution in worldwide.

Remarks. *Gonodactylus botti* was originally described from Jakarta, Indonesia, has only been reliably reported from the western Indian Ocean. The single record of *G. botti* from the Pacific is that of Moosa (1991) for a 23 mm TL female from New Caledonia specimen. According to the description of Moosa's (1991), this species has a strongly inflated median carina on the telson and doesn't have accessory median carinae, that author suggests that it is maybe *Gonodactylellus annularis*, a species which was misidentified as *G. botti* by Moosa & Erdmann (1994). Moreover, *G. botti* doesn't have strongly inflated telson carinae at the size of TL 23 mm. The disjunct distribution of *G. botti* is anomalous, and despite intensive sampling in Indonesia, the species has not been found there. The type material *G. botti* may have originated in the western Indian Ocean rather than the published type locality, Jakarta, Indonesia. It is necessary to re-examine the morphological characteristics based on a large number of specimens.

CHAPTER 3.

TAXONOMIC REVISION OF THE SELECTED STOMATOPOD GROUP RELATED TO CARINA

3-1. Taxonomic review of the seven genera (Squilloidea: Squillidae)

INTRODUCTION

Squilloids differ from other superfamilies by the presence of 4 or more closely spaced intermediate denticle on the telson. Characteristics of the median carina of the carapace, and thoracic and abdominal somite, lateral process of thoracic somite 5 are used as main identification keys in Squilloids species. Depending on whether the anterior bifurcation of the median carina is interrupted or uninterrupted, it can be divided into *Oratosquilla* and *Miyakella* groups and *Erugosquilla*, *Nanosquilla*, *Busquilla*, *Alima*, *Oratosquillina*, *Aerosquilla*, and *Quollastria*. Depending on whether it is single or bilobed, more than half of the 55 genera belonging to this family are divided. According to Ahyong's comment (2012), the morphological traits were not well developed before the stomatopod grew to a certain size and these morphological traits have allometric variations. In this part, a taxonomic review for selected 7 genera belonging to squillidae, was conducted.

MATERIALS AND METHODS

Morphological terminology largely follows Ahyong (2001, 2012). The barcoding region of the mitochondrial cytochrome oxidase subunit 1 gene was sequenced from the specimens of *Squilloids* species from throughout its range for comparison with published sequences from each nominal species, previously identified and recorded as the species to compare. It was selected as the outgroup owing to the close relationship between respective species. Also, 18 Korean *Oratosquilla oratoria* specimens which have variations of lateral processes of thoracic somites 5–8, anterior bifurcation of median carina of carapace, and inferodistal spine of raptorial

claw carpus were sequenced. And they were compared with seven published sequences from *Oratosquilla fabricii*, *Miyakella* (as *Miyakea*) *holoschista*, and *Miyakella* (as *Miyakea*) *nepa* were selected as the outgroup owing to the close relationship between each genus (Ahyong & Harling 2000; Ahyong & Jarman 2009; Porter et al. 2010). Respective GenBank Accession numbers are follow as: MH168267.1 (*Oratosquilla fabricii*), MH168248.1 (*Miyakella* (as *Miyakea*) *holoschista*), and KM034808.1, FJ229781.1, MF173603.1, MH168269.1, FJ229777.1 (*Miyakella* (as *Miyakea*) *nepa*),

SYSTEMATIC ACCOUNTS

Family Squillidae Latreille, 1802

Diagnosis. Telson with distinct median carina; submedian teeth movable or fixed; with 4 or more intermediate denticles. Cornea with 2 rows of hexagonal ommatidia in the midband. Maxillipeds 3–4 with propodi ovate, not ribbed distally. Body depressed, articulation compact. Raptorial claw with ischiomeral articulation terminal, dactylus bearing four or more teeth; propodus with 3 proximal movable spines. Uropodal protopod with two primary spines; articulation of exopod segments terminal.

Selected groups within 55 genera belonging to Squillidae: 7 genera (*Oratosquilla* Manning, 1968; *Levisquilla* Manning, 1977; *Anchisquilla* Manning 1968; *Cloridopsis* Manning, 1968; *Miyakella* Ahyong & Low, 2013; *Squilloides* Manning, 1968; *Kempella* Low & Ahyong, 2010).

Remarks. Squillidae is the most diverse stomatopod family, currently containing 46 genera (Ahyong, 2001; 2002; 2004). Among them, 7 genera belonging to squillids requiring taxonomic revision were selected. The identification keys of these genera

are characteristics of the median carina of the carapace, and thoracic and abdominal somite, lateral process of thoracic somite 5. Especially, the identification of the stomatopods can be changed according to the different interpretation of these carinae. According to Ahyong's comment (2012), the morphological traits were not well developed before the stomatopod grew to a certain size. In the case of *Oratosquilla fabricii*, its developmental changes are as follows: after it has developed into a 35 mm size, anterolateral spines on the carapace are well developed, the anterior bifurcation of the median carina on the carapace is usually interrupted, the carpus on the raptorial claw is irregular, the inferodistal margin on the merus of the raptorial claw is angular, the lobes on lateral processes of thoracic somites 5–7 are better defined and the abdominal carinae are spined as follows. after it has developed into a 48 mm size, submedian carinae of abdominal somite 4 are armed posteriorly. When the overall size does not reach 55 mm, adult diagnostic characters are not shown. Median carina on the rostral plate more closely resembles a low tubercle, the median carina of the carapace is entire at the base of the anterior bifurcation, the carpus of the raptorial claw is distinctly tuberculate and the inferodistal angle is produced to a blunt tooth, the anterior lobes of the lateral processes of thoracic somites 6–7 relatively slender, the penes are well developed. Therefore, in the case of species of comparatively small size, additional ancillary morphological traits must be additionally identified. To accomplish, this chapter describes major morphological traits and additional traits that can be used incidentally.

Allometric changes of main morphological characters in Squillids

Anterior bifurcation of median carina of carapace

In squillids, anterior bifurcation of the median carina of the carapace is used as key characters in the identification of the species. However, it is not fully developed before it develops into the adult size of each species. Until the adult size (TL 69 mm) is reached, a correct interpretation of the morphological trait can be made (Fig. 77). Before being developed into an adult, the identification of the species can be changed according to the different interpretation of the anterior

bifurcation of the median carina of the carapace. Therefore, the interpretation of the morphological trait of the corresponding species should be accompanied by information on the size and the developmental state of the endopod of the first pleopod of the individual.

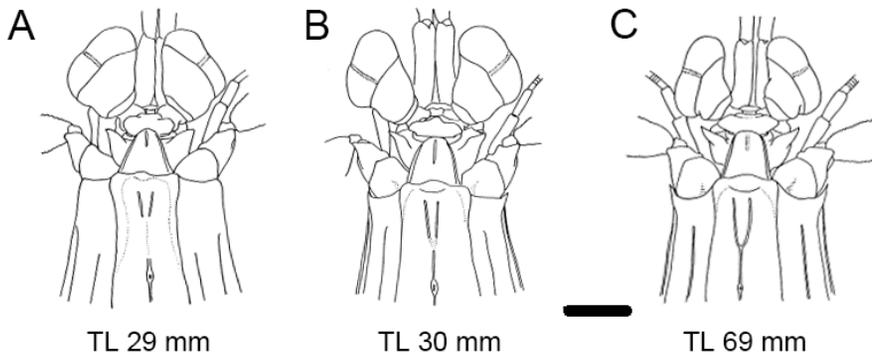


Fig. 77. *Oratosquilla fabricii* (Holthuis, 1941); A, anterior cephalon of postlarva TL 29 mm (stn DW1241); B, anterior cephalon of juvenile TL 30 mm (stn DW1214); C, anterior cephalon of adult TL 63 mm. Scale bars: A–B= 1.5 mm; C= 3 mm. Modified from Ahyong (2002).

Lateral processes of thoracic somites 5–8

In squillids, lateral processes of thoracic somites 5–8 are used as key characters in the identification of the species. Whether the lateral processes of thoracic somites 5–8 is divided into two is a very important morphological trait in squillids. However, it is not fully developed before it develops into the adult size of each species. Before being developed into an adult, the identification of the species can be changed according to the different interpretation of the lateral processes of thoracic somites 5–8. In order to interpret the corresponding morphological trait, an examination must be made with the individual in lateral view, not dorsal view. Also, it should be accompanied by information on the size and the developmental state of the endopod of the first pleopod of the individual.

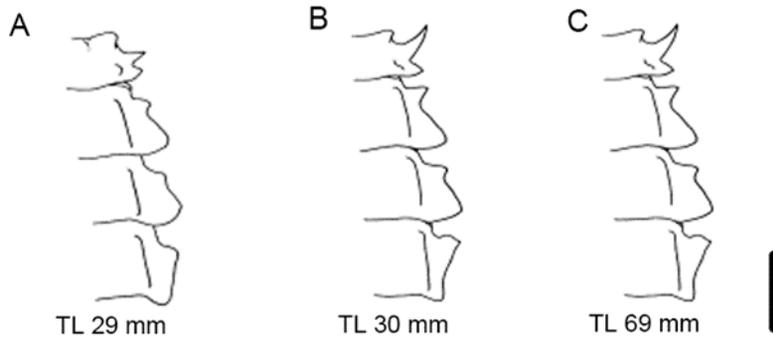


Fig. 78. Lateral processes of thoracic somites 5–8 of *Oratosquilla fabricii* (Holthuis, 1941); A, postlarva TL 29 mm (stn DW1241); B, juvenile TL 30 mm (stn DW1214); C, adult TL 63 mm. Scale bars: A–B= 1.5 mm; C= 3 mm. Modified from Ahyong (2002).

Inferodistal spine of raptorial claw carpus

In squillids, it is used as a key character depending on the presence or absence of inferodistal spine of raptorial claw carpus. However, it is not fully developed before it develops into the adult size of each species. Before being developed into an adult, the identification of the species can be changed according to the different interpretation of the inferodistal spine of raptorial claw carpus. Therefore, the interpretation of the morphological trait of the corresponding species should be accompanied by information on the size and the developmental state of the endopod of the first pleopod of the individual.

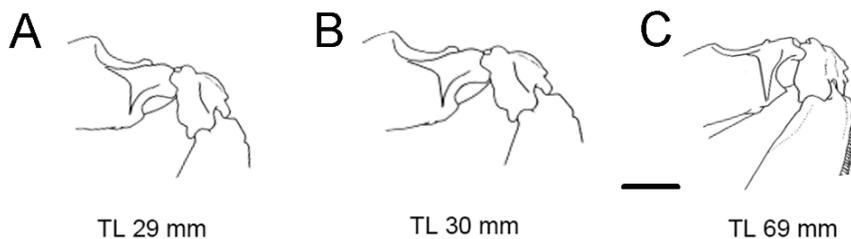


Fig. 79. Raptorial claw carpus of *Oratosquilla fabricii* (Holthuis, 1941); A, postlarva TL 29 mm (stn DW1241); B, juvenile TL 30 mm (stn DW1214); C, lateral process of thoracic somites 5–8 of adult TL 63 mm. Scale bars: A–B= 1.5 mm; C= 3 mm. Modified from Ahyong (2002).

RESULTS

Molecular data

18 sequences from Korean *Oratosquilla oratoria* specimens which have variations of lateral processes of thoracic somites 5–8, anterior bifurcation of median carina of carapace, and inferodistal spine of raptorial claw carpus show internal divergence in COI of 0.0–0.7 %. Mean divergence between *Oratosquilla oratoria* group and Out group lades was 9–10.7%, corresponding to separate species. Observed intra-specific and inter-specific divergences among *Oratosquilla oratoria* and other species are consistent with those observed for other species of Stomatopoda at <2.4%, >3.0%, respectively (Tang et al. 2010). More accurate examination for characteristics and a comprehensive interpretation considering development is necessary.

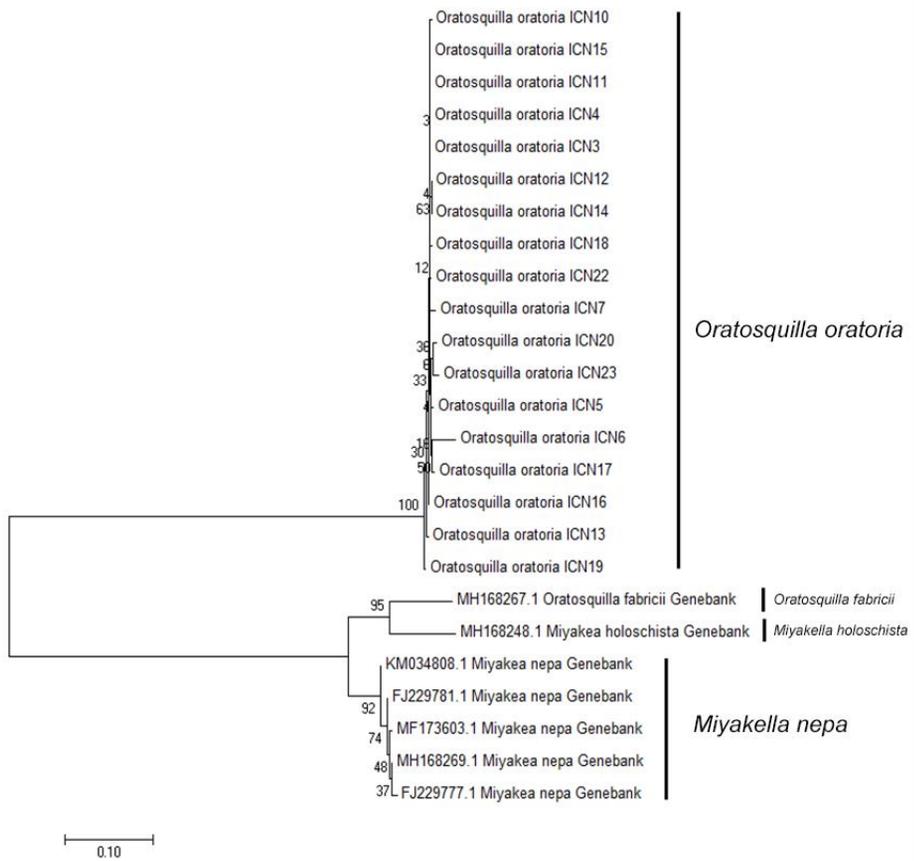


Fig. 80. Neighbor-joining (NJ) tree of COI sequences from 18 Korean *Oratosquilla oratoria* and Outgroup (*Oratosquilla fabricii*, *Miyakella* (as *Miyakea*) *holoschista*, and *Miyakella* (as *Miyakea*) *nepa*).

Genus *Oratosquilla* Manning, 1968

Oratosquilla Manning, 1968: 120, 133. (type species *Squilla oratoria* de Haan, 1844, by original designation. Gender feminine).

Diagnosis. Eye large, strongly bilobed, distinctly broader than and set obliquely on stalk, Ocular scales separate. Carapace with anterolateral spine; Median carina distinct, not interrupted at base of anterior bifurcation; branches of anterior bifurcation distinct, opening anterior to dorsal pit; posterolateral margin rounded. Raptorial claw dactylus with 6 teeth, outer margin without basal notch; carpus dorsal carina bi- or tri-tuberculate; merus outer inferodistal angle with or without spine. Mandibular palp 3-segmented. Maxillipeds 1–4 with epipod. Pleopod 1 endopod in adult males with posterior endite; hook process blunt distally. Thoracic somites 6–8 with distinct submedian and intermediate carinae. Thoracic somites 5–6 lateral processes bilobed. Carina of abdominal somites 1–6 distinct. Telson submedian teeth with fixed apices; prelateral lobe present; dorsolateral surface with curved rows of shallow pits; without supplementary longitudinal carinae; ventral surface with short postanal carina. Uropodal protopod inner margin crenulate.

Composition. *O. fabricii* (Holthuis, 1941), *O. mauritiana* (Kemp, 1913), and *O. oratoria* (de Haan, 1844).

Key to the species of *Oratosquilla* Manning, 1968

1. Submedian carina of abdominal somite 4 without posterior spine
..... *O. oratoria*
- Submedian carinae of abdominal somites 4–6 with posterior spines
..... 2
2. Anterior lobe of lateral process of thoracic somite 7 blunt
..... *O. mauritania*
- Anterior lobe of lateral process of thoracic somite 7 point to blunt (if the total length
is more than 55 mm) *O. fabricii*

33. *Oratosquilla oratoria* (De Haan, 1844) (Figs. 81–82)

Squilla oratoria de Haan, 1844 (atlas): pl. 51, fig. 2 [type locality: Japan]; Kemp, 1913: 3, 10, 23, 66, pl. 5, figs. 54–56 [part]; Manning, 1965: 259–260.

Squilla affinis Berthold, 1845: 46 [type locality: China].

Oratosquilla oratoria: Manning, 1971: 4, 6–8, fig. 2; Yamaguchi & Baba, 1993: 183–186, figs. 14, pl. 3a, b; Manning, 1995: 25, 224, figs. 136a, b, 137; Ahyong et al., 1999: 49, 52, figs. 6f–I; Ahyong, 2001: 283–285: fig. 138; Ahyong, 2012: 92–93: fig. 41.

Material examined

Non type material

KOREA: Sorae Port, 69, Poguro, Namdong-gu, Incheon (37°21'47.9"N 126°36'41.3"E): 10 females (85–108 mm), 12 males (128–150 mm), commercial fishing trawlers, 25 April 2018.

Suldo Port, Yeomsan-myeon, Yeonggwang-gun, Jeollanam-do (35°12'44.4"N 126°22'32.0"E): 11 females (110–130 mm), 12 males (15–79 mm), commercial fishing trawlers, 20 June 2009.

Gyodongnam 2-gil, Yeosu-si, Jeollanam-do (34°44'18.0"N 127°43'54.3"E): 18 females (100–125 mm), 5 males (77–95 mm), commercial fishing trawlers, 18 June 2010.

Diagnosis. Rostral plate (Fig. 82) trapezoid; apex truncate to curved. Raptorial claw (Fig. 82) robust; dactylus with 6 teeth; merus with outer inferodistal tooth. Carapace (Fig. 82) with median carina uninterrupted at base of anterior bifurcation; branches of anterior bifurcation distinct, opening anterior to dorsal pit; posterior median projection obtuse. Thoracic somite 5 (Fig. 82) lateral process bilobed. Thoracic somite 6 lateral process bilobed; anterior lobe slender. Thoracic somite 7 (Fig. 82) lateral process anterior lobe triangular. Abdominal somite 4 (Fig. 82) unarmed posteriorly. Telson (Fig. 82) subquadrate, broader than long, bearing a couple of three pairs of primary teeth; median carina interrupted proximally, with posterior spine; dorsal surface with curved rows of shallow pits; denticles rounded, each with dorsal tubercle, with 2–3 submedian denticles, 6–9 intermediate denticles, 1 lateral denticle; prelateral lobe as long as margin of lateral teeth. Uropodal protopod (Fig. 82) with lobe on outer margin of inner spine rounded.

Habitat. Muddy or sandy-mud substrates in the depth 10–20 m (Ahyong, 2012).

Distribution. Southern Russia, Korea, Japan, China, Hong Kong and Vietnam; introduced to south-eastern Australia and north-western New Zealand (Ahyong, 2012).



Fig. 81. Distribution of *Oratosquilla oratoria* (De Haan, 1844). Legend: star = type locality; circle = distribution in worldwide.

Remarks. *Oratosquilla oratoria* is similar with other species in the genus in having the bilobed lateral processes of thoracic somites 5–6 and in having the anterior bifurcation of the median carina of the carapace uninterrupted basally and opening anterior to the dorsal pit. However, this species differs from congeners by the combination of the armed outer inferodistal margin of the merus of the raptorial claw and unarmed submedian carinae on abdominal somite 4. The Korean specimens agree well with published accounts (Ahyong, 2001; 2012) except those following characteristics: In the Korean specimens, 1) the apex of the rostral plate is usually truncate but is occasionally rounded, 2) the anterior lobe of thoracic somite 7 varies from blunt to sharp, and 3) the median carina of carapace is sometimes faint. These features, like the *O. fabricii*, are found to be less developed before reaching 30 mm based on a number of Korean specimens. Therefore, when identifying the corresponding species, the size should be confirmed, and the parts corresponding to the objective morphological trait should be additionally confirmed and integrated to interpret the traits. In other words, whether thoracic somites 6–7 is divided into one or two, whether the median carina of the carapace is faint or absent, the number of denticles in general, and the developmental state of the endopod of the first pleopod should be confirmed. In the case of *Oratosquilla oratoria*, lateral processes of

thoracic somites 6–7 are all bilobed. If the median carina of the carapace is not without a trace, it should be judged to be in a faint case. The number of denticles is submedian denticles are 5–6, intermedian denticles are 4–6, lateral denticles are 4–6, marginal denticles 1–5. If the endopod of the first pleopod is not well developed, it is either female or has not yet developed into the adult.



Fig. 82. *Orotosquilla oratoria*, male. Whole animal, 150 mm, MADBK600103001. Scale bar = 10 mm.

34. *Oratosquilla fabricii* (Holthuis, 1941) (Fig. 83)

Squilla fabricii Holthuis, 1941: 927–929, fig. 1 [type locality: Telok Dalan, Nias, Indonesia].

Oratosquilla fabricii: Manning, 1995: 25, 225, 227; Ahyong&Erdmann, 2003: 342; Ahyong et al., 2008: 142–144, figs. 112–114.

Non type material

Taiwan: 1 female, TL 64 mm, Dasi fishing port, Yilan Conty, 24 September 1996.

Diagnosis. Rostral plate wider than long but appering elongate; apex rounded. Raptorial claw robust; dactylus with 6 teeth; merus with outer inferodistal tooth. Carapace with median carina interrupted or interuupted at base of anterior bifurcation; branches of anterior bifurcation distinct, opening anterior to dorsal pit; posterior median projection obtuse. Thoracic somite 5 lateral process bilobed. Thoracic somite 6 lateral process bilobed; anterior lobe elongate, triangular. Thoracic somite 7 lateral process with small triangular anterior lobe triangular, apex pointed to blunt, and broad and triangular posterior lobe. Thoracic somite 8 anterior margin triangular, apex sharp; sternal keel rounded. Abdominal somite 4 armed posteriorly. Telson subquadrate, broader than long, bearing a couple of three pairs of primary teeth; median carina interrupted proximally, with posterior spine; dorsal surface with curved rows of shallow pits; denticles rounded, each with dorsal tubercle, with 4–6 submedian denticles, 2–6 intermediate denticles, 1–6 lateral denticle; prelateral lobe shorter than margin of lateral teeth. Uropodal protopod with lobe on outer margin of inner spine rounded, narrower than adjacent spines.

Habitat. Muddy or sandy-mud substrates in sheltered waters such as embayments and estuaries in the depth 5–50 m (Ahyong, 2012).

Distribution. Figi, French Polynesia, Guam, Hawaii, Indonesia, Taiwan, Philippines, New Caledonia, New Zealand (Ahyong, 2012),



Fig. 83. Distribution of *Oratosquilla fabricii* (Holthuis, 1941). Legend: star = type locality; circle = distribution in worldwide.

Remarks. *Oratosquilla fabricii* closely resembles *O. oratoria* (De Haan, 1844) in having the bilobed lateral processes of thoracic somites 5–6 and the armed outer inferodistal margin of the merus of the raptorial claw. However, this species is easily distinguished from the other by the presence of the armed submedian carina on abdominal somite 4.

Additionally, when interpreting the morphological traits identifying the corresponding species, as mentioned in the part ‘morphological character in *Oratosquilla*’, a comprehensive combination of morphological traits is needed. As noted by Ah Yong (2012), that several of the juvenile characters of *Oratosquilla fabricii* are retained by adults of *Quollastria* Ah Yong, 2001, and *Oratosquillina* Manning, 1995. Hence, species of *Oratosquillina* and *Quollastria* bear the interrupted anterior bifurcation of the median carina of the carapace and an uninterrupted dorsal carpal carina of the raptorial claw. As noted by Ah Yong (2001), adults of *Busquilla* retain many features of postlarval or juvenile *Oratosquilla*. According to the description of Ah Yong (2012), the species develops slowly, and until TL 55 mm, the corresponding morphological trait is properly expressed.

Therefore, when identifying the corresponding species, the size should be confirmed, and the parts corresponding to the objective morphological trait should

be additionally confirmed and integrated to interpret the traits. In other words, whether submedian carina on abdominal somite 4 is armed or unarmed, anterior lobe of the lateral process of thoracic somites 7 is pointed to blunt or just blunt, and the developmental state of the endopod of the first pleopod should be confirmed. In the case of *O. fabricii*, submedian carina on abdominal somite 4 is armed. The anterior lobe of the lateral process of thoracic somites 7 is always pointed to blunt. If the endopod of the first pleopod is not well developed, it is either female or has not yet developed into the adult.

35. *Oratosquilla mauritiana* (Kemp, 1913) (Fig. 84)

Squilla mauritiana Kemp, 1913: 66, 68.

Oratosquilla mauritiana: Manning, 1995: 220; Ahyong, 2001: 283.

Type material

Mauritius: IM 4269/4, female and male, no further information.

Diagnosis. Rostral plate wider than long; apex rounded. Raptorial claw robust; dactylus with 6 teeth; merus with outer inferodistal tooth. Carapace with median carina interrupted or interrupted at base of anterior bifurcation; branches of anterior bifurcation distinct, opening anterior to dorsal pit; posterior median projection obtuse. Thoracic somite 5 lateral process bilobed. Thoracic somite 6 lateral process bilobed; anterior lobe elongate, triangular. Thoracic somite 7 lateral process with small triangular anterior lobe blunt, rounded. Abdominal somites 4–6 armed posteriorly. Telson subquadrate, broader than long, bearing a couple of three pairs of primary teeth; median carina interrupted proximally, with posterior spine; dorsal surface with curved rows of shallow pits; denticles rounded, each with dorsal tubercle; prelateral lobe present. Uropodal protopod inner margin crenulate.

Habitat. Muddy or sandy-muddy bottoms (Schram & Müller, 2004).

Distribution. Madagascar; Mauritius (Schram & Müller, 2004).



Fig. 84. Distribution of *Oratosquilla mauritiana* (Kemp, 1913). Legend: star = type locality; circle = distribution in worldwide.

Remarks. *Oratosquilla mauritiana* closely resembles *O. fabricii* (Holthuis, 1941) in having armed the submedian carina of abdominal somites 5–6 and the armed outer inferodistal margin of the merus of the raptorial claw. However, this species is easily distinguished from the other by the presence of the pointed-to blunt anterior lobe of the lateral process of thoracic somite 7.

This species has been recorded only from Mauritius of Madagascar, compared with other congeners which have a relatively broad distribution. Further sampling is required to better determine the distribution of *O. mauritiana*.

Genus *Levisquilla* Manning, 1977

Levisquilla Manning, 1977: 422 (type species *Squilla inermis* Manning, 1965, by original designation and monotypy. Gender feminine).

Diagnosis. Eye small, elongate; cornea bilobed, broader than stalk in dorsal view. Ocular scales broad; truncate; partially fused. Antennular somite 1 not greatly elongate; dorsal process trianguloid with spiniform apex. Carapace with anterolateral

spine; median carina absent; marginal carina indistinct reflected; lateral carina reduced or absent; posterolateral margin rounded. Raptorial claw dactylus with 6 teeth; carpus undivided; merus without outer inferodistal spine. Mandibular palp absent. Maxillipeds 1–4 with epipod. Pleopod 1 endopod in adult males with posterior endite; hook process with distal point. Thoracic somite 5 lateral process a short recurved spine basally. Thoracic somites 6–7 lateral process not bilobed or single. Abdominal somites 1–5 without submedian carinae. Telson submedian teeth with movable apices; prelateral lobe present. Uropodal protopod inner margin lined with slender spines.

Composition. *L. jurichi* (Makarov, 1979a); *L. inermis* (Manning, 1965); and *L. minor* (Jurich, 1904).

Key to the species of *Levisquilla* Manning, 1977

1. Dorsal surface of telson without mid-carinae. Ventral surface of telson without postanal carina (>TL 29 mm) *L. inermis*
 - Dorsal surface of telson with mid-carinae. Ventral surface of telson with postanal carina in adult size 2
2. Telson without accessory median carina *L. minor*
 - Telson without accessory median carina (TL 11–12 mm) *L. jurichi*

36. *Levisquilla inermis* (Manning, 1965) (Figs. 85–86)

Squilla inermis Manning, 1965: 255–257, fig. 2 [type locality: Enoshima, Sagami Bay, Japan]; 1977: 422.

Squilla lata: Komai, 1927: 310, pl. 14, figs. 1, 1b [not *S. lata* Brooks, 1886].

Levisquilla inermis: Manning, 1995: 24, 209–210; Ahyong, 2001: 271, fig. 132; Ahyong et al., 2008: 131, figs. 104–105; Ahyong, 2012b: 248; Ariyama et al., 2014: 35–37, fig. 6.

Material examined

Non type materials

Korea: NIBRIV0000150629, female (TL 25 mm), Seosaeng-myeon, Ulju-gun, Ulsan, South Korea, 35°20'24.4"N, 129°19'13.4"E, coll. J.S Hong, 21 October 1998; NIBRIV0000837750, female (TL 13.5 mm), Seosaeng-myeon, Ulju-gun, Ulsan, South Korea, 35°20'24.4"N, 129°19'13.4"E, coll. S.J Song, 24 October 2006; MADBK 600202_001, male (TL 18.5 mm), Seosaeng-myeon, Ulju-gun, Ulsan, South Korea, 35°20'24.4"N, 129°19'13.4"E, coll. S.J Song, 22 May 2007. MADBK 600202_002, female (TL 18.5 mm), Hwanggi-dong, Gwangyang, Jeollnam-do, South Korea, 34°53'31.3"N, 127°39'57.7"E, coll. S.J Song, 18 November 2003.

Diagnosis. Anterior margin of ophthalmic somite (Fig. 86) rounded. Each lateral process of thoracic somites 6–7 trianguloid, rounded posterolaterally. Anterolateral margin of thoracic somite 8 angular, with blunt apex. Telson (Fig. 86) prelateral lobe faintly indicated, shorter than or longer than margin of lateral tooth; dorsolateral surface without supplementary carinae; postanal carina absent. Uropodal protopod inner margin (Fig. 86) with 6–10 slender spines; protopod terminal spines with rounded lobe on outer margin of inner spine, without rounded proximal lobe; exopod proximal segment outer margin with 7–9 movable spines.

Habitat. Silty sand substrates in depth of 53–108 m (Ahyong, 2001).

Distribution. Japan, Taiwan, Vietnam, Australia (Manning, 1995; Ahyong, 2001; Ahyong et al., 2008) and Korea.



Fig. 85. Distribution of *Levisquilla inermis* (Manning, 1965). Legend: star = type locality; circle = distribution in worldwide.

Remarks. According to the description of Ahyong (2001), *L. inermis* shows allometric changes in the shape of the distal movable spine on the outer margin of the proximal uropodal exopod segment, ranging from spinular in the smallest specimen to spatulate in larger specimens. A single specimen (TL 29.9 mm) reported from Japan (Ariyama et al., 2014) also has a spatulate distal spine. The specimens examined reflect these allometric changes; the spine is most prominently spinular in the smallest specimen (TL 13.5 mm) and becomes spatulate in the larger specimens (> TL 18.5 mm). The largest specimen examined (TL 25 mm) has a distinctly spatulate, and slightly more curved distal spine compared to smaller specimens.

Levisquilla inermis is distinguished from other congeners by the absence of supplementary mid-dorsal carinae on the telson and absence of the postanal carina. The specimens examined generally agree well with published accounts (Manning, 1965; Ahyong, 2001; Ahyong et al., 2008) except that the lateral process of thoracic somite 5 is less prominently recurved anteriorly, probably a reflection of their smaller size (TL 25 mm or less) (than previously figured specimens (all with TL 29 mm or greater) (e.g., Ahyong, 2001).

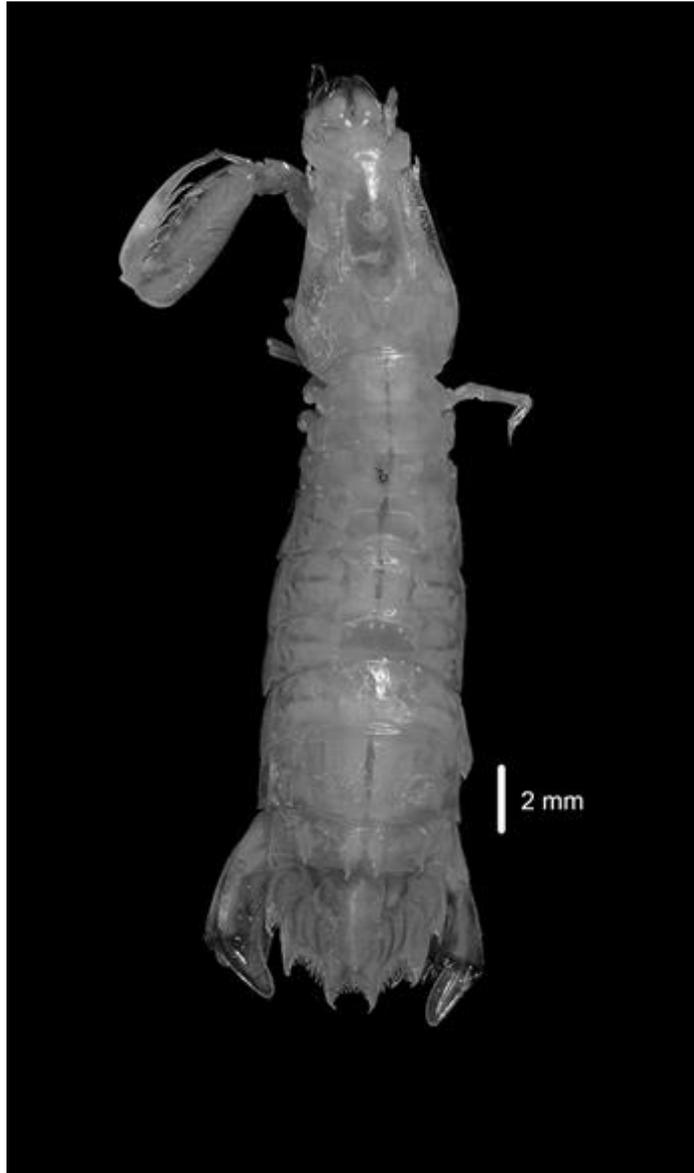


Fig. 86. *Levisquilla inermis*, female, TL 25 mm, NIBRIV0000150629.

37. *Levisquilla jurichi* (Makarov, 1979a) (Figs. 87–88)

Clorida jurichi Makarov, 1979a: 40, fig. 1 [type locality: Tonkin Bay, Vietnam].

Levisquilla jurichi: Manning, 1995: 25, 209–210; Ahyong, 1997: fig. 1A, 3K;

Ahyong, 2001: 271–274, fig. 133; Ahyong & Naiyanetr, 2002: 299; Ahyong, 2016: 464–465, fig. 4F.

Material examined

Non type material

Korea: MADBK 600205_001, female, (TL 13 mm), Junggye-ri, Byeonsan-myeon, Buan-gun, Jeollabuk-do, South Korea, 35°39'00.0"N, 126°27'22.3"E, coll. S.-K Lee, 4 September 2017.

Diagnosis. Anterior margin of ophthalmic somite (Fig. 88) triangular. Each lateral process of thoracic somites 6–7 subtruncate, rounded anterolaterally. Anterolateral margin of thoracic somite 8 rounded. Telson (Fig. 88) prelateral lobe faint, shorter than or longer than margin of lateral tooth; dorsolateral surface with supplementary carinae; the region between submedian and intermediate teeth terminating in small spine; postanal carina present. Uropodal protopod (Fig. 88) inner margin with 6–11 spines; protopod terminal spines with rounded lobe on outer margin of inner spine, without rounded proximal lobe; exopod proximal segment outer margin with 5–7 movable spines.

Habitat. Sand and mud strates in depth of 9–43 m (Ahyong, 2001).

Distribution. Andaman Sea, Vietnam, Singapore, New Caledonia, Australia (Ahyong, 2001, 2016), and from Korea.



Fig. 87. Distribution of *Levisquilla jurichi* (Makarov, 1979a). Legend: star = type locality; circle = distribution in worldwide.

Remarks. According to the description of Ahyong (2001), the primary diagnostic characters of *L. jurichi* are well developed even in TL 11–12 mm juveniles, although the mid-dorsal carinae on the telson are fewer in number than those of larger specimens. The specimen examined differs slightly from Ahyong's (2001) account of the species in having six submedian denticles as a result of the innermost denticles having multifid apices (a juvenile feature commonly observed in squilloids) and fewer supplementary longitudinal carinae on the telson than in a TL 51 mm specimen figured by Ahyong (2001: fig. 133). Considering the small size of the Korean specimen (TL 13 mm), the observed differences may be attributable to its immaturity. Within genus *Levisquilla*, *Levisquilla jurichi* differs from *L. inermis* by the presence of supplementary carina on the dorsolateral surface of the telson (smooth in *L. inermis*), and can be distinguished from *L. minor* by the presence of one instead of two lobes between the terminal spines of the protopod of the uropod. Also, *L. jurichi* has three to five submedian denticles on either side of the midline and numerous supplementary longitudinal carinae on the telson. The specimens examined generally agree well with published accounts (Manning, 1995; Ahyong, 1997; 2001; Ahyong & Naiyanetr, 2002; Ahyong, 2016).

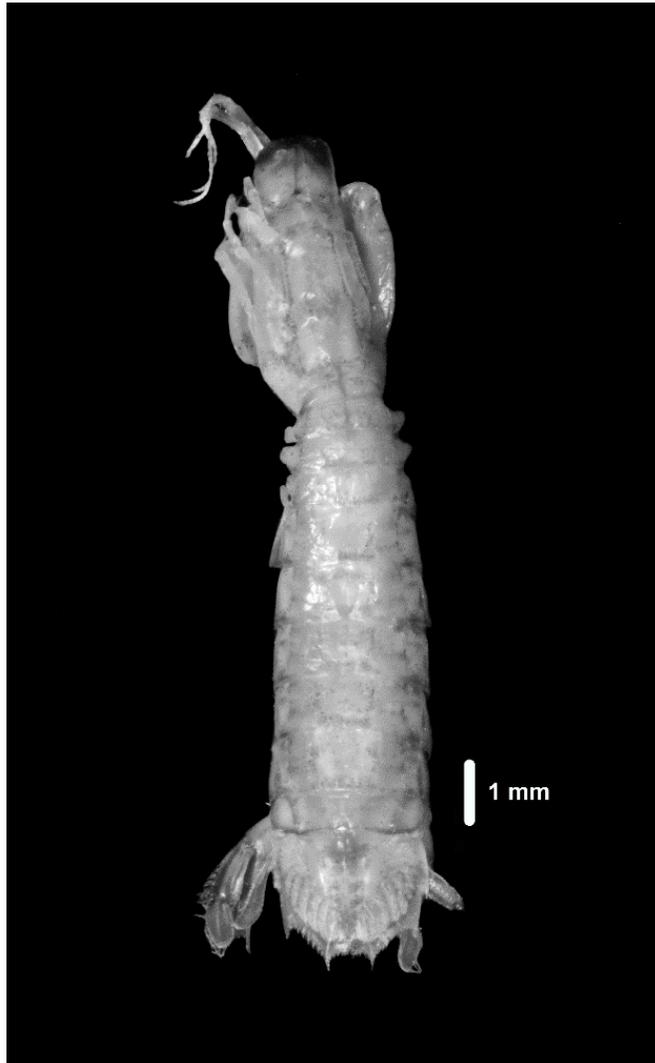


Fig. 88. *Levisquilla jurichi*, female, TL 13 mm, MADBK 600205_001.

38. *Levisquilla minor* (Jurich, 1904) (Fig. 89)

Squilla minor Jurich, 1904: 364–366, pl. 25, figs. 4–4a.

Levisquilla inermis: Manning, 1995: 24, 209; Ahyong, 2001: 271.

Non type material

Tanzania: ZMB 13254, 1 female, 1 male, Bay of Zanzibar, no further information.

Diagnosis. Antennular somite 1 not greatly elongate; dorsal process trianguloid with spiniform apex. Lateral processes of thoracic somites 6–7 single. Telson dorsolateral surface without supplementary carinae, sometimes with a row of widely spaced tubercles; postanal carina present; submedian teeth with movable apices; prelateral lobe present. Uropodal protopod inner margin lined with slender spines.

Habitat. Muddy sand (Schram & Müller, 2004).

Distribution. Tanzania (Zanzibar), Madagascar, the Philippines (Schram & Müller, 2004).



Fig. 89. Distribution of *Levisquilla minor* (Jurich, 1904). Legend: star = type locality; circle = distribution in worldwide.

Remarks. *L. minor* is morphologically similar to *L. jurichi* in having the median carinae on the dorsal surface of the telson and postanal carina on the ventral surface of telson. However, it can be distinguished from the other by the presence of two lobes between the terminal spines of the protopod of uropod and the absence of accessory median carina on the telson. The specimens examined generally agree well with published accounts (Manning, 1995; Ahyong, 2001).

Genus *Anchisquilla* Manning, 1968

Anchisquilla Manning, 1968: 120, 127–128. (type species *Squilla fasciata* de Haan, 1844, by original designation. Gender feminine).

Diagnosis. Eye small, elongate; cornea bilobed, distinctly broader than stalk. Anterior margin of ophthalmic somite triangular. Carapace with anterolateral spine; lateral carinae and reflected marginal carinae present only; posterolateral margin rounded. Raptorial claw dactylus with 6 teeth. Mandibular palp 3-segmented. Maxillipeds 1–4 with epipod. Thoracic somites 6–8 without submedian carinae. Each lateral process of thoracic somites 5–7 single. Abdominal somites 1–5 without submedian carinae. Pleopod 1 endopod in males with posterior endite; hook process with distal point. Telson flattened, with 3 pairs of primary teeth; submedian teeth with fixed apices; prelateral lobe present; dorsolateral surface with curved supplementary carinae; ventral surface with long postanal carina and with or without supplementary carinae. Uropodal protopod inner margin lined with slender spines.

Composition. *A. subfasciata* (Tate, 1883), *A. chani* Ahyong, 2001, *A. fasciata* (de Haan, 1844), and *A. fasciaticauda* Liu & Wang, 1998.

Postanal carina of telson ventral surface in *Anchisquilla*

In *Anchisquilla* species, characteristics of the dorsal surface are used as key characters in the identification of the species. The characteristics of the accessory median carina, prelateral lobe, and dorsolateral carinae, which are present in a telson, were used as the main key characters. However, Ahyong (2001) noted that Australian specimens referable to *A. fasciata* to differ from material from Thailand, Taiwan, and Japan in having more numerous ventral telson carinae. By this characteristics, *Squilla subfasciata* (Tate, 1883), a synonym of *A. fasciata*, was removed from synonymy and recognized for *A. subfasciata* (Fig. 90A). Like fig. 90, *Anchisquilla* species has various characteristics of postanal carina on the telson ventral surface. *A. subfasciata* is distinguished from *A. fasciata* (Fig. 90B) by the presence of 4 or 5

instead of 1 or 2 carinae flanking the postanal carina. *A. chani* (Fig. 90C) differs from other species by the at most tubercles or 3 short carinae laterally.

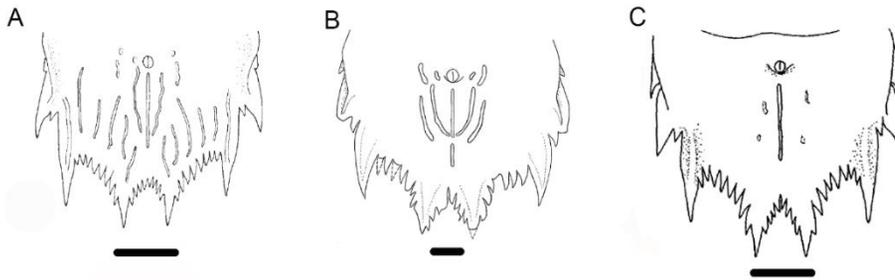


Fig. 90. Telson, ventral view. A, *Anchisquilla subfasciata* (Tate, 1883); male holotype TL 56 mm (SAM C 182); B, *Anchisquilla fasciata* (de Haan, 1844); female, TL 27 mm (MADBK 600204_001); C, *Anchisquilla chani* Ahyong, 2001; female holotype TL 52 mm (AM P55592). Scales bars: A= 3 mm, B = 1.0 mm, C = 2.5 mm. A, C

Key to the species of *Anchisquilla* Manning, 1968

1. Dorsal surface of telson without accessory median carina. Dorsolateral carina faint or distinct posteriorly only *A. fasciaticauda*
- Dorsal surface of telson with accessory median carina and distinct dorsolateral carina 2
2. Telson prelateral lobe terminating in a distinct spine; ventral surface with low tubercles *A. chani*
- Telson prelateral lobe with blunt apex; ventral surface with longitudinal carinae 3
3. Telson ventral surface with 1–2 longitudinal carinae lateral to postanal carina *A. fasciata*
- Telson ventral surface with 4–5 longitudinal carinae lateral to postanal carina *A. subfasciata*

39. *Anchisquilla fasciata* (de Haan, 1844) (Figs. 91–93)

Squilla fasciata de Haan, 1844: pl. 51, fig. 4 [type locality: Japan].

Anchisquilla fasciata: Manning, 1968: 120, 127; 1977: 420; 1991: 8; 1995: 166, 169, pl. 29, figs. 98–100; Yamaguchi & Baba, 1993: 181–182, fig. 12; Ahyong & Naiyanetr, 2002: 289–290; Ahyong et al., 2008: 69–70, fig. 48, 49; Ahyong, 2012b: 248; Ahyong & Kumar, 2018: 385–386.

Material examined.

Non type materials

Korea: NIBRIV000071695, female (TL 27 mm), Gwangyang port, Gwangyang-si, Jeollanam-do, South Korea, 34°54'30.3"N, 127°41'02.1"E, coll. J.S Hong, 1 November 2006; MADBK 600204_001, male (TL 50 mm), Gwangyang port, Gwangyang-si, Jeollanam-do, South Korea, 34°54'30.3"N, 127°41'02.1"E, 1 August 2007.

Diagnosis. Carapace (Fig. 92) without median carina, with longitudinal groove in position of intermedian carina. Outer margin of dactylus of raptorial claw (Fig. 92) without proximal notch. Each lateral process of thoracic somites 6–7 (Fig. 92) rounded. Anterolateral margin of thoracic somite 8 rounded. Abdominal somites 1–5 (Fig. 92) with blunt tubercle proximally between intermedian and lateral carinae. Telson (Fig. 92) dorsolateral surface with entire accessory median and numerous curved longitudinal carinae, often short; prelateral lobe with blunt apex; postanal carina (Fig. 93) long, with low tubercles proximally and longitudinal carinae laterally. Uropodal protopod (Fig. 92) inner margin armed with 7–14 spines; exopod proximal segment outer margin with 7–10 movable spines; exopod distal segment dark.

Habitat. Sandy, shelly or gitty mud and gravel substrates in depth of 7–55 m (Ahyong, 2001).

Distribution. Western Indian Ocean to India, Philippines, Vietnam, Taiwan, Japan (Ahyong et al., 2008), and Korea.



Fig. 91. Distribution of *Anchisquilla fasciata* (de Haan, 1844). Legend: star = type locality; circle = distribution in worldwide.

Remarks. *Anchisquilla fasciata* is morphologically close to *A. fasciaticauda* Liu & Wang, 1998 and *A. chani* Ahyong, 2001, but is distinguished from the two species by the presence of an accessory median carina and a blunt prelateral lobe on the telson. *Anchisquilla subfasciata* (Tate, 1883) also closely resembles *A. fasciata* but differs in having more numerous carinae flanking the postanal carinae on the telson (four or more rather than one or two; Ahyong, 2008).

Anchisquilla fasciata is known from the Western Indian Ocean to the Philippines, Vietnam, Taiwan, Korea, and Japan (Ahyong, 2001; Ahyong et al., 2008; Hwang et al., 2019). The specimens examined morphologically agree with the material from other areas including Japan and Taiwan, although the postanal carina is interrupted (Fig. 93), rather than entire, and is almost connected with a pair of the most proximal carinae among the two pairs of carinae flanking the postanal carina.



Fig. 92. *Anchisquilla fasciata*, female, TL 27 mm, MADBK 600204_001.

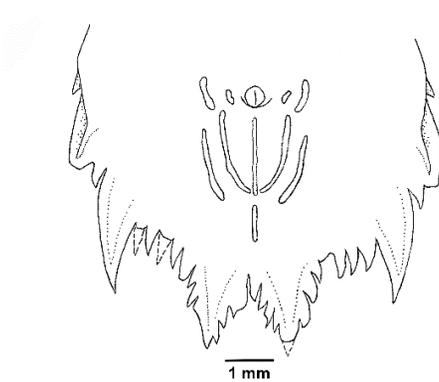


Fig. 93. *Anchisquilla fasciata*; telson, ventral view, female, TL 27 mm, MADBK 600204_001.

40. *Anchisquilla subfasciata* (Tate, 1883) (Figs. 94–95)

Squilla subfasciata Tate, 1883: 52, pl. 2, figs. 1a–d [type locality: Gulf St. Vincent, S Australia].

Squilla fasciata: Hale, 1924: 496; 1927: 30, 32, fig. 21; Stephenson, 1952: 5; Stephenson and McNeill, 1955: 240–241, 258, 261 [not *S. fasciata* de Haan, 1844].

Anchisquilla fasciata: Ahyong, 2001: 196, 198, fig. 96; Ahyong and Davie, 2002: 72–73 [not *A. fasciata* (de Haan, 1844)].

Material examined

Non type material

Australia: AMP 21655, female, TL 53 mm, Queensland, south east corner of Gulf of Carpentaria, coll. CSIRO Division of Fisheries and Oceanography, 23 December 1963.

Diagnosis. Carapace (Fig. 95) without median carina, with longitudinal groove in position of intermedian carina. Outer margin of dactylus of raptorial claw (Fig. 95) without proximal notch. Each lateral process of thoracic somites 6–7 (Fig. 95) rounded. Anterolateral margin of thoracic somite 8 rounded. Abdominal somites 1–5 (Fig. 95) with blunt tubercle proximally between intermedian and lateral carinae. Telson (Fig. 95) dorsolateral surface with entire accessory median and numerous curved longitudinal carinae, often short; prelateral lobe with blunt apex; postanal carina long, with additional 4–5 carinae laterally. Uropodal protopod (Fig. 95) inner margin armed with 7–14 spines; exopod proximal segment outer margin with 7–10 movable spines; exopod distal segment dark.

Habitat. Sand and mud substrates in depth of 49 m (Ahyong, 2001).

Distribution. Australia (Gulf of Carpentaria), Vietnam (Gulf of Tonkin), and Oman (Ahyong, 2008).



Fig. 94. Distribution of *Anchisquilla subfasciata* (Tate, 1883). Legend: star = type locality; circle = distribution in worldwide.

Remarks. *Anchisquilla subfasciata* is morphologically close to *A. fasciata* (de Haan, 1844) in having a blunt prelateral lobe on the telson and entire accessory median carina. According to the description of Ah Yong (2001), Australian specimens referable to *A. fasciata* to differ from material from Thailand, Taiwan and Japan in having more numerous ventral telson carinae. By this characteristics, *Squilla subfasciata* Tate, 1883, a synonym of *A. fasciata*, was removed from synonymy and recognized for *A. subfasciata*. *A. subfasciata* is distinguished from *A. fasciata* by the presence of 4 or 5 instead of 1 or 2 carinae flanking the postana carina. The specimen examined generally agrees well with these characteristics.



Fig. 95. *Anchisquilla subfasciata*, female, TL 53 mm, AMP 21655.

41. *Anchisquilla chani* Ahyong, 2001 (Figs. 96–97)

Anchisquilla chani Ahyong, 2001: 194–196, fig. 95; Ahyong & Davie, 2002: 72.

Material examined

Type material

Holotype: Australia: AMP 55593, female, TL 63 mm, Northern, Arafura Sea, coll. T. Wassenberg, 23 November 1991.

Diagnosis. Carapace (Fig. 97) without median carina, with longitudinal groove in position of intermedian carina; lateral carinae indicated anteriorly and posteriorly; Outer margin of dactylus of raptorial claw with shallow proximal notch. Each lateral process of thoracic somites 6–7 (Fig. 97) rounded. Anterolateral margin of thoracic somite 8 (Fig. 97) rounded. Abdominal somites 1–5 (Fig. 97) with blunt tubercle proximally between intermedian and lateral carinae. Telson (Fig. 97) broader than long; prelateral lobe distinct, as long as margin of lateral tooth, terminating in spine; dorsolateral surface with accessory median carina comprising a broken line of elongate tubercles, and numerous supplementary longitudinal carinae, often broken anteriorly; postanal carina long, at most with low tubercles or 3 short carinae laterally; ventrolateral carina extending to base of lateral tooth. Uropodal protopod (Fig. 97) inner margin armed with 9–12 spines; exopod proximal segment outer margin with 7 movable spines; exopod distal segment dark.

Habitats. Sand and mud substrates in the depth of 49 m (Ahyong, 2001).

Distribution. Australia (Gulf of Carpentaria), Vietnam (Gulf of Tonkin), and Oman (Ahyong, 2008).



Fig. 96. Distribution of *Anchisquilla chani* Ahyong, 2001. Legend: star = type locality; circle = distribution in worldwide.

Remarks. *Anchisquilla chani* is morphologically similar to *A. fasciata* in having and accessory median carina and distinct longitudinal carinae. However, *A. chani* differs from the other by the presence of the following features: 1) the accessory median carina of the telson is broken into a line of tubercles instead of being entire or only disrupted proximally, 2) the outer, proximal margin of the dactylus of the raptorial claw is notched instead of entire, 3) the distal apex of the prelateral lobe is distinctly spiniform instead of a blunt, and 4) the ventral surface of the telson lateral to the postanal carina bears several short, low carinae or tubercles instead of longitudinal carinae. The specimen examined generally agrees well with these characteristics.



Fig. 97. *Anchisquilla chani*, AMP 55593, female, TL 63 mm.

42. *Anchisquilla fasciaticauda* Liu & Wang, 1998 (Figs. 98–99)

Anchisquilla fasciaticauda Liu & Wang, 1998: 588–590, 593–594, fig. 1; Ahyong, 2001: 194.

Material examined

Non type material

Fiji: AMP 21655, male, TL 60 mm, south of Viti Levu, coll. P. Bouchet, B. Richer de Forges, 15 August 1998.

Diagnosis. Carapace (Fig. 99) without median carina, with longitudinal groove in position of intermedian carina. Outer margin of dactylus of raptorial claw without proximal notch. Each lateral process of thoracic somites 6–7 (Fig. 99) rounded. Anterolateral margin of thoracic somite 8 (Fig. 99) rounded. Abdominal somites 1–5 (Fig. 99) with blunt tubercle proximally between intermedian and lateral carinae. Telson (Fig. 99) dorsolateral surface without accessory median; dorsolateral carinae distinct, posteriorly only. Uropodal exopod (Fig. 99) distal segment dark.

Habitat. Bottom muddy sand in depth of 44–176 m. (Schram & Müller, 2004).

Distribution. South China Sea (Schram & Müller, 2004).



Fig. 98. Distribution of *Anchisquilla fasciaticauda* Liu & Wang, 1998. Legend: star = type locality; circle = distribution in worldwide.

Remarks. Among *Anchisquilla* species, *Anchisquilla fasciaticauda* is easily distinguished from other congeners by the absence of accessory median carina on the dorsal surface of the telson and indicated only posteriorly distinct dorsolateral carinae. The specimen examined generally agrees well with these characteristics.



Fig. 99. *Anchsquilla fasciaticauda*, male, TL 60 mm, AMP 21655.

Genus *Squilloides* Manning, 1968

Squilloides Manning, 1968: 131. (type species *Squilla leptosquilla* Brooks, 1886, by original designation. Gender feminine).

Diagnosis. Eye small; cornea strongly bilobed, set obliquely on stalk. Ocular scales separate. Dorsal processes of antennular somite trianguloid; apices acute, directed anterolaterally. Mandibular palp absent. Maxillipeds 1–4 each with epipod. Carapace with anterolateral angle spines; with or without intermediate carinae and anterior portion of lateral carinae; median carina without anterior bifurcation. Raptorial claw

dactylus with 4 teeth; carpus dorsal carina undivided; merus without outer inferodistal spine. Pleopod 1 endopod in males with posterior endite; hook process with distal point. Lateral process of thoracic somite 5 single, directed anterolaterally; ventral spine stout, directed anteroventrally. Lateral process of thoracic somites 6–7 single, broadly rounded anteriorly, acute posteriorly. Abdominal somites 1–6 with carinae. Telson trianguloid; submedian teeth with fixed apices; prelateral lobe absent; dorsolateral surface without pits or supplementary carinae. Uropodal protopod with spine anterior to endopod articulation; inner margin of protopod crenulate.

Composition. *S. leptosquilla* (Brooks, 1886); and *S. tenuispinis* (Wood-Mason, 1875).

Morphological variation in *Squilloides*

In *Squilloides* species, the most important variation is in the orientation of the lateral process of thoracic somite 5 ranging from being directed laterally to anterolaterally, a feature used by Kemp (1911) to distinguish *S. leptosquilla* from *S. tenuispinis* (Wood-Mason, 1875) (Fig. 100). Sexual dimorphism in the size of the intermediate teeth of the telson is present like Fig. 101.

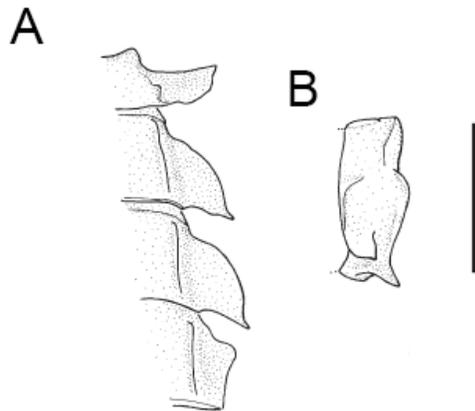


Fig. 100. Lateral process of thoracic somite 5 of *Squilloides leptosquilla* (Male, TL 77 mm, NIWA); A, dorsal view; B, lateral view. Scale bars A–B = 5.0 mm. Modified from Ahyong (2001).

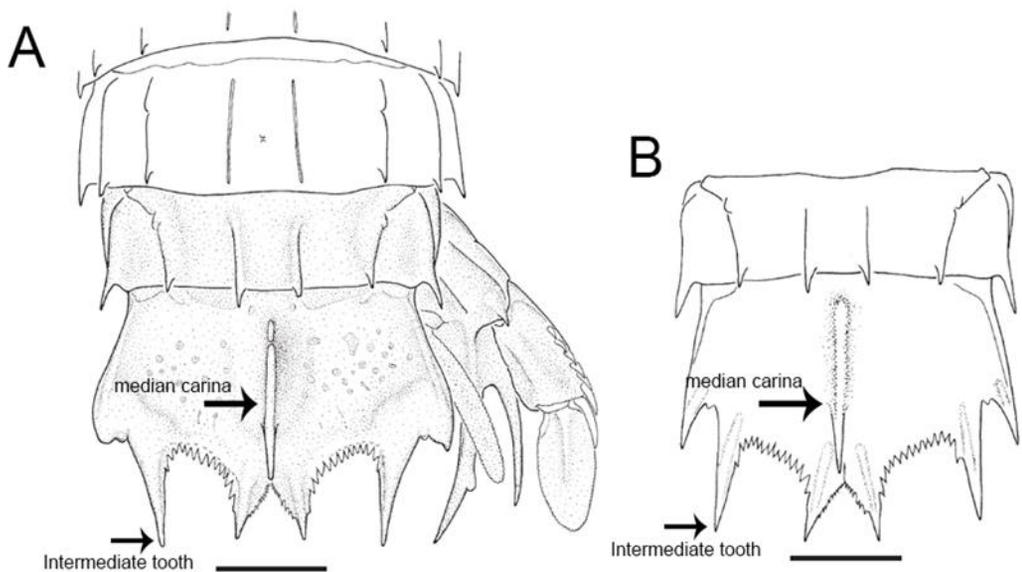


Fig. 101. Telson variation of *Squilloides leptosquilla*. A, abdominal somites 5–6, telson and right uropod (Male, TL 77 mm, NIWA); B, abdominal somite 6 and telson (Female, TL 79 mm, TMCS-0032). Scale bars A–B = 5.0 mm. Modified from Ahyong (2008).

Key to the species of *Squilloides* Manning, 1968

- 1. Carapace with intermediate carina *S. leptosquilla*
- Carapace without intermediate carina *S. tenuispins*

43. *Squilloides leptosquilla* (Brooks, 1886) (Fig. 102)

Squilloides leptosquilla Brooks, 1886: 30–34, pl. 1: figs. 1–2 [type locality: Celebes Sea, Philippines].

Squilloides leptosquilla: Manning, 1991: 15; 1995: 26; Ahyong, 2001: 310, 312, fig. 150; 2008: 176–179, figs. 142–143.

Type material

Holotype: NHM 1894.10.16.7, male, TL 66 mm, Philippine Islands, *Challenger* stn 204B, no further information.

Diagnosis. Carapace with intermediate carinae. Abdominal somite with respective carinae; abdominal somite 6 bearing submedian carina; abdominal somites 3–6 bearing intermediate carinae; abdominal somites 1–6 bearing intermediate carinae; abdominal somites 1–5 bearing marginal carinae. Telson denticles present, as follows: 12–19 submedian denticles, 8–14 intermediate denticles, 1 lateral denticle. Uropodal exopod proximal segment outer margin with 7–9 movable spines.

Habitat. Soft substrates in depth of 170–754 m (Ahyong, 2008). Moosa (1986) mentioned the bathymetric range as 170–754 m, as a depth of the entire specimens.

Distribution. Australia (Ahyong, 2001), Philippines (Brooks, 1886; Moosa, 1986), Indonesia (Hansen, 1926), the Andaman Islands (Kemp, 1913), and Korea.



Fig. 102. Distribution of *Squilloides leptosquilla* (Brooks, 1886). Legend: star = type locality; circle = distribution in worldwide.

Remarks. In *Squilloides* species, the length of the rostral plate, the lateral process

of thoracic somite 5, and the median carina of the telson varies. The two preceding characters can be changed according to allometric growth. In general, the characters of the rostral plate can be changed according to allometric growth in the relative length of the rostral plate and anterior margins of the basal portion. The rostral spine is proportionally longest in small specimens and becomes shorter with increasing body size and can become proportionally thicker. Also, the anterior margin of the basal portion of the rostral plate slopes more posteriorly in smaller specimens and become transverse or even slightly concave with increasing body size. The case of the length of the rostral plate also is similar. In other stomatopods, the degree of the median carina of the telson is known to be different according to sex. Among *Squilloides* species, *S. leptosquilla* differs from *S. tenuispinis* by the presence of the intermediate carinae on the carapace. These differences may be referable to size since all specimens of *S. tenuispinis* reported by Kemp are below 62 mm TL. So it should that prove size related or variable, the two species will have to be synonymized. Sexual dimorphism in the relative lengths of the intermediate primary teeth of the telson observed together in both species, reported by Moosa (1986) for Philippine specimens, is also evident.

44. *Squilloides tenuispinis* (Wood-Mason, 1891) (Fig. 103)

Squilloides tenuispinis Wood-Mason, 1891: 271; Ahyong, 2001: 311.

Type material

Holotype: Burna: IM 5801/9, male, IM 3081/5, female, Ganjam coast, Madras & off Chebuda, no further information.

Diagnosis. Carapace without intermediate carinae. Abdominal somite with respective carinae; abdominal somite 6 bearing submedian carina; abdominal somites 3–6 bearing intermediate carinae; abdominal somites 1–6 bearing intermediate carinae; abdominal somites 1–5 bearing marginal carinae. Telson denticles present, as follows: 12–19 submedian denticles, 8–14 intermediate

denticles, 1 lateral denticle. Uropodal exopod proximal segment outer margin with 7–9 movable spines.

Habitat. The information is not available.

Distribution. India and Burma (Schram & Müller, 2004).



Fig. 103. Distribution of *Squilloides tenuispinis* (Wood-Mason, 1891). Legend: star = type locality; circle = distribution in worldwide.

Remarks. Features distinguishing *S. tenuispinis* and *S. leptosquilla* are discussed under the account of the former. *S. tenuispinis* differs from *S. leptosquilla* by the absence of the intermediate carinae on the carapace. Other features that are mainly observed between them, it should that prove size-related or variable, the two species will have to be synonymized. *S. tenuispinis* differs from *S. leptosquilla* by the absence of the intermediate carinae on the carapace.

Genus *Kempella* Low & Ahyong, 2010

Kempella Low & Ahyong, 2010: 68. (type species *Squilla mikado* Kemp & Chopra, 1921, by original designation. Gender feminine).

Diagnosis. Eye small; cornea distinctly bilobed. Carapace with anterolateral spine; median carina distinct, uninterrupted at base of anterior bifurcation, branches of anterior bifurcation distinct, opening anterior to dorsal pit; posterolateral margin angular. Raptorial claw dactylus with 6 teeth; carpus dorsal carina undivided; merus without outer inferodistal spine. Pleopod endopod in males with posterior endite; hook process with distal point. Lateral process of thoracic somite 5 a single slender spine directed laterally; ventral spine directed ventrolaterally. Lateral processes of thoracic somites 6–7 bilobed. Mandibular palp 3-segmented. Maxillipeds 1–4 with epipod. Abdominal somites 1–5 with lateral carinae bicarinate. Telson submedian teeth with fixed apices; prelateral lobe present; dorsolateral surface without longitudinal carinae. Uropodal protopod inner margin crenulate.

Composition. *K. mikado* (Kemp & Chopra, 1921); and *K. stridulans* (Wood-Mason, in Alcock, 1894).

Remarks. *K. mikado* and *K. stridulans* are easily distinguished by the presence of median carina of the rostral plate and a pair of dark patches on abdominal somite 5. The character used by Chopra (1939) and Manning (1995), the relative length of the anterior bifurcation in relation to the remainder of the median carina of the carapace, varies in *Kempella* species and thus is not useful a diagnostic character (Ahyong, 2001). This confirms that it is reasonable to use a constant and invariable factor as a diagnosis key character rather than a trait that can change with growth, such as relative size and ratio.

Key to the species of *Kempella* Low & Ahyong, 2010

- 1. Rostral plate with median carina. Abdominal somites with pair of dark patches *K. mikado*
- Rostral plate without median carina. Abdominal somites without pair of dark patches *K. stridulans*

45. *Kempella mikado* (Kemp & Chopra, 1921) (Figs. 104–105)

Squilla stridulans: Kemp, 1913: 78 [part, Japanese specimens only, not *S. stridulans* Wood-Mason, 1895].

Squilla mikado Kemp & Chopra, 1921: 301, fig. 2; Komai, 1927: 320; Manning, 1965: 257–259, 262, pl. 12: fig. a.

Squilla zanzibarica Chopra, 1939: 143–148, figs. 2, 4.

Oratosquilla mikado: Manning, 1971b: 3.

Kempina zanzibarica: Manning, 1981: 298–300, fig. 1.

Kempina mikado: Manning, 1978: 40, fig. 23a–c; Moosa, 1986: 400–402, fig. 10; Manning, 1991: 14; 1995: 24, 208; Graham et al., 1993a: 24, 64; 1993b: 73.

Kempina cf mikado: Cannon et al., 1987: 63; Ahyong, 2001: 266–268: fig. 130.

Kempella mikado: Kang et al., 2016: 234–236, fig. 2; Hwang et al., 2019: in press.

Material examined.

Non type material

Australia: AM P43206, female, TL 130 mm, Queensland, due east of Mooloolaba, coll. J. McIllwain, 4 August 1994.

Diagnosis. Rostral plate (Fig. 105) with median carina. Carapace (Fig. 105) with undivided portion of median carina anterior to dorsal pit from about one-third to one fifth of distance between dorsal pit and anterior margin. Thoracic somite 5 (Fig. 105) with lateral process as single slender spine directed laterally; ventral spine directed ventrolaterally. Thoracic somites 6–7 (Fig. 105) bilobed; thoracic somite 6 lateral process anterior lobe trapezoid, apex acute; posterior lobe triangular; anterior margin straight to convex, apex acute. Thoracic somite 7 (Fig. 105) lateral process anterior lobe trapezoid to spiniform, apex acute; posterior lobe, triangular, anterior margin straight to slightly convex, apex acute. Abdominal somite 5 (Fig. 105) with pair of large dark dorsal patches. Uropodal exopod (Fig. 105) proximal segment with 10–

12 movable spines on outer margin.

Habitat. Manning (1991) noted a bathymetric range of 58 m to 753–804 m for *K. mikado*. Level, sandy or sandy-mud substrates from nearshore to the outer continental shelf and slope in depths of 30–570 m. In case of Australian specimens, this species has often been taken with *Anchisquilloides mcneilli* (Ahyong, 2001).

Distribution. Australia, Japan, Philippines, New Caledonia, Vietnam (Ahyong, 2001), Taiwan (Ahyong et al., 2008), and Korea.



Fig. 104. Distribution of *Kempella mikado* (Kemp & Chopra, 1921). Legend: star = type locality; circle = distribution in worldwide.

Remarks. Among *Kempella* species, *K. mikado* is morphologically similar to *K. stridulans* (Wood-Mason, in Alcock, 1894) in having following characteristics: (1) the single, spiniform lateral process of thoracic somite 5 and (2) strongly bilobed lateral processes of thoracic somites 6–7. However, *K. mikado* can be easily distinguished from the other by the presence of median carina of the rostral plate and a pair of dark patches on the abdominal somites. In case of this species, Chopra (1939) and Manning (1995) used the relative length of the anterior bifurcation in relation to the remainder of the median carina of the carapace as an identification key. However, these characteristic varies and thus are unreliable as a diagnosis character.



Fig. 105. *Kempella mikado*, female, TL 130 mm, AM P43206.

46. *Kempella stridulans* (Wood-Mason, in Alcock, 1894) (Figs. 106–107)

Squilla stridulans Wood-Mason, in Alcock, 1894: 409; Ghosh & Manning, 1988: 659.

Kempina stridulans: Moosa, 1986: 402–403; Manning, 1991: 14.

Kempella stridulans: Low & Ahyong, 2010: 68.

Material examined

Taiwan: AM P67935, female, TL 64 mm, Yilan County, Dasi fishing port, coll. Shane T. ahyong, 25 May 1998.

Diagnosis. Rostral plate (Fig. 107) without median carina. Carapace (Fig. 107) with undivided portion of median carina anterior to dorsal pit from about one-third to one fifth of distance between dorsal pit and anterior margin. Thoracic somite 5 (Fig. 107) with lateral process as single slender spine directed laterally; ventral spine directed ventrolaterally. Thoracic somites 6–7 (Fig. 107) bilobed. Abdominal somite 5 (Fig. 107) without pair of large dark dorsal patches. Uropodal exopod (Fig. 107) proximal segment with 10–11 movable spines on outer margin.

Habitat. Bottom soft brown mud (Ghosh, 1973).

Distribution. Gulf of Aden, India, Philippines (Schram & Müller, 2004).



Fig. 106. Distribution of *Kempella stridulans* (Wood-Mason, in Alcock, 1894). Legend: star = type locality; circle = distribution in worldwide.

Remarks. *Kempella stridulans* can be easily distinguished from only congener, *K. mikado* by the absence of a median caruba on the rostral plate and a pair of dark

submedian patches on abdominal somite 5. The specimen examined generally agrees well with these characteristics.



Fig. 107. *Kempella stridulans*, female, TL 64 mm, AM P 67935.

Genus *Cloridopsis* Manning, 1968

Cloridopsis Manning, 1968: 120, 128. (type species *Squilla scorpio* Latreille, 1828, by original designation. Gender masculine).

Diagnosis. Eye small, elongate; cornea bilobed, broader than and set obliquely on stalk. Ocular scales separate. Dorsal processes of antennular somite trianguloid, with acute apices, directed anterolaterally. Carapace with anterolateral spine; median carina interrupted; anterior bifurcation absent; without posterior median projection; posterolateral margin rounded. Raptorial claw dactylus with 5–6 teeth; carpus dorsal carina undivided; merus without outer inferodistal spine. Mandibular palp present or absent. Maxillipeds 1–3 with epipod. Pleopod 1 endopod in males with posterior endite; hook process with distal point. Thoracic somites 6–8 with submedian and intermediate carinae. Lateral process of thoracic somite 5 as single slender spine recurved anteriorly; ventral spine directed ventrally. Lateral process of thoracic somites 6–7 single, rounded. Telson submedian teeth with movable apices; prelateral lobe present; dorsolateral surface without longitudinal carinae; ventral surface without postanal carina. Uropodal protopod inner margin crenulate.

Composition. *C. bengalensis* (Tiwari & Biswas, 1952); *C. dubia* (H. Milne Edwards, 1837); *C. gibba* (Nobili, 1903); *C. scorpio* (Latreille, 1828); *C. immaculata* (Kemp, 1913); and *C. terrareginensis* (Stephenson, 1953).

Variation of the lateral process of the fifth thoracic somite in *Cloridopsis*

The lateral process of the fifth thoracic somite (Figs. 108A–C) varies. Even though sex and size are the same, its shape is strong falcate or anterior spine shape. In the case of spine shape, it is very sharp or less sharp according to individuals.

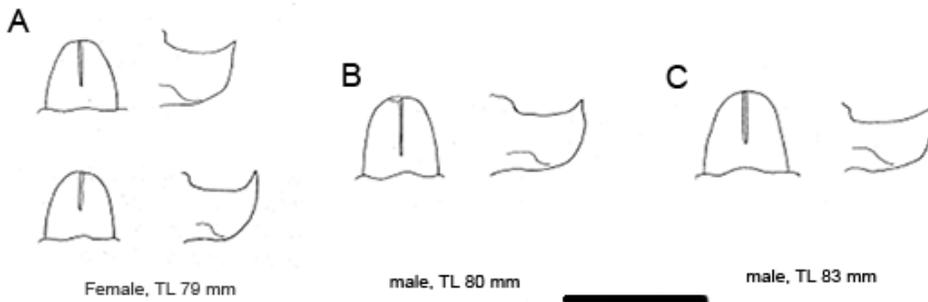


Fig. 108. *Cloridopsis scorpio*. A–C, rostral plate and right lateral process of thoracic somite 5. A, female, TL 79 mm; B, male TL 80 mm, C, male TL 83 mm. Modified from Ahyong (1999).

Habitat preference in *Cloridopsis*

Species of *Cloridopsis* occur in shallow inshore waters with substantial terrigenous influence. Kemp (1913), Tiwari & Ghosh (1973), Manning (1979) and Ahyong et al. (1999) each reported *Cloridopsis* from estuarine habitats.

Key to the species of *Cloridopsis* Manning, 1968

1. First to third of maxillipeds with eipod *C. dubia*
- First to second of maxillipeds with eipod 2
2. Mandibular palp present 3
- Mandibular palp absent 4
3. Lateral process of thoracic somite 5 with large black patch basally. Raptorial claw dactylus with 5 teeth *C. terrareginensis*
- Lateral process of thoracic somite 6 without large black patch basally. Raptorial claw dactylus with 6 teeth *C. bengalensis*
4. Corea narrow than stalk *C. gibba*
- Corea broader than stalk 5

5. Lateral process of thoracic somite 5 without large black patch basally
 *C. immaculata*
 - Lateral process of thoracic somite 5 with large black patch basally
 *C. scorpio*

47. *Cloridopsis scorpio* (Latreille, 1828) (Figs. 109–110)

Squilla scorpio Latreille in Latreille et al., 1828: 472; Lee & Wu, 1966: 48.

Cloridopsis scorpio: Manning, 1995: 24, 196; Ah Yong et al., 1999: 42–46, fig. 4; Ah Yong et al., 2008: 94, fig. 70; Ah Yong, 2012b: 248; Ah Yong, 2016: 460, 464, fig. 4D.

Material examined

Non type material

Korea: MADBK 600203_001, female (TL 74.5 mm), Ho-ri, Palbong-myeon, Seosan-si, Chungcheongnam-do, South Korea, 36°55'24.2"N, 126°19'26.3"E, commercial fishing trawlers, 20 October 2011.

Diagnosis. Maxillipeds 1–2 with epipod. Mandibular palp present. Eye (Fig. 110A) elongate; cornea broader than stalk. Rostral plate (Figs. 110A, B) with median carina. Raptorial claw dactylus with 5 teeth. Mandibular palp 2-segmented. Lateral process of thoracic somite 5 (Figs. 110A, C) broad, apex sharp, directed anteriorly, with black patch basally; ventrally with blunt angular lobe. Telson (Fig. 110A) prelateral lobe longer than margin of lateral tooth; respective denticles present; 1–2 submedian denticles, 4–6 intermedian denticles, and 1 lateral denticle. Uropodal protopod (Fig. 110A) with 6–7 movable spines.

Habitat. Mud and muddy sand (Schram & Müller, 2004).

Distribution. Western Indian Ocean to Malaysia, Indonesia, Vietnam, China, Japan (Ah Yong et al., 1999), and Korea (Hwang et al., 2019).



Fig. 109. Distribution of *Cloridopsis scorpio* (Latreille, 1828). Legend: star = type locality; circle = distribution in worldwide.

Remarks. Among *Cloridopsis* species, *C. scorpio* resembles *C. terrareginensis* (Stephenson, 1953) in having following characteristics: 1) five teeth on the dactylus of the raptorial claw, and 2) a dorsal black patch on the lateral process of thoracic somite 5. *C. scorpio*, however, can be easily distinguished from *C. terrareginensis* by the absence of a mandibular palp. The specimen examined generally agrees well with those characteristics.

As mentioned earlier, an intraspecific variation of the lateral process of the fifth thoracic somite has been reported (Ahyong et al., 1999) and the form of the lateral process of thoracic somite 5 varies from an anterolaterally directed angular lobe to anteriorly directed spine. In the specimen examined, the rostral plate is elongated with a broadly rounded apex and the lateral process of thoracic somite 5 is anterolaterally directed (Fig 110A, B, C) which is within the reported range of variation in *C. scorpio*.

Cloridopsis species favor shallow inshore waters with substantial terrigenous influence (Ahyong, 2001). The specimen examined was also collected from an estuarine region, which has terrigenous influence and relatively low salinity. Evidently, species of *Cloridopsis* tolerate or are even well adapted to relatively low salinities.

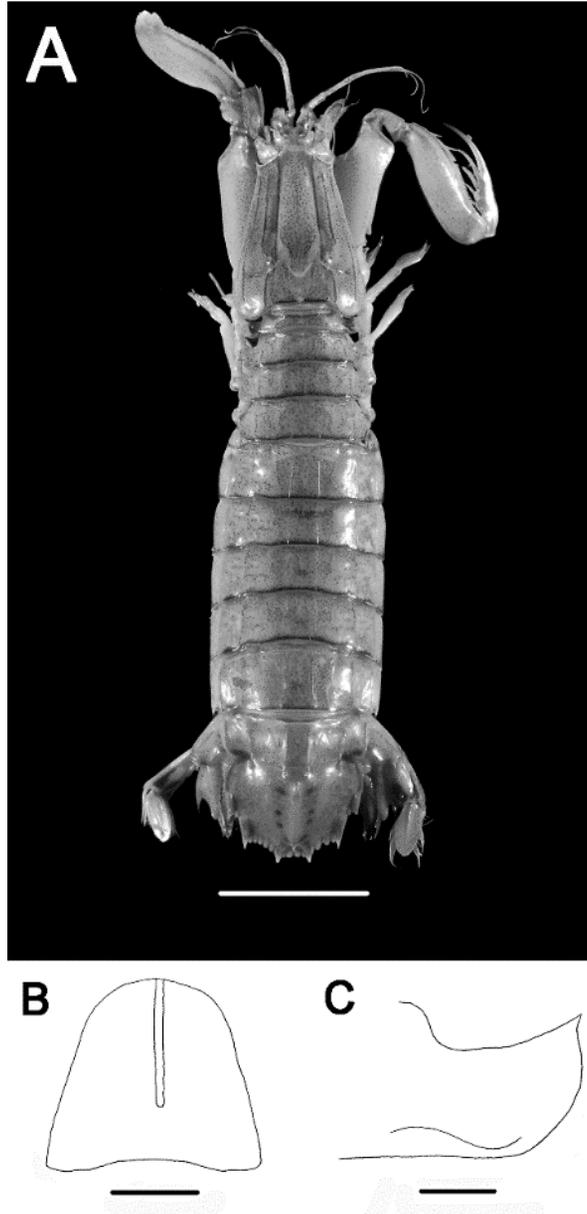


Fig. 110. *Cloridopsis scorpio*, female, TL 74.5 mm, MADBK600203_001. A, dorsal view; B, rostral plate; C, right lateral process of thoracic somite 5. Scale bars: A = 15 mm, B–C = 1.0 mm

48. *Cloridopsis terrareginensis* (Stephenson, 1953) (Figs. 111–112)

Squilla terrareginensis Stephenson, 1953: 208–213, fig. 3A, B [type locality: Barron River, Cairns, Queensland, Australia]; Stephenson & McNeill, 1955: 242; Manning, 1968: 128.

Squilla scorpio: White, 1847: 84; Miers, 1880: 18 [part, Australian specimens only]; Stephenson & McNeill, 1955: 242 [not *Squilla scorpio* Latreille, 1828].

Cloridopsis terrareginensis: Manning, 1995: 24, 196; Ahyong, 2001: 242–243, fig. 119.

Material examined

Non type material

Australia: AM P12267, Queensland, Cairns, female, TL 83 mm, coll. H. Flecker, 25 April 1953.

Diagnosis. Maxillipeds 1–2 with epipod. Mandibular palp absent. Eye (Fig. 112) elongate; cornea broader than stalk. Rostral plate (Fig. 112) with median carina. Raptorial claw dactylus with 5 teeth. Mandibular palp 2-segmented. Lateral process of thoracic somite 5 (Fig. 112) broad; apex sharp, directed anteriorly, with black patch basally; ventrally with blunt angular lobe. Telson (Fig. 112) prelateral lobe longer than margin of lateral tooth; respective denticles present; 1–2 submedian denticles, 4–6 intermedian denticles, and 1 lateral denticle. Uropodal protopod (Fig. 112) with 6–8 movable spines.

Habitat. Burrows in intertidal and subtidal mudflats in depth of 25 m (Schram & Müller, 2004).

Distribution. Australia and Papua New Guinea.



Fig. 111. Distribution of *Cloridopsis terrareginensis* (Stephenson, 1953). Legend: star = type locality; circle = distribution in worldwide.

Remarks. Features distinguishing *C. terrareginensis* and *C. scorio* are discussed under the account of the former. *C. terrareginensis* differs from *C. scorio* by the presence of the intermediate carinae on the carapace. The specimen examined generally agrees well with those characteristics.



Fig. 112. *Cloridopsis terrareginensis*, female, TL 83 mm, AM P12267.

49. *Cloridopsis immaculata* (Kemp, 1913) (Figs. 113–114)

Cloridopsis immaculata Kemp, 1913: 45, pl. 2, fig. 31; Manning, 1991: 10; Ahyong, 2001: 242.

Material examined

Non type material

Indonesia: AM P 64267, male, TL 44 mm, Empang Kamal, Palembang, coll. A.A. Racek, 14 May 1954.

Diagnosis. Maxillipeds 1–2 with epipod. Mandibular palp absent. Eye (Fig. 114) elongate; cornea (Fig. 114) distinctively broader than stalk. Rostral plate (Fig. 114) with median carina. Raptorial claw dactylus with 5 teeth. Mandibular palp 2-segmented. Lateral process of thoracic somite 5 (Fig. 114) broad; apex sharp, directed anteriorly, without black patch basally; ventrally with blunt angular lobe.

Habitat. Mangrove swamps (traps in prawn ponds), brackish water (Schram & Müller, 2004).

Distribution. Burma, India, Singapore (Jurong), and Pakistan (Schram & Müller, 2004).

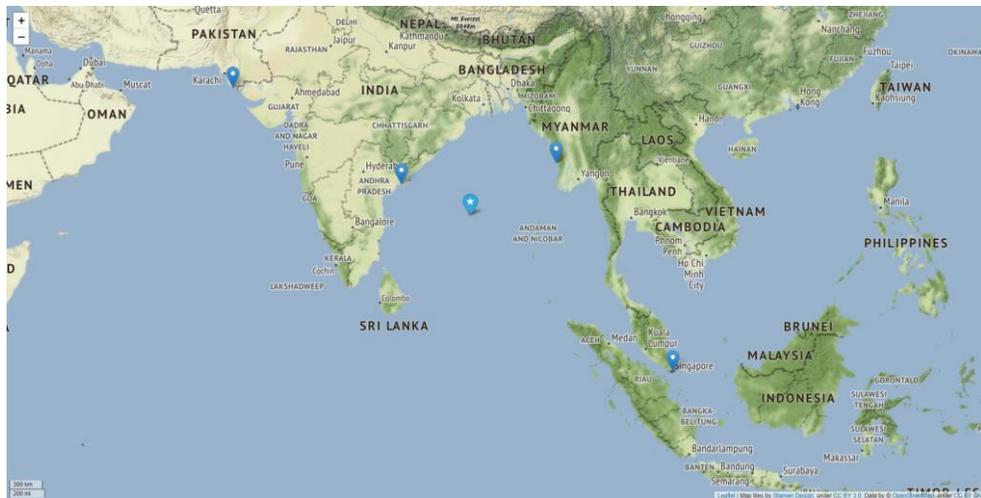


Fig. 113. Distribution of *Cloridopsis immaculata* (Kemp, 1913). Legend: star = type locality; circle = distribution in worldwide.

Remarks. Among *Cloridopsis* species, *C. immaculata* is morphologically similar with *C. scorio* by the presence of the broader cornea and absence of the mandibular palp. *C. immaculata*, however, can be easily distinguished from *C. scorio* by the absence of a black patch of the lateral process of thoracic somite 5. The specimen examined generally agrees well with those characteristics.



Fig. 114. *Cloridopsis immaculata*, male, TL 44 mm, AM P 64267.

50. *Cloridopsis gibba* (Nobili, 1903) (Fig. 115)

Squilla gibba Nobili, 1903: 30–31, fig. 3; Kemp, 1913: 28–30, pl. 1, figs. 5–12.

Cloridopsis gibba: Ahyong, 2001: 242.

Type material

Holotype: 1 male, Pulo Burong, Sarawak Musuem, no further museum.

Diagnosis. Maxillipeds 1–2 with epipod. Mandibular palp absent. Eye small; cornea distinctively narrower than stalk. Raptorial claw dactylus with 5–6 teeth. Mandibular palp 2-segmented. Lateral process of thoracic somite 5 broad; apex sharp, directed anteriorly. Telson submedian teeth with movable apices; prelateral lobe present; dorsolateral surface without longitudinal carinae; ventral surface without postanal carina. Uropodal protopod inner margin crenulate.

Habitat. The information is not available.

Distribution. Malaysia (Pulo Burong, Borneo) (Schram & Müller, 2004).



Fig. 115. Distribution of *Cloridopsis gibba* (Nobili, 1903). Legend: star = type locality; circle = distribution in worldwide.

Remarks. Among *Cloridopsis* species, *C. gibba* is morphologically similar with *C. scorpio* and *C. terrareginensis* by the absence of the mandibular palp. *C. gibba*, however, can be easily distinguished from congeners by the presence of narrower cornea.

51. *Cloridopsis bengalensis* (Tiwari & Biswas, 1952) (Fig. 116)

Cloridopsis bengalensis Tiwari & Biswas, 1952: 352–353, figs. 1b–c; Ahyong, 2001: 242; Ahyong & Naiyanetr: 295–296.

Type material

Holotype: India: IM C3013/1, male, Salt Lakes, lower Bengal, no further information.

Diagnosis. Maxillipeds 1–2 with epipod. Mandibular palp present. Raptorial claw dactylus with 6 teeth. Lateral process of thoracic somite 5 broad; apex sharp, directed anteriorly, without black patch basally. Telson submedian teeth with movable apices; prelateral lobe present; dorsolateral surface without longitudinal carinae; ventral surface without postanal carina. Uropodal protopod inner margin crenulate.

Habitat. Esuarine habitats; mangrove swamps, found in a long horizontal burrow about 10 centimeters below the surface (Manning, 1978).

Distribution. India and Thailand (Schram & Müller, 2004).



Fig. 116. Distribution of *Cloridopsis bengalensis* (Tiwari & Biswas, 1952). Legend: star = type locality; circle = distribution in worldwide.

Remarks. Among *Cloridopsis* species, *C. bengalensis* is morphologically similar *C. immaculata* in having the mandibular palp. *C. bengalensis* however, can be easily distinguished from *C. immaculata* by the presence of a black patch of the lateral process of thoracic somite 5 and five teeth of raptorial claw dactylus.

52. *Cloridopsis dubia* (H. Milne Edwards, 1837) (Fig. 117)

Squilla dubia H. Milne Edwards, 1837: 522.

Cloridopsis dubia: Manning, 1967: 105; Manning & Heard, 1997: 312–313, fig. 12.

Type material

Holotype: coast of America, MNHN Sto 434, male, no further information.

Diagnosis. Maxillipeds 1–3 with epipod. Eye small, elongate; cornea bilobed, broader than and set obliquely on stalk. Ocular scales separate. Dorsal processes of antennular somite trianguloid, with acute apices, directed anterolaterally. Carapace with anterolateral spine; median carina interrupted; anterior bifurcation absent;

without posterior median projection; posterolateral margin rounded. Raptorial claw dactylus with 5–6 teeth; carpus dorsal carina undivided; merus without outer inferodistal spine. Mandibular palp present or absent. Maxillipeds 1–3 with epipod. Pleopod 1 endopod in males with posterior endite; hook process with distal point. Thoracic somites 6–8 with submedian and intermediate carinae. Lateral process of thoracic somite 5 as single slender spine recurved anteriorly; ventral spine directed ventrally. Lateral process of thoracic somites 6–7 single, rounded. Telson submedian teeth with movable apices; prelateral lobe present; dorsolateral surface without longitudinal carinae; ventral surface without postanal carina. Uropodal protopod inner margin crenulate.

Habitat. Usually on shallow mud flats on both sides of the American continent; salt lake, low tide near entrance of Panama Canal; mouth of river (Schram & Müller, 2004).

Distribution. Brazil, British Honduras, South Carolina, Columbia, Cuba, Dominican, Ecuador, Georgia, Guatemala, El Salvador, Mexico, entrance of Panama Canal, Peru, Trinidad, and Venezuela (Schram & Müller, 2004).

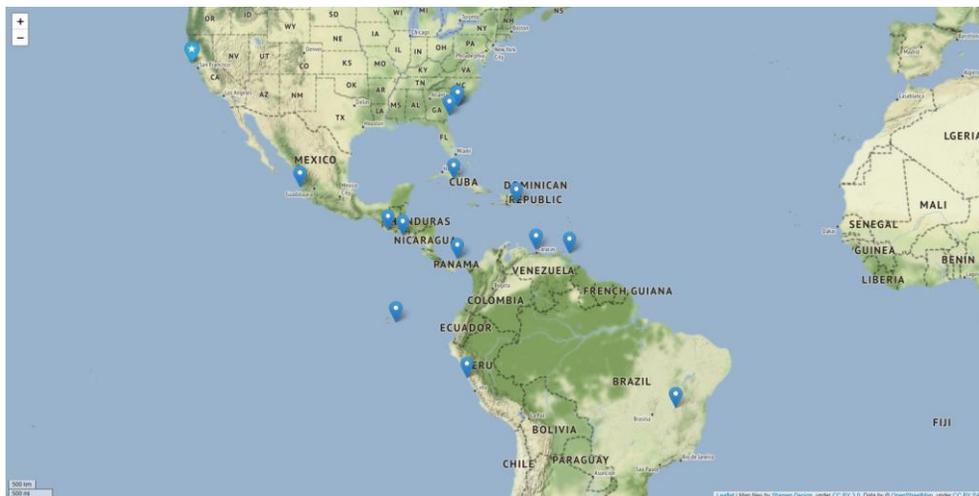


Fig. 117. Distribution of *Cloridopsis dubia* (H. Milne Edwards, 1837). Legend: star = type locality; circle = distribution in worldwide.

Remarks. Among *Cloridopsis* species, *C. dubia* can be easily distinguished from congeners by the presence of epipod of all the first to third of maxillipeds. Other *Cloridopsis* species have each epipod only in the first to the second of maxillipeds.

Genus *Miyakella* Ah Yong & Low, 2013

Miyakella Ah Yong & Low, 2013: 99–100. (type species *Squilla nepa* Latreille, 1828, by original designation. Gender feminine).

Diagnosis. Mandibular palp 3-segmented. Maxillipeds 1–4 with epipod. Cornea bilobed. Ocular scales separate. Carapace with anterolateral spine; median carina present, uninterrupted at base of anterior bifurcation; branches of anterior bifurcation present, opening posterior to dorsal pit; posterolateral margin rounded. Raptorial claw dactylus with 6 teeth; carpus dorsal carina with irregular tubercles; outer surface of merus with inferodistal spine. Pleopod 1 endopod in male without posterior endite; hook process blunt. Thoracic somites 6–8 with distinct submedian and intermediate carinae. Lateral processes of thoracic somites 5–7 bilobed. Telson submedian teeth with fixed apices; prelateral lobe present; dorsolateral surface without longitudinal carinae.

Composition. *M. holoschista* (Kemp, 1911); and *M. nepa* (Latreille, 1828).

Remarks. *Miyakella* species is similar to *Oratosquilla* and *Oratosquillina* within Squillidae in having bilobed lateral processes on thoracic somite 5–7 and six teeth on the dactylus and an outer inferodistal spine on the merus of the raptorial claw. *Miyakella* species, however, differs from *Oratosquilla* and *Oratosquillina* by the presence of the dorsal pit enclosed by the branches of the anterior bifurcation of the median carina of the carapace and absence of the posterior endite of the endopod on the first pleopod in adult males whereas *Oratosquilla* and *Oratosquillina* species has

anterior bifurcation of the median carina of the carapace opens anterior to the dorsal pit and the posterior endite of the endopod of the first pleopod is present in adult males. The specimens examined herein generally agree well with those characteristics.

Key to the species of *Miyakella* Ahyong & Low, 2013

1. Carapace with portion of median carina between cervical groove and anterior bifurcation not bicarinate. Abdominal somite 4 with submedian carinae armed posteriorly *M. nepa*
- Carapace with portion of median carina between cervical groove and anterior bifurcation bicarinate. Abdominal somite 4 with submedian carinae unarmed posteriorly *M. holoschista*

53. *Miyakella nepa* (Latreille, 1828) (Figs. 118–119)

Squilla nepa Latreille, 1828: 471 (type localities: Xiamen, China, by present neotype designation); Kemp, 1913: 3, 10, 22, 30, 195, pl. 4: fig. 49; Holthuis, 1941: 245–246; Stephenson & McNeill, 1955: 243; Manning, 1968: 31–32, fig. 10.

Oratosquilla nepa: Manning, 1968: 31–32, fig. 10; 1971: 3; Manning, 1991: 12.

Miyakea nepa: Manning, 1995; Ahyong et al., 1999: 47, 52, fig. 6a–d; Ahyong, 2001: 279–281.

Material examined.

Non type material

Australia: AM P21642, 6 females, TL 79–113 mm, Queensland, south east corner of Gulf of Carpentaria, coll. CSIRO Division of Fisheries and Oceanography, 9 September 1963.

Diagnosis. Carapace (Fig. 119) with portion of median carina between cervical

groove and anterior bifurcation not finely bicarinate. Submedian carina of abdominal somite 4 armed posteriorly. Abdominal somite 4–5 (Fig. 119) with dark transverse dorsal patch. Telson denticles present, following as: 2–3 submedian denticles, 7–10 intermediate denticles, 1 lateral denticle. Uropodal exopod (Fig. 119) outer margin with 8–10 movable spines.

Habitat. Level sand and mud substrates; shallow sublittoral in depth of less than 25 m (Ahyong, 2001).

Distribution. Australia, French Polynesia, New Caledonia, Taiwan, Philippines, and Vietnam (Ahyong, 2001).



Fig. 118. Distribution of *Miyakella nepa* (Latreille, 1828). Legend: star = type locality; circle = distribution in worldwide.

Remarks. *Miyakella nepa* is morphologically similar to *M. holoschista* in having the dorsal pit enclosed by the branches of the anterior bifurcation of the median carina of the carapace and in lacking the posterior endite of the endopod on the first pleopod in males. *M. nepa*, however, can be easily distinguished from only its congener by the presence of the simple, not bicarinate anterior bifurcation of the median carina of the carapace and posteriorly armed submedian carina of abdominal somite 4. The

specimen examined generally agrees well with those characteristics.



Fig. 119. *Miyakella nepa*, female, TL 93 mm, AM P21642.

54. *Miyakella holoschista* (Kemp, 1911) (Figs. 120–121)

Miyakella holoschista Kemp, 1911: 97; Manning, 1995: 214–215, fig. 130c, 131; Ahyong, 2001: 279.

Material examined

Non type material

India: AM P65699, male, TL 64 mm, Tranquebar, Tamil Nadu, south India, coll. N.K. Ng & A.S. Fernando, 16 March 2001.

Diagnosis. Carapace (Fig. 121) with portion of median carina between cervical groove and anterior bifurcation bicarinate. Submedian carina of abdominal somite 4 (Fig. 121) unarmed. Thoracic somites 6–8 (Fig. 121) with distinct submedian and intermediate carinae. Lateral processes of thoracic somites 5–7 (Fig. 121) bilobed. Telson (Fig. 121) submedian teeth with fixed apices; prelateral lobe present; dorsolateral surface without longitudinal carinae.

Habitat. The information is not available. Collection depth is shallow water (Schram & Müller, 2004).

Distribution. Indonesia, Philippines, South Africa, Sri Lanka, Tahiti, and Vietnam (Schram & Müller, 2004).



Fig. 120. Distribution of *Miyakella holoschista* (Kemp, 1911). Legend: star = type locality; circle = distribution in worldwide.

Remarks. Features distinguishing *M. holoschista* and *M. nepa* are discussed under the account of the former. Dorsal pit enclosed by the branches of the anterior

bifurcation of the median carina of the carapace, the difference between these two species, can be observed more clearly when they are in a relatively dry condition. The specimen examined generally agrees well with those characteristics.



Fig. 121. *Miyakella holoschista*, male, TL 64 mm, AM P65699.

3-2. Taxonomic review of the genus *Faughnia* (Parasquilloidea: Parasquillidae)

INTRODUCTION

Parasquilloids differ from gonodactyloids by the presence of an asymmetrically bilobed cornea, stout propodus on the raptorial claw, and three primary spines of the uropodal protopod. Among them, *Faughnia* Serène, 1962, is one of two genera of Parasquillidae Manning, 1995, distinguished from other parasquillids by the presence of indistinct instead of distinct reflected marginal carinae on the carapace and the absence of submedian carinae on abdominal somites 1–5. In parasquilloids, characteristics of the rostral plate and presence or absence of reflected marginal carine of the carapace and submedian carinae on abdominal somites 1–5. In this part, a taxonomic review for *Faughnia* species, which uses these characteristics, were conducted.

MATERIALS AND METHODS

Morphological terminology largely follows Ahyong (2001, 2012). All specimen measurements are given in millimeters (mm). Total length (TL) was measured along the dorsal midline from the apex of the rostral plate to the apex of the submedian tooth of the telson, and carapace length (CL) along the dorsal midline and the rostral plate are excluded. The abdominal-width-carapace-length index (AWCLI) is given as $100 \times \text{abdominal somite 5 width} / \text{carapace length}$.

SYSTEMATIC ACCOUNTS

Superfamily Parasquilloidea Manning, 1995

Family Parasquillidae Manning, 1995

Genus *Faughnia* Serène, 1962

Faughnia Serène, 1962: *Faughnia* Serène, 1962: 12. (Type species *Pseudosquilla haani* Holthuis, 1959, replacement name for preoccupied *Squilla empusa* de Haan, 1844, by original designation and monotypy. Gender feminine).

Diagnosis. Body subcylindrical; articulation compact. Rostral plate without long anterior spine. Carapace with indistinct reflected marginal carinae and distinct cervical groove. Raptorial claw carpus dorsal margin with 2 blunt teeth directed ventrally. Abdominal somites 1–5 with indistinct intermediate, lateral and marginal carinae; without submedian carinae. Telson with minute submedian denticles.

Composition. *F. formosae* Manning & Chan, 1997; *F. haani* (Holthuis, 1959); *F. profunda* Manning & Makarov, 1978; and *F. serenei* Moosa, 1982.

Remarks. In parasquilloids, the number of the dorsal carina of telson, presence or absence of reflected marginal carina of the carapace and submedian carinae on abdominal somites 1–5, and characteristics of the rostral plate are used as key characters in identification of the species. Among them, *Faughnia* species are distinguished from other parasquillids by the presence of indistinct instead of distinct reflected marginal carinae on the carapace and the absence of submedian carinae on abdominal somites 1–5. Through the present study, a taxonomic review of these species, consider additional morphological traits (characteristics of rostral plate), was conducted.

Key to the species of *Faughnia* Serène, 1962

1. Telson with median and 5 pairs of carinae. Carinae of submedian, intermediate and lateral teeth extending onto surface of telson. Uropodal protopod denticulate inner margin, with well-developed spinules flanked proximally by 4 smaller spinules *F. formosae*
- Telson with median and at most 3 pairs of carinae. Carinae of submedian, intermediate and lateral teeth not extending onto surface of telson. Uropodal protopod with smooth or crenulate inner margin 2
2. Carapace with anterolateral angles produced anteriorly, forming an acute angle. Abdominal somites 5–6 with posteriorly armed intermediate carinae *F. profunda*
- Carapace with anterolateral angles not produced anteriorly, forming an obtuse angle 3
3. Telson without accessory median carina, with anterior intermediate and marginal carinae only. Abdominal somite 5 with intermediate carina armed posteriorly *F. serenei*
- Telson with distinct, entire, accessory median carina in addition to anterior intermediate and marginal arinae. Abdominal somite 5 with intermediate carina unarmed posteriorly *F. haani*

55. *Faughnia formosae* Manning & Chan, 1997 (Figs. 122–123)

Pseudosquilla empusa: Komai, 1927: 325, 346, fig. 1; Dong et al., 1983: 90, fig. 3 [not *Squilla empusa* de Haan, 1844].

Faughnia formosae Manning and Chan, 1997: 546–551, figs. 1–4; Moosa, 2000: 422; Ahyong & Naiyanetr, 2002: 289.

Material examined

Non type material

Korea: 1 male, TL 132 mm, Jeju Island, Seogwipo-si, Daejeong-eup, Hamori, Moseulpo port, 10 September 2006.

Diagnosis. Carapace (Fig. 123) with indistinct reflected marginal carina; anterolateral angles rounded, not produced anteriorly. Telson (Fig. 123) as long as broad, with 3 pairs of primary teeth (submedian, intermediate, lateral); with 2 spiniform intermediate denticles, 1 spiniform lateral denticle. Dorsal surface (Fig. 123) with median carina and 5 pairs of longitudinal carinae (accessory median, anterior submedian, and lateral slightly interrupted, anterior intermediate and marginal uninterrupted) in addition to carinae of all primary teeth extending onto surface of telson. Ventral surface of telson smooth, without postanal carina. Uropodal protopod (Fig. 123) bearing well-developed spinules, outermost largest, flanked proximally by 4 smaller spinules as well as some denticulation on inner margin; exopod proximal segment outer margin with 8 movable spines.

Habitat. Sand and mud in depth of 100–200 m (Ahyong et al., 2008).

Distribution. Japan, Taiwan, Philippines, Thailand, and Korea (Jeju Island) (Hwang et al., 2013).



Fig. 122. Distribution of *Faughnia formosae* Manning & Chan, 1997. Legend: star = type locality; circle = distribution in worldwide.

Remarks. Other *Faughnia* species have a smooth or crenulate inner margin of uropodal protopod, while *F. formosae* is easily distinguished from its congeners by the presence of well developed spinules on inner margin of the uropodal protopod. Also, *F. formosae* has the median carina and 5 pairs of carinae on the dorsolateral surfaces of the telson while other *Faughnia* species have at most 3 pairs of carinae besides the median carina. The specimen examined generally agrees well with those characteristics except that the width of the rostral plate was 2.6 times as long as the median length in the present specimen, whereas width was only ‘more than twice median length’ in the original description of Manning and Chan (1997).



Fig. 123. *Faughnia formosae*, male, TL 132 mm.

56. *Faughnia haani* (Holthuis, 1959) (Figs. 124–125)

Squilla empusa de Haan, 1844: pl. 51, fig. 6 [preoccupied by *Squilla empusa* Say, 1818; type locality: Japan].

Pseudosquilla empusa: Miers, 1880: 4, 1884: 567; Kemp, 1913: 3, 95–96, 104.

Pseudosquilla haani Holthuis, 1959: 179 [replacement name for *Squilla Empusa* de Haan, 1844, preoccupied] [type locality: Japan].

Parasquilla haani: Lee & Wu, 1966: 44, figs. 2A–D.

Faughnia haani: Manning & Makarov, 1978: 521; Yamaguchi & Baba, 1993: 178–179, fig. 10; Manning & Chan, 1997: 551–552, figs. 2, 4; Ahyong, 2001:179–181, fig. 89.

Material examined.

Non type material

Japan: AM P72347, 1 male, TL 55 mm, no further data, coll. H. Fujita, 10 June 1989.

Diagnosis. Carapace (Fig. 125) with indistinct reflected marginal carina; anterolateral angles rounded, not produced anteriorly. Telson (Fig. 125) as long as broad, with 3 pairs of primary teeth (submedian, intermediate, lateral); with 2 spiniform intermediate denticles, 1 spiniform lateral denticle. Dorsal surface (Fig. 125) with median carina and 3 pairs of longitudinal carinae (accessory median, anterior intermediate and marginal uninterrupted); carina of submedian tooth extending onto surface of telson; carina of intermedian and lateral teeth short, not extending onto surface of telson. Ventral surface of telson smooth, without postanal carina. Uropodal protopod (Fig. 125) inner proximal margin crenulate; exopod proximal segment outer margin with 7–8 movable spines.

Habitat. Manning & Chan (1997) noted a bathymetric range of 73 m to 100–200 m. Sand and mud substrates at depths between 78– 88 m and 110–111 m (Ahyong,

2001).

Distribution. Australia, Hong Kong, Japan, Taiwan (Ahyong, 2001).



Fig. 124. Distribution of *Faughnia haani* (Holthuis, 1959). Legend: star = type locality; circle = distribution in worldwide.

Remarks. Among *Faughnia* species which have the median carina and at most 3 pairs of carinae on the telson, *F. haani* is easily distinguished from its congeners by the presence of rounded anterolateral angle of the carapace and accessory median, anterior intermediate and marginal carinae, unarmed intermediate carina on the abdominal somite 5. The specimen examined generally agrees well with those characteristics except that the anterior margin of the rostral plate is more obtusely angled than figured in the description of Yamaguchi and Baba (1993).

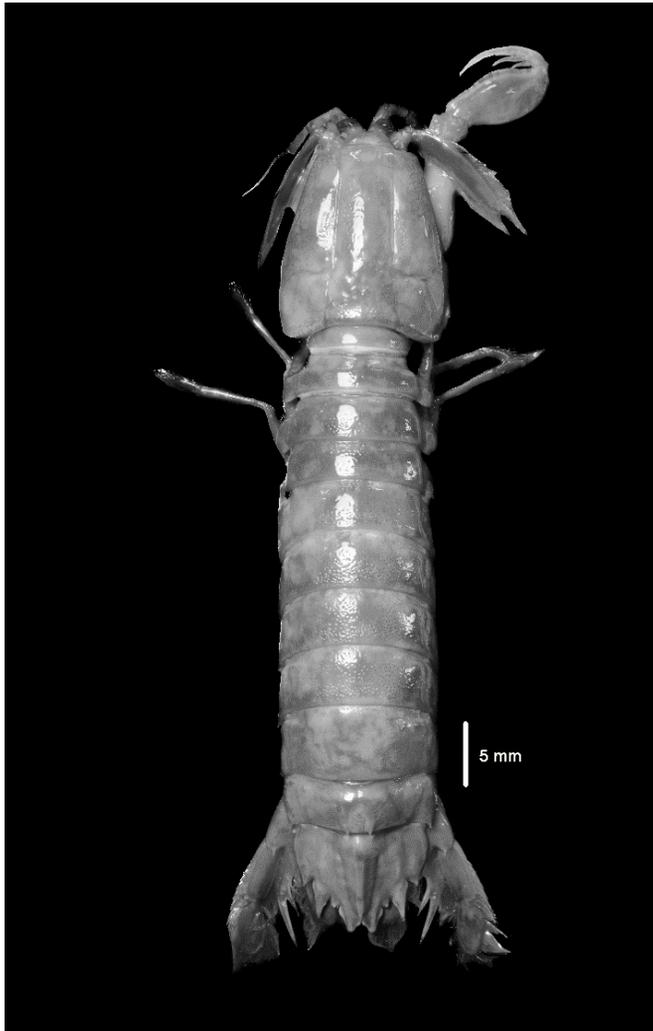


Fig. 125. *Faughnia haani*, male, TL 55 mm, AM P72347.

57. *Faughnia serenei* Moosa, 1982 (Figs. 126–127)

Faughnia serenei Moosa, 1982: 600, figs. 1–5 [type locality: Gulf of Thailand, South China Sea]; 1986: 385; Manning & Chan, 1997: 552–553, figs. 3, 4; Ahyong, 2001:181–182, fig. 90.

Material examined

Non type material

Australia: AM P56914, 1 male, TL 127 mm, Queensland, east of Swains Reef, coll. D. Bray, M. Westneat, J. Williams, and D.J. Smith, 07 June 1996.

Diagnosis. Carapace (Fig. 127) with indistinct reflected marginal carina; anterolateral angles broadly rounded, not produced anteriorly. Telson (Fig. 127) as long as broad with 3 pairs of primary teeth (submedian, intermediate, lateral); with 2 spiniform intermediate denticles, 1 spiniform lateral denticle. Dorsal surface (Fig. 127) with median carina and 2 pairs of longitudinal carinae (anterior intermediate and marginal uninterrupted); carina of submedian, intermediate and lateral teeth short, not extending onto surface of telson. Uropodal protopod (Fig. 127) inner proximal margin dentate; exopod proximal segment outer margin with 7–9 movable spines.

Habitat. Manning & Chan (1997) reported a bathymetric range between 73–92 m and 170–230 m. Sand and mud substrates at depths of 200–310 m (Ahyong, 2001).

Distribution. Australia, Japan, Taiwan, Philippines, and Thailand (Manning & Chan, 1997; Ahyong, 2001).



Fig. 126. Distribution of *Faughnia serenei* Moosa, 1982. Legend: star = type locality; circle = distribution in worldwide.

Remarks. *F. serenei* is morphologically similar with *F. haani* in having not acute, obtuse anterolateral angles of carapace. *F. serenei* is easily distinguished from *F. haani* by the absence of accessory median carina on the telson and the presence of armed intermediate carina of abdominal somite 5. The specimen examined generally agrees well with those characteristics including the anterior margin of the rostral plate.



Fig. 127. *Faughnia serenei*, male, TL 127 mm, AM P56914.

58. *Faughnia profunda* Manning & Makarov, 1978 (Fig. 128)

Faughnia profunda Manning & Makarov, 1978: 518–522, fig. 1; Ahyong, 2001: 179.

Non type material

Holotype: Madagascar: MNHN Sto 799, male, no further information.

Diagnosis. Carapace with indistinct reflected marginal carina; anterolateral angles acute, produced anteriorly. Telson as long as broad with 3 pairs of primary teeth (submedian, intermediate, lateral); with 2 spiniform intermediate denticles, 1 spiniform lateral denticle. Dorsal surface with median carina and 3 pairs of longitudinal carinae (accessory median, anterior intermedian interrupted; carina of submedian, intermediate and lateral teeth short, not extending onto surface of telson. Uropodal protopod inner proximal margin dentate; exopod proximal segment outer margin with 8–9 movable spines.

Habitat. The information is not available. The collection depth is 225–385 m (Schram & Müller, 2004).

Distribution. Kenya, Madagascar, and Mozambique (Schram & Müller, 2004).



Fig. 128. Distribution of *Faughnia profunda*. Legend: star = type locality; circle = distribution in worldwide.

Remarks. Among *Faughnia* species which have the median carina and at most 3 pairs of carinae on the telson, *F. profunda* is easily distinguished from its congeners by the presence of acute anterolateral angle of the carapace and armed intermediate carina on the abdominal somite 5. Compared with *F. serenei*, rostral plate characteristics is very similar and it is the trapezoidal shape and is broader than long.

**3-3. Taxonomic review of the genus *Acanthosquilla*
(Lysiosquilloidea: Nannosquillidae)
and the genus *Acaenosquilla* (Lysiosquilloidea: Tetrasquillidae)**

INTRODUCTION

Lysiosquilloids comprise 4 families and this superfamily is easily distinguished from other superfamilies in having a combination of following characteristics: (1) subquadrate propodi of maxilliped 3–4 and distal ribbing, (2) round point of hook process of petasma, (3) short, posteriorly rounded dorsal process of antennular somite, and (4) low or swelling median boss of telson. Among them, a taxonomic review for *Acaenosquilla* belonging to Tetrasquillids and *Acanthosquilla* belonging to Nannosquillids. Among them, which uses carina on the dorsal surface of telson and carapace as an identification key, were conducted. In these species, lysiosquillids have a relatively low or swelling median boss or carina on the dorsal surface of telson. In the case of the boss or carina is not too low or relatively weakly swollen, the identification of the species can be changed according to the different interpretation of the boss or carina. It is also very difficult to interpret traits in specimens with very dark coloration. In this part of chapter 3, the morphological traits identifying *Acaenosquilla* and *Acanthosquilla* species are re-examined and described in detail.

MATERIALS AND METHODS

Morphological terminology largely follows Ahyong (2001, 2012). All specimen measurements are given in millimeters (mm). Total length (TL) was measured along the dorsal midline from the apex of the rostral plate to the apex of the submedian tooth of the telson, and carapace length (CL) along the dorsal midline and the rostral plate are excluded. The abdominal-width-carapace-length index (AWCLI) is given as $100 \times \text{abdominal somite 5 width} / \text{carapace length}$.

Morphological characters in *Acaenosquilla* and *Acanthosquilla*

Although *Acanthosquilla* species belonging to the family Nannosquillidae and *Acaenosquilla* species belonging to the family Tetrasquillidae belonging to different families, they have a common point in that the morphological characteristics of the spine of the telson is used as an identification key. The number of the spines (5–11), the shape in which the spines are arranged (transverse or fan-shaped shape) and postanal carina of ventral surface (sharp or blunt) are important in the interpretation of morphological traits.

SYSTEMATIC ACCOUNTS

Superfamily Lysiosquilloidea Giesbrecht, 1910

Family Tetrasquillidae Manning & Camp, 1993

Genus *Acaenosquilla* Manning, 1991

Acaenosquilla Manning, 1991: 6. (type species *Lysiosquilla latifrons* de Haan, 1844, by original designation. Gender feminine).

Diagnosis. Eye with cornea bilobed, set transversely on stalk. Antennal protopod with one ventral papilla. Mandibular palp 3-segmented. Maxillipeds 1–5 with epipod. Rostral plate broader than long, with short “basal portion and apical spine”; with ventral carina or spine. Raptorial claw robust; dactylus with 6–7 teeth; propodus with 4 proximal movable spines. Distal segment of pereopod 1 subcircular. Distal segment of endopod of pereopod 2 ovate. Distal segment of endopod pereopod 3 slender. Abdominal somite 6 with posterolateral spine. Telson submedian teeth with movable apices; with 4 intermediate and 1 lateral denticle; dorsal surface with flat median elevation terminating in 3 acute spines; with marginal and several posteriorly armed carinae. Telson ventral surface with long postanal spine. Uropodal protopod with ventral spine anterior to endopod articulation.

Composition. *A. brazieri* (Miers, 1880); and *A. latifrons* (de Haan, 1844).

Remarks. Among Lysiosquilloids, Tetrasquillids can be easily distinguished from other families by the combination of the following characteristics: (1) the presence of basally uninflated dactylus, (2) the presence of slender primary teeth of telson, (3) the absence of erect spines on dorsal surface of telson, (4) the absence of strong dorsal proximal fold on dorsal margin of uropodal endopod. Among them,

Acaenosquilla is morphologically similar to two other tetrasquillid genera, *Heterosquillopsis*, and *Kasim* in having a postanal spine on telson ventral surface and subcircular or ovate endopods of the pereopod 1–2. However, *Acaenosquilla* differs from *Kasim* in having a distinctively broad rostral plate (versus longer than broad in *Kasim*) and differs from *Heterosquillopsis* in having six to seven instead of eight teeth on the dactylus of the raptorial claw, and two instead of four pairs of fixed primary teeth on the telson. Within *Acaenosquilla* species, the shape of a mesial lobe of the cornea and the presence or absence of carinae in lateral to median prominence of telson are used as identification keys. In the case of the carina is not too low or relatively weakly swollen, the identification of the species can be changed according to the different interpretation of the carina. Also, it is difficult to interpret traits in specimens with very dark coloration. When interpreting morphological characteristics, the carinae of the dorsal surface of telson should be additionally observed in lateral view and, together with other additional characteristics, should be interpreted comprehensively.

Key to the species of *Acaenosquilla* Manning, 1991

- 1. Mesial lobe of cornea conical, with apical tubercle. Telson with 1–3 sharp carinae in lateral to median prominence *A. brazieri*
- Mesial lobe of cornea rounded, without apical tubercle. Telson without carinae in lateral to median prominence *A. latifrons*

59. *Acaenosquilla brazieri* (Miers, 1880) (Fig. 129)

Lysiosquilla Brazieri Miers, 1880: 11, 125, pl. I: figs. 3–6 [type locality: Port Jackson, New South Wales, Australia].

Lysiosquilla latifrons: Kemp, 1913: 128 [part]; Stephenson & McNeill, 1955: 248 [not *Lysiosquilla latifrons* de Haan, 1844].

Lysiosquilla latifrons brazier: Stephenson, 1962: 38–39, figs. 1e, f, pl. 1: figs. A–D.

Acaenosquilla brazier: Manning, 1991: 6; 1995: 123; Ahyong, 2001: 172–173, fig. 85.

Type material

Holotype: NHM 79.8, female, TL 99 mm, Australia, Port Jackson, coll. J. Brazier.

Diagnosis. Cornea bilobed, with apical tubercle; mesial lobe conical. Rostral plate broader than long; ventral surface with carina and anteriorly directed spine. Dactylus of raptorial claw with 6–7 teeth; outer margin sinuous. Abdominal somite 6 with long posterolateral spine, with 1 spine and 1 triangular lobe anterior to uropodal articulation. Telson with distinct primary teeth, with 8–10 submedian denticles in slightly convex row; intermediate denticles acute, second and fourth longer than first to third; lateral denticle elongate; dorsal median elevation flat, sharply defined, terminating in 3 acute spines; laterally with 2 smooth, longitudinal carinae, terminating in a slender spine, inner carina anteriorly continuous with median elevation and separated posteriorly by deep depression, with 1–3 armed, intervening carinae; posterior surface between dorsal and marginal margin with 2–11 tubercles or spines. Proximal segment of uropodal exopod with 6–7 movable spines on outer margin.

Habitat: Ahyong (2001) reported a collection depth between 36 m and 54–59 m.

Distribution. Australia (the vicinity of Sydney to the New South Wales-Queensland border and the Coral Sea) (Manning, 1991; Ahyong, 2001).



Fig. 129. Distribution of *Acaenosquilla brazieri* (Miers, 1880). Legend: star = type locality; circle = distribution in worldwide).

Remarks. *A. brazieri* is morphologically similar to *A. latifrons* (de Haan, 1844), but is easily distinguished by the shape of the mesial lobe of the cornea and the presence of carinae on the dorsal surface of the telson. In *A. brazieri*, the mesial lobe of the cornea is distinctly conical with a low apical tubercle rather than rounded. Also, this species has one to three carinae lateral to the median prominence of the telson. When three carinae are observed in lateral view, these terminate with sharp spines at the end and these spines of carinae confirm its existence. The specimen examined generally agrees well with these characteristics.

60. *Acaenosquilla latifrons* (de Haan, 1844) (Figs. 130–131)

Squilla latifrons de Haan, 1844: pl. 51, fig. 3.

Lysiosquilla latifrons: Komai, 1927: 333–335, pl. 14, fig. 3.

Acaenosquilla latifrons: Manning, 1991: 6, fig. 4; Ahyong, 2001: 171; Ahyong, 2012: 247; Hwang et al., 2019: in press.

Heterosquilloides latifrons: Yamaguchi and Baba, 1993: 187–188, fig. 15.

Material examined

Non type material

Korea: MADBK 600501_001, female (TL 34 mm), Sam-do, Bomok-dong, Segwipo-si, Jejudo, South Korea, 33°13'46.3"N, 126°35'55.7"E, coll. S.H Kim, 13 June 2011.

Diagnosis. Cornea (Fig. 131) bilobed; mesial lobe rounded. Rostral plate broader than long; ventral surface with carina and anteriorly directed spine. Dactylus of raptorial claw (Fig. 131) with 7 teeth; outer margin sinuous. Abdominal somite 6 (Fig. 131) with long posterolateral spine, with 1 spine and 1 triangular lobe anterior to uropodal articulation. Telson (Fig. 131) with distinct primary teeth, with 8–9 submedian denticles in slightly convex row; intermediate denticles acute; lateral denticle elongate; without carinae in lateral to median prominence. Proximal segment of uropodal exopod (Fig. 131) with 7 movable spines on outer margin.

Distribution. Japan and Korea (Manning, 1991; Ah Yong, 2001; Hwang et al., 2019).



Fig. 130. Distribution of *Acaenosquilla latifrons* (de Haan, 1844). Legend: star = type locality; circle = distribution in worldwide).

Remarks. Features distinguishing *A. latifrons* and *A. brazieri* are discussed under the account of the former. *A. latifrons* differs from *A. brazieri* by the shape of the mesial lobe of the cornea and the absence of carinae on the dorsal surface of the

telson. Carinae on the dorsal surface of the telson, the difference between these two species, can be observed more clearly when they are in lateral view as well as a relatively dry condition. The specimen examined generally agrees well with those characteristics.

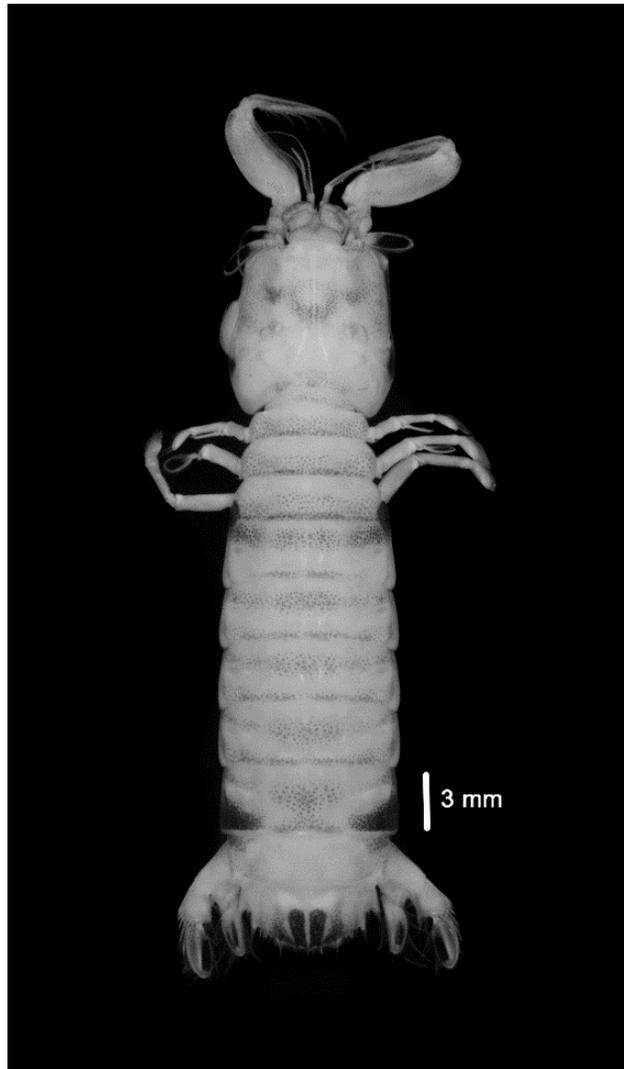


Fig. 131. *Acaenosquilla latifrons*, female, TL 34 mm, MADBK 600501_001.

Family Nannosquillidae Manning, 1980

Genus *Acanthosquilla* Manning, 1963

Acanthosquilla Manning, 1963: 319. (type species *Lysiosquilla multifasciata* Wood-Mason, 1895, by original designation. Gender feminine).

Diagnosis. Cornea broadened, faintly bilobed. Rostral plate with single median spine. Antennal protopod with ventral papilla, without mesial papilla. Ischium of raptorial claw unarmed distally. Abdominal somite 6 with posterolateral spines; posterior margin of sternum unarmed. Mandibular palp three-segmented. Maxillipeds 1–5 with epipod. Telson posterodorsal surface with fan-shaped row of posteriorly directed spines above marginal armature; with 2 or 4 pairs of fixed primary teeth and movable submedian teeth; submedian denticles forming inverted V-shape in posterior view. Uropodal protopod terminating in 2 slender spines, without ventral spine anterior to endopod articulation.

Composition. *A. crosnieri* Ahyong, 2002; *A. derijardi* Manning, 1970; *A. manningi* Makarov, 1979b; *A. melissae* Ahyong, 2008; *A. multispinosa* Blumstein, 1974; *A. multifasciata* (Wood-Mason, 1895); *A. tigrina* (Nobili, 1903); and *A. wilsoni* Moosa, 1973.

Remarks. Among Lysiosquilloids, Nannosquillids can be easily distinguished from other families by the combination of the following characteristics: (1) the presence of strong dorsal proximal fold on the dorsal margin of uropodal endopod, (2) the presence of basally uninflated dactylus, (3) the absence of erect spines on the dorsal surface of telson. Among them, *Acanthosquilla* species differs from other genera by the combination of following characteristics: (1) the presence of a broadened cornea, (2) the presence of a triangular to subpentagonal rostral plate, an inverted V-shaped or semicircular row of submedian denticles on the telson, and (3) the absence of mesial papillae on the antennal protopod. Within *Acanthosquilla* species, abdominal

somite 6 (the presence or absence of spinules on the dorsal surface and ventral posterior margin) and telson characteristics (the number of fixed primary teeth on the margin, the number spine on the posterodorsal surface) are used as identification keys. In particular, the number spine on the posterodorsal surface can be faint or destroyed, the identification of the species can be changed according to the different interpretation of the characteristics. Also, it is difficult to interpret traits in specimens with very dark coloration. When interpreting morphological characteristics, the spine of the dorsal posterodorsal surface of telson should be additionally observed in lateral view and, together with other additional characteristics, should be interpreted comprehensively.

Key to the species of *Acanthosquilla* Manning, 1963

- 1. Telson margin with 2 pairs of fixed primary teeth and 4 intermediate denticles 2
- Telson margin with 4 pairs of fixed primary teeth and each intermediate denticles between each primary teeth 3
- 2. Telson posterior surface of telson covering two clusters of three-four numerous spines *A. manningi*
- Telson posterior surface of telson covering transverse arrangement of spines 4
- 3. Abdominal somite 6 posterior margin unarmed except for posterolateral spines; ventral posterior margin with spines *A. tigrina*
- Abdominal somite 6 posterior margin with 2-3 spinules and posterolateral spines; ventral posterior margin without spines *A. wilsoni*
- 4. Posterodorsal surface of telson with 5 posteriorly directed spines above primary teeth and denticles 5
- Posterodorsal surface of telson with 7 or more posteriorly directed spines above primary teeth and denticles 6
- 5. Uropodal protopod without distal spines adjacent to endopod articulation

- *A. multifasciata*
- Uropodal protopod with two distal spines adjacent to endopod articulation
..... *A. crosnieri*
6. Posterodorsal surface of telson with 7 posteriorly directed spines above primary teeth and denticles 8
- Posterodorsal surface of telson with 9–11 posteriorly directed spines above primary teeth and denticles *A. multispinosa*
7. Raptorial claw outer lobe small, extending to the base of the first occlusal tooth
..... *A. melissae*
- Raptorial claw outer lobe large, extending to the base of the fourth or fifth occlusal tooth *A. derijardi*

61. *Acanthosquilla derijardi* Manning, 1970 (Figs. 132–133)

Acanthosquilla derijardi Manning, 1970: 1431, tab. 1, 1434–1438, fig. 2; Manning, 1995: 141; Ahyong, 2001: 144–145, fig. 70; Ahyong & Davie, 2002: 55.

Acanthosquilla sirindhorn Naiyanetr, 1995: 409–417, pl. 1, figs. 1–2.

Material examined

Non type material

Malaysia: AM P16285, female, TL 70 mm, Sandakan fish market, North Borneo, coll. C. Phui Kong, 05 November 1959.

Diagnosis. Rostral plate (Fig. 133) longer than broad, trapezoid to subpentagonal, with single apical median spine. Raptorial claw dactylus with 5–6 teeth; outer margin with basal notch; distal lobe triangular, larger than proximal lobe. Abdominal somite 6 without spinules on posterior margin adjacent to posterolateral spine. Telson (Fig. 133) with 2 pairs of fixed primary teeth (lateral and intermediate); dorsal surface with 7 posteriorly directed spines in fan shaped row above marginal armature. Telson

(Fig. 133) denticles present, following as: 3–4 submedian denticles, 4 intermediate denticels (first and third slightly smaller than second and fourth). Uropodal protopod (Fig. 133) with smooth inner margin, without distal spines adjacent to endopod articulation; exopod proximal segment outer margin with 6 movable spines.

Habitat: Soft substrates in the depth of 33 m (Ahyong, 2001).

Distribution. Australia, Japan, and New Caledonia (Ahyong, 2001).



Fig. 132. Distribution of *Acanthosquilla derijardi* Manning, 1970. Legend: star = type locality; circle = distribution in worldwide).

Remarks. *A. derijardi* is morphologically similar to *A. multifasciata* (Wood-Mason, 1895) in having 2 pairs of fixed primary teeth and 4 intermediate denticles. *A. derijardi*, however, can be easily distinguished from its congeners by the presence of more than 5 spines dorsally above the posterior margin of the telson. *A. derijardi* has a fan-shaped row of 7 spines on the posterodorsal surface of the telson. When a fan-shaped row of spines should be additionally observed in lateral view, they are clearly observed in dry condition. The specimen examined generally agrees well with these characteristics.



Fig. 133. *Acanthosquilla derijardi*, female, TL 70 mm, AM P16285.

62. *Acanthosquilla multifasciata* (Wood-Mason, 1895) (Figs. 134–135)

Lysiosquilla multifasciata Wood-Mason, 1895: 1–2, figs. 22–24.

Lysiosquilla valdiviensis: Jurich, 1904: 372, pl. 26: fig. 2.

Acanthosquilla multifasciata: Holthuis, 1967: 4; Moosa, 1991: 183; Manning, 1995: 143–147, pls. 25, 26, figs. 78b, 80b, 81a, b, e, f, 82a, b, 83–86; Ah Yong, 2001: 144–146, fig. 71; Ah Yong & Naiyanetr, 2002: 289; Ah Yong et al., 2008: 47–48, figs. 35–37; Ah Yong, 2012b: 244, 247; Ariyama et al., 2014: 28–31, fig. 3, Hwang et al., 2019.

Material examined

Non type material

Australia: AM P57040, female, TL 67 mm, Queensland, north east Gulf of Carpentaria, coll. T. Wassenberg, 1990.

Korea: MADBK 600401_001, male (damaged, cephalothorax missing, TS7 to telson remaining; TL estimated at 37 mm), Sam-do, Bomok-dong, Segwipo-si, Jeju-do, South Korea, 33°13'46.3"N, 126°35'55.7"E, coll. S.H Kim, 14 October 2010.

Diagnosis. Rostral plate (Fig. 135) longer than broad, trapezoid to subpentagonal, with single apical median spine. Ocular scales rounded, separate. Raptorial claw (Fig. 135) dactylus with 5–6 teeth; outer margin with basal notch, distal lobe triangular, distinctly larger than proximal lobe. Abdominal somite 6 (Fig. 135) without spinules on posterior margin adjacent to posterolateral spine. Telson (Fig. 135) with 2 pairs of fixed primary teeth (lateral and intermediate); dorsal surface with 5 posteriorly directed spines in fan shaped row above marginal armature; Telson (Fig. 135) denticles present, following as: 3–4 submedian denticles, 4 intermediate denticels. Uropodal (Fig. 135) protopod with smooth inner margin, without distal spines adjacent to endopod articulation; exopod proximal segment outer margin with 6 movable spines.

Habitat. Chopra (1939) reported *A. multifasciata* collected from a depth of 73 m. Also, they were collected from burrows in mud or sand substrates, from the shore down to 43 m (Ah Yong, 2001).

Distribution. Red Sea to Australia, South China Sea, Taiwan, Japan, Hawaii (Heard & Manning, 1990; Ah Yong, 2001), and Korea.



Fig. 134. Distribution of *Acanthosquilla multifasciata* (Wood-Mason, 1895). Legend: star = type locality; circle = distribution in worldwide.

Remarks. Among *Acanthosquilla* species, *A. multifasciata* can be easily distinguished from other congeners by the presence of the following telson characters: 1) two instead of three pairs of fixed primary teeth (lateral and intermediate), 2) four intermediate denticles, 3) an arcuate row of five instead of seven posteriorly directed spines on the posterodorsal surface above the posterior marginal armature, and 4) the unarmed margin adjacent to the uropodal endopod articulation. The specimen examined generally agrees well with these characteristics.

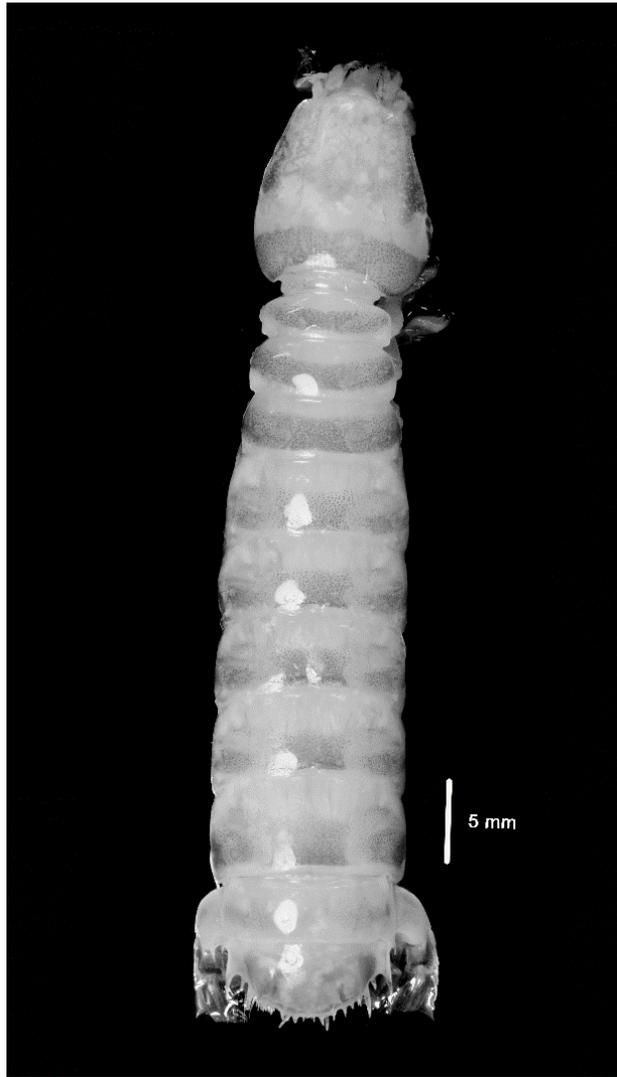


Fig. 135. *Acanthosquilla multifasciata*, female, TL 67 mm, AM P57040.

63. *Acanthosquilla melissae* Ahyong, 2008 (Figs. 136–137)

Acanthosquilla derijardi: Ahyong, 2001: 144; Ahyong & Davie, 2002: 55
[Shelburne Bay specimens only; not *A. derijardi* Manning, 1970].

Acanthosquilla melissae Ahyong, 2008: 48–51: fig. 3.

Material examined***Type material***

Paratype: Australia: AM P54463, female, TL 46 mm, Shelburne Bay (11°41.4'S, 143°00.4'E), 33 m, coll. T. Wassenberg, January 1993.

Diagnosis. Rostral plate (Fig. 137) longer than broad, with trapezoid proximal portion and single long apical median spine. Ocular scales (Fig. 137) rounded, separate, inclined anteriorly. Raptorial claw (Fig. 137) dactylus with 6 teeth; outer proximal margin with small proximal lobe and larger, triangular distal lobe. Abdominal somite 6 (Fig. 137) posterior margin smooth; posterolateral spine long, slender, with slender ventrolateral spine and short blunt angular lobe anterior to uropodal articulation; Telson (Fig. 137) with 2 pairs of fixed primary teeth (lateral and intermediate); dorsal surface with pair of mid-dorsal pits and 7 well spaced posteriorly directed spines in transverse row above marginal armature. Uropodal protopod (Fig. 137) with smooth inner margin, without distal spines adjacent to endopod articulation; exopod proximal segment outer margin with 6 movable spines.

Habitat. The information is not available.

Distribution. Australia (Shelburne Bay of Queensland and Dampier Archipelago of Western region) (Ahyong, 2008).



Fig. 136. Distribution of *Acanthosquilla melissae* Ah Yong, 2008. Legend: star = type locality; circle = distribution in worldwide.

Remarks. Among *Acanthosquilla* species, *A. melissae* is morphologically similar to *A. derijardi* in having 2 pairs of fixed primary teeth and 4 intermediate denticles of the telson and it was originally reported as a variation of *A. derijardi* (Ah Yong, 2001). However, it can be easily distinguished from the other species by the presence of the following characteristics: (1) seven spines in transverse row on the upper posterior margin and fewer spines on the dorsal surface of telson, (2) a relatively smaller outer triangular lobe of raptorial claw, and (3) a more elongate rostral spine. The specimen examined generally agrees well with these characteristics.

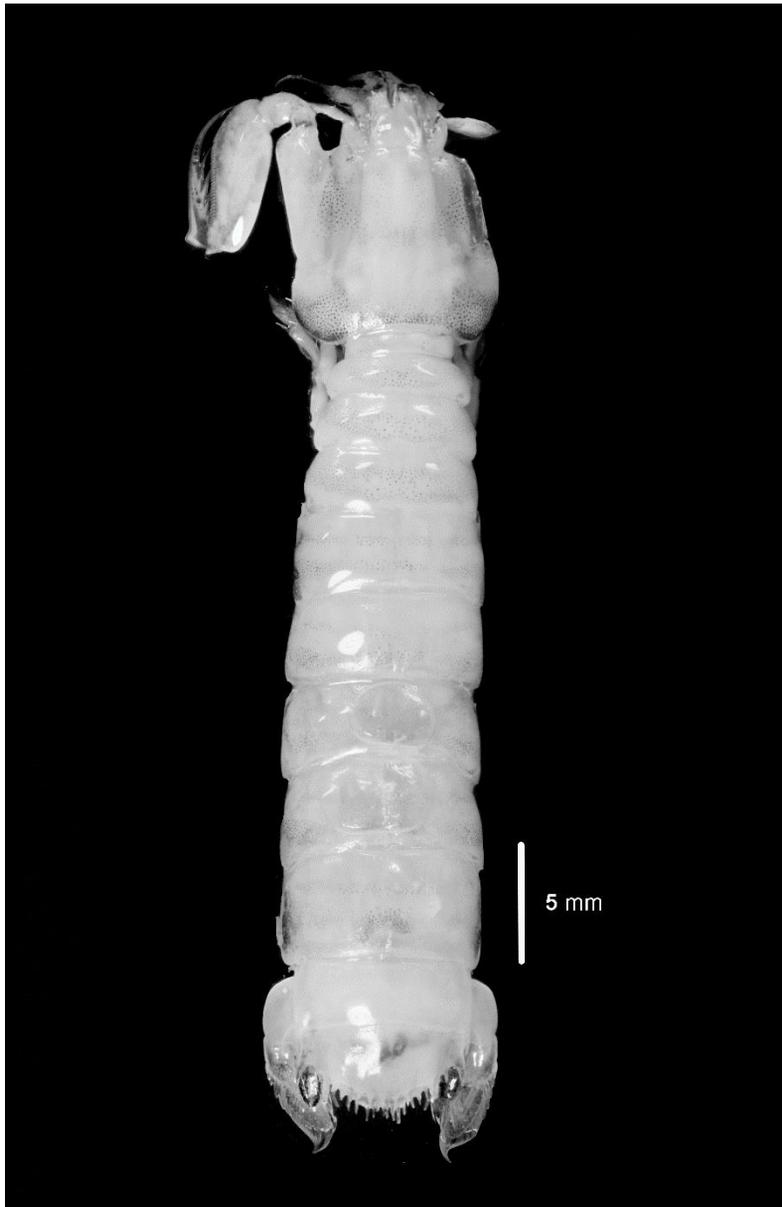


Fig. 137. *Acanthosquilla melissae*, female, TL 46 mm, AM P54463.

64. *Acanthosquilla manningi* Makarov, 1979b (Fig. 138)

Acanthosquilla manningi Makarov, 1978: 177, fig. 1 [type locality: Tonkin Bay, Vietnam].

Material examined*Non type material*

Taiwan: NTOU, 1 male, TL 60 mm, Donggang fishing port, Pingtung County, 5 August 1996.

Diagnosis. Rostral plate longer than broad, with trapezoid proximal portion and single long apical median spine. Ocular scales rounded, separate. Raptorial claw dactylus with 6 teeth. Abdominal somite 6 posterior margin smooth; posterolateral spine long, slender, with slender ventrolateral spine and short blunt angular lobe anterior to uropodal articulation; Telson with 2 pairs of fixed primary teeth (lateral and intermediate); upper posterior margin with median spine and two clusters of three-four spines above field of numerous spines. Uropodal protopod with smooth inner margin, without distal spines adjacent to endopod articulation; exopod proximal segment outer margin with 5 movable spines.

Habitat. Not known, but presumably soft substrates suitable for burrow construction (Ahyong et al., 2008).

Distribution. Vietnam, and Taiwan (Ahyong et al., 2008).



Fig. 138. Distribution of *Acanthosquilla manningi* Makarov, 1979b. Legend: star = type locality; circle = distribution in worldwide.

Remarks. Among *Acanthosquilla* species, *A. manningi* can be readily distinguished from the congeners by having two clusters of three–four numerous spines covering the posterior surface of the telson instead of the transverse arrangement of spines on the upper posterior margin. The specimen examined generally agrees well with these characteristics.

65. *Acanthosquilla crosnieri* Ahyong, 2002 (Fig. 139)

Acanthosquilla crosnieri Ahyong, 2002: 359–361, fig. 7.

Type material

Marquesas: MNHN, 1 male, TL 33 mm, Hiva Oa, stn DW1213, 18–20 m, 29 August 1997.

Diagnosis. Rostral plate longer than broad, subpentagonal with short apical median spine. Ocular scales narrow, separate, inclined anteriorly. Raptorial claw dactylus with 5 teeth. Abdominal somite 6 posterior margin smooth; posterolateral spine long,

slender, with slender ventrolateral spine and short blunt angular lobe anterior to uropodal articulation; Telson with 2 pairs of fixed primary teeth (lateral and intermediate); dorsal surface with pair of mid-dorsal pits and five well spaced posteriorly directed spines in fan-shaped row above marginal armature. Uropodal protopod inner margin with two slender ventral spines adjacent to endopod articulation; exopod proximal segment outer margin with 6 movable spines.

Habitat. The information is not available.

Distribution. Known only from the Marquesas (type locality) (Ahyong, 2002).

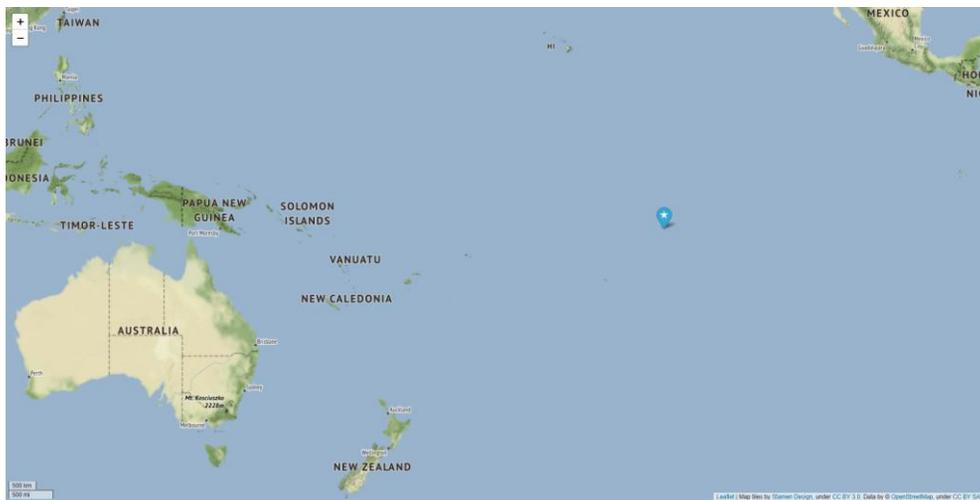


Fig. 139. Distribution of *Acanthosquilla crosnieri* Ahyong, 2002. Legend: star = type locality; circle = distribution in worldwide.

Remarks. *Acanthosquilla crosnieri* is morphologically similar to *A. multifasciata* from the Indo-West Pacific in almost all respects, but differs in bearing slightly narrower corneae, in bearing two fixed spines under the articulation of the uropodal endopod. The specimen examined generally agrees well with these characteristics.

66. *Acanthosquilla tigrina* (Nobili, 1903) (Fig. 140)

Acanthosquilla tigrina Nobili, 1903: 28 [type locality: Santubong, Borneo]; Naiyanetr,

1980: 42; Ah Yong, 2001: 144; Ah Yong & Naiyanetr, 2002: 289.

Non type material

Phuket: ZRC 1999.2346, 1 male, TL 42 mm, Naiyang Beach, 21 April 1997.

Diagnosis. Rostral plate with single median spine. Ocular scales narrow, separate, inclined anteriorly. Abdominal somite 6 posterior margin smooth; posterolateral spine long, slender, with slender ventrolateral spine; ventral posterior margin with spines. Telson with 4 pairs of fixed primary teeth, each with intervening denticle; dorsal surface with flat median elevation terminating in 3 acute spines; with marginal and several posteriorly armed carinae. Uropodal protopod with ventral spine anterior to endopod articulation.

Habitat. Intertidal sand flats (Schram & Müller, 2004).

Distribution. Indo-West Pacific; India, Thailand, Malaysia, Borneo (Sarawak) (Schram & Müller, 2004).



Fig. 140. Distribution of *Acanthosquilla tigrina*. Legend: star = type locality; circle = distribution in worldwide.

Remarks. Among *Acanthosquilla* species, *A. tigrina* is morphologically similar to

A. wilsoni by the presence of 4 pairs of fixed primary teeth and denticles, but differs in bearing unarmed posterior margin and armed ventral posterior spine on the abdominal somite 6.

67. *Acanthosquilla wilsoni* Moosa, 1973 (Fig. 141)

Acanthosquilla wilsoni Moosa, 1973: 15–17, fig. 2; 1986: 389, fig. 6; Ahyong, 2001: 144.

Type material

Indonesia: S 836, 1 male, TL 38.66 mm, west of Babi Island, Whakamaru, Aru, 17 June 1970.

Diagnosis. Rostral plate longer than broad, with trapezoid proximal portion and single long apical median spine. Abdominal somite 6 dorsally with 2–3 spinules along posterior margin adjacent to posterolateral spine; ventral posterior margin without spines. Telson broader than long; with 4 pairs of fixed primary teeth, each with intervening denticle; dorsal surface with pair of mid-dorsal pits and 6–7 well spaced posteriorly directed spines in transverse row above marginal armature. Uropodal protopod with smooth inner margin, without distal spines adjacent to endopod articulation; exopod proximal segment outer margin with 6 movable spines.

Habitat. Muddy bottom (Moosa, 1973).

Distribution. Indonesia and Philippines (Schram & Müller, 2004).



Fig. 141. Distribution of *Acanthosquilla wilsoni* Moosa, 1973. Legend: star = type locality; circle = distribution in worldwide.

Remarks. Features distinguishing *A. tigrina* and *A. wilsoni* are discussed under the account of the former. These two species are clearly distinguished by the characteristics of abdominal somite 6 (unarmed posterior margin and posteriorly armed ventral margin).

68. *Acanthosquilla multispinosa* Blumstein, 1974 (Fig. 142)

Acanthosquilla multispinosa Blumstein, 1974: 113–115, fig. 1.

Type material

Holotype: Vietnam: 1 female, TL 28 mm, Gulf of Tonkin, 31 July 1961.

Diagnosis. Rostral plate longer than broad, with ovate proximal portion and single long apical median spine. Abdominal somite 5 with posterolateral spine. Telson broader than long; with 2 pairs of fixed primary teeth (lateral and intermediate); dorsal surface with pair of mid-dorsal pits and 9–11 well spaced posteriorly directed spines in transverse row above marginal armature. Uropodal protopod with smooth inner margin, without distal spines adjacent to endopod articulation; exopod

proximal segment outer margin with 6 movable spines.

Habitat. The information is not available.

Distribution. Babi Island of Indonesia (type locality) (Blumstein, 1974).



Fig. 142. Distribution of *Acanthosquilla multispinosa* Blumstein, 1974. Legend: star = type locality; circle = distribution in worldwide.

Remarks. *A. multispinosa* is morphologically similar to *A. multifasciata* and *A. derijardi* in having 2 pairs of fixed primary teeth and 4 intermediate denticles. But *A. multispinosa* differs from *A. multifasciata* by the presence of an arcuate row of 9–11 instead of 5 posteriorly directed spines on the posterodorsal surface above the posterior marginal armature. *A. derijardi* has 7 posteriorly directed spines on the telson.

CHAPTER 4.

FAUNAL STUDY OF KOREAN STOMATOPODS

INTRODUCTION

Stomatopods or mantis shrimps are predatory crustaceans found mostly in tropical and subtropical regions and characterized by having remarkably developed second maxillipeds modified as powerful raptorial appendages (Ahyong et al., 2008). More than 480 described species are known, distributed in seven superfamilies and seventeen families, of which only eight species in three superfamilies have been recorded from Korean waters: *Chorisquilla orientalis* Hwang, Ahyong & Kim, 2018; *Gonodactylaceus falcatus* (Forskål, 1775); *Odontodactylus japonicus* (de Haan, 1844); *Taku spinosocarinatus* (Fukuda, 1909) (Gonodactyloidea Giesbrecht, 1910); *Faughnia formosae* Manning & Chan, 1997 (Parasquilloidea Manning, 1995); *Kempella mikado* (Kemp & Chopra, 1921); *Oratosquilla oratoria* (de Haan, 1844); and *Squilloides leptosquilla* (Brooks, 1886) (Squilloidea Latreille, 1802) (Kim and Rho, 1972; The Korean Society of Systematic Zoology, 1997; Hwang et al., 2013; Kang et al., 2016; Hwang et al., 2018a, b; 2019).

MATERIALS AND METHODS

Specimens were collected from Korean waters by SCUBA diving and commercial fishing trawlers, and preserved in 95% ethanol. A stereomicroscope (MZ8; Leica, Wetzlar, Germany) was used for observation and sorting. Photographs of specimens were recorded using a Nikon D200 digital camera and processed with the focus-stacking program Helicon Focus (Helicon Soft, Kharkov, Ukraine). The specimens examined herein are deposited in the Marine Arthropod Depository Bank of Korea (MADBK) and the National Institute of Biological Resources, Incheon, Korea (NIBR).

Among Korean stomatopod species, if additional taxonomic studies about corresponding species are required, detailed descriptions of the Korean specimen of corresponding species were made for providing information on Korean species.

Checklist of Korean Stomatopoda

SYSTEMATIC ACCOUNTS

Phylum Arthropoda von Siebold, 1848 절지동물 문

Subphylum Crustacea Brünnich, 1772 갑각 아문

Class Malacostraca Latreille, 1802 연갑 강

Subclass Hoplocarida Calman, 1904 연갑 아강

Order Stomatopoda Latreille, 1817 구각 목

*Superfamily Lysiosquilloidea Giesbrecht, 1910 등근갯가재 상과

*Family Nannosquillidae Manning, 1980 줄무늬갯가재 과

*Genus *Acanthosquilla* Manning, 1963 줄무늬갯가재 속

*1. *Acanthosquilla multifasciata* (Wood-Mason, 1895) 줄무늬갯가재

*Family Tetrasquillidae Manning & Camp, 1993 두줄등근갯가재 과

*Genus *Acaenosquilla* Manning, 1991 두줄등근갯가재 속

*2. *Acaenosquilla latifrons* (de Haan, 1844) 두줄등근갯가재

Superfamily Squilloidea Latreille, 1802 갯가재 상과

Family Squillidae Latreille, 1802 갯가재 과

*Genus *Levisquilla* Manning, 1977 무늬갯가재 속

*3. *Levisquilla inermis* (Manning, 1965) 민무늬갯가재

*4. *Levisquilla jurichi* (Makarov, 1979a) 잔무늬갯가재

*Genus *Anchisquilla* Manning, 1968 잔돌기갯가재 속

*5. *Anchisquilla fasciata* (de Haan, 1844) 잔돌기갯가재

*Genus *Cloridopsis* Manning, 1968 민물갯가재 속

*6. *Cloridopsis scorpio* (Latreille in Latreille et al., 1828) 민물갯가재

Genus *Kempella* Low & Ah Yong, 2010 큰점박이갯가재 속

7. *Kempella mikado* (Kemp & Chopra, 1921) 큰점박이갯가재

Genus *Oratosquilla* Manning, 1968 갯가재 속

8. *Oratosquilla oratoria* (De Haan, 1844) 갯가재

Genus *Squilloides* Manning, 1968 사니갯가재 속

9. *Squilloides leptosquilla* (Brooks, 1886) 사니갯가재

Superfamily Gonodactyloidea Giesbrecht, 1910 가위갯가재 상과

Family Gonodactylidae Giesbrecht, 1910 흑돌기갯가재 과

Genus *Gonodactylaceus* Manning, 1995 흑돌기갯가재 속

10. *Gonodactylaceus falcatus* (Forskål, 1775) 흑돌기갯가재

Family Takuidae Manning, 1995 가위갯가재 과

Genus *Taku* Manning, 1995 가위갯가재 속

11. *Taku spinosocarinatus* (Fukuda, 1909) 가위갯가재

Family Protosquillidae Manning, 1980 가시꼬리갯가재 과

Genus *Chorisquilla* Manning, 1969 가시꼬리갯가재 속

12. *Chorisquilla orientalis* Hwang, Ahyong & Kim, 2018 가시꼬리갯가재

Family Odontodactylidae Manning, 1980

Genus *Odontodactylus* Bigelow, 1893

13. *Odontodactylus japonicus* (de Haan, 1844)

Superfamily Parasquilloidea Manning, 1995 돌기갯가재 상과

Family Parasquillidae Manning, 1995 돌기갯가재 과

Genus *Faughnia* Serène, 1962 돌기갯가재 속

14. *Faughnia formosae* Manning & Chan, 1997 다섯돌기갯가재

The marked with an asterisk (*) indicates newly reported species from Korea by the author.

A Key to species of Korean Stomatopods

1. Maxillipeds 3–4 propodi subquadrate, broader than long, each with distal ribbing 2
- Maxillipeds 3–4 propodi ovate, without distal ribbing 3
2. Telson without postanal spine *Acanthosquilla multifasciata*
- Telson with postanal spine *Acaenosquilla latifrons*
3. Telson with at least 4 intermediate denticles 4
- Telson with 2 intermediate denticles 10
4. Thoracic somites 6–7 lateral process bilobed 5
- Thoracic somites 6–7 lateral process single 6
5. Raptorial claw merus without inferodistal spine. Abdominal somite 5 with pair of large dark dorsal patches *Kempella mikado*
- Raptorial claw merus with inferodistal spine. Abdominal somite 5 without large dark dorsal patches *Oratosquilla oratoria*
6. Uropodal protopod inner margin lined with spines 7
- Uropodal protopod inner margin crenulate or smooth 8
7. Telson submedian teeth with fixed apices *Anchisquilla fasciata*
- Telson submedian teeth with articulated apices 9
8. Raptorial claw dactylus with 4 teeth. Thoracic somite 5 lateral process without black patch *Squilloides leptosquilla*
- Raptorial claw dactylus with 5 teeth. Thoracic somite 5 lateral process with black patch *Cloridopsis scorpio*
9. Telson without longitudinal carinae on either side of median carina; ventral surface without postanal carina *Levisquilla inermis*
- Telson with longitudinal carinae on either side of median carina; ventral surface with postanal carina *Levisquilla jurichi*
10. Uropodal protopod with 3 primary spines. Ischiomeral articulation of raptorial claw terminal; dactylus outer proximal margin uninflated, not forming ‘smashing’ club *Faughnia formosae*

- Uropodal protopod with 2 primary spines. Ischiomeral articulation of raptorial claw terminal; dactylus outer proximal margin inflated, forming ‘smashing’ club 11
- 11. Rostral plate trispinous or with broad trapezoid basal portion and slender median spine. Raptorial claw dactylus without teeth on occlusal margin 12
- Rostral plate subtriangular to rounded, without median spine. Raptorial claw dactylus without 5 or more small teeth on occlusal margin
 *Odontodactylus japonicus*
- 12. Uropodal exopod bearing stout, anteriorly recurved, immovable distal spines on outer margin *Taku spinosocarinatus*
- Uropodal exopod bearing slender, straight, movable distal spines on outer margin 13
- 13. Rostral plate with broad trapezoid basal portion and slender median spine. Telson mid-dorsal surface with 5 longitudinal carinae; lateral margin of without row of spines *Gonodactylaceus falcatus*
- Rostral plate trispinous. Telson dorsal surface of telson with 3 bosses covered in short spinules; lateral margin with row of 8-14 spines
 *Chorisquilla orientalis*

SYSTEMATICS ACCOUNTS

*Superfamily Lysiosquilloidea Giesbrecht, 1910 등근갯가재 상과

*Family Nannosquillidae Manning, 1980 줄무늬갯가재 과

*Genus *Acanthosquilla* Manning, 1963 줄무늬갯가재 속

*1. *Acanthosquilla multifasciata* (Wood-Mason, 1895) 줄무늬갯가재

(Figs. 143–144)

Lysiosquilla multifasciata Wood-Mason, 1895: 1–2, figs. 22–24.

Lysiosquilla valdiviensis: Jurich, 1904: 372, pl. 26: fig. 2.

Acanthosquilla multifasciata: Holthuis, 1967: 4; Moosa, 1991: 183; Manning, 1995: 143–147, pls. 25, 26, figs. 78b, 80b, 81a, b, e, f, 82a, b, 83–86; Ah Yong, 2001: 144–146, fig. 71; Ah Yong & Naiyanetr, 2002: 289; Ah Yong et al., 2008: 47–48, figs. 35–37; Ah Yong, 2012b: 244, 247; Ariyama et al., 2014: 28–31, fig. 3; Hwang et al., 2019: in press.

Material examined

MADBK 600401_001, male (damaged, cephalothorax missing, thoracic somite 7 to telson remaining; TL estimated at 37 mm), Sam-do, Bomok-dong, Segwipo-si, Jeju do, South Korea, 33°13'46.3"N, 126°35'55.7"E, coll. S.H Kim, 14 October 2010.

Distribution. Red Sea to Australia, South China Sea, Taiwan, Japan, Hawaii (Heard & Manning, 1990; Ah Yong, 2001), and now from Korea.

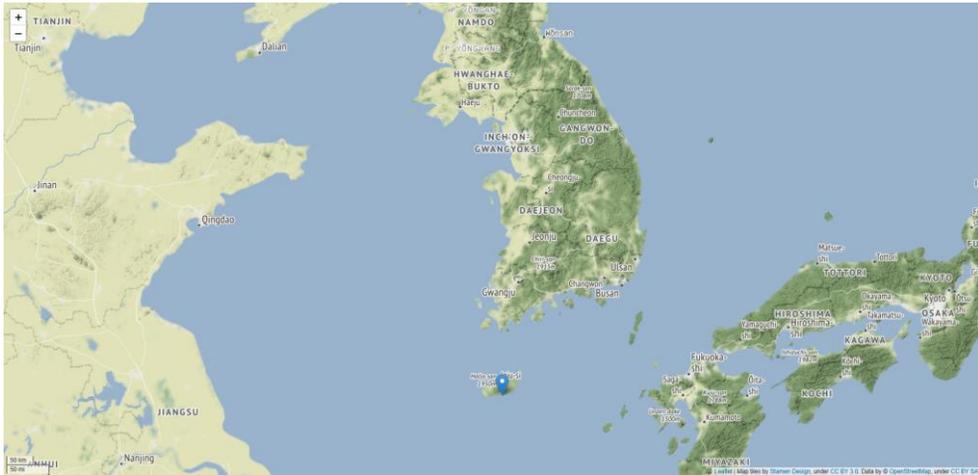


Fig. 143. Distribution of *Acanthosquilla multifasciata* (Wood-Mason, 1895) in Korea.

Remarks. The present specimen is readily identified as *Acanthosquilla multifasciata* based on the presence of the following telson characters: 1) two pairs of fixed primary teeth (lateral and intermediate), 2) four intermediate denticles, 3) an arcuate row of five posteriorly directed spines on the posterodorsal surface above the posterior marginal armature (figs. 144A, 144B), and 4) the unarmed margin adjacent to the uropodal endopod articulation (Ahyong, 2001, 2002).

In addition, *A. multifasciata* is readily distinguished from the lysiosquilloid *Acaenosquilla latifrons* (reported below) by the presence of a transverse black band on each thoracic and abdominal somite; its Korean name, meaning stripe, was given according to these characteristics.

The present specimen represents a significant northward range extension of *A. multifasciata* and is the first record of both the family and superfamily (together with *Acaenosquilla latifrons*, below) from Korea.

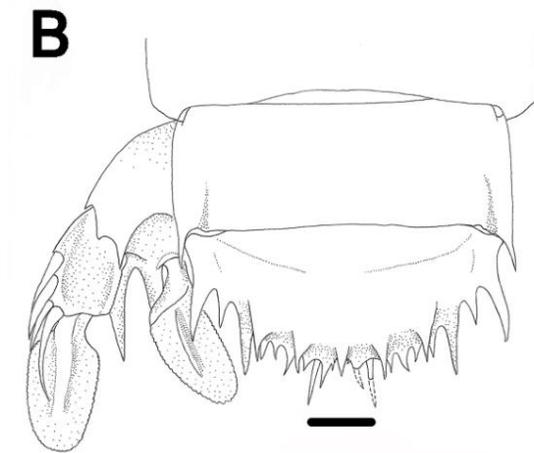


Fig. 144. *Acanthosquilla multifasciata*, male, TL 28.4 mm, MADBK 600401_001, specimen lacking carapace). A, body, dorsal view; B, telson, in dorsal view. Scale bars: A = 4.0 mm, B = 1.0 mm.

*Family Tetrasquillidae Manning & Camp, 1993 두줄등근갯가재 과

*Genus *Acaenosquilla* Manning, 1991 두줄등근갯가재 속

*2. *Acaenosquilla latifrons* (de Haan, 1844) 두줄등근갯가재

(Figs. 145–146)

Squilla latifrons de Haan, 1844: pl. 51, fig. 3.

Lysiosquilla latifrons: Komai, 1927: 333–335, pl. 14, fig. 3.

Acaenosquilla latifrons: Manning, 1991: 6, fig. 4; Ah Yong, 2001: 171; Ah Yong, 2012b: 247.

Heterosquilloides latifrons: Yamaguchi and Baba, 1993: 187–188, fig. 15; Hwang et al., 2019: in press.

Material examined

MADBK 600501_001, female (TL 34 mm), Sam-do, Bomok-dong, Segwipo-si, Jeju-do, South Korea, 33°13'46.3"N, 126°35'55.7"E, coll. S.H Kim, 13 June 2011.

Distribution. Japan (Manning, 1991; Ah Yong, 2001) and now from Korea.

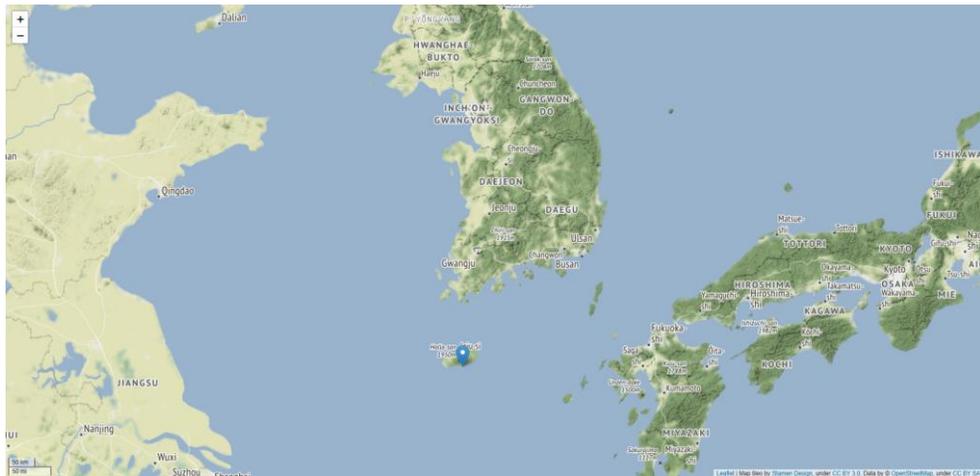


Fig. 145. Distribution of *Acaenosquilla latifrons* (de Haan, 1844) in Korea.

Remarks. *Acaenosquilla latifrons* is morphologically similar to *A. brazieri* (Miers, 1880), but is easily distinguished by the shape of the mesial lobe of the cornea and the absence of carinae on the dorsal surface of the telson. In *A. latifrons*, the mesial lobe of the cornea is rounded rather than distinctly conical with a low apical tubercle (Ahyong, 2001). *Acaenosquilla brazieri* has one to three carinae lateral to the median prominence of the telson. A feature present in the Korean specimen, which was also observed by Komai (1927) but not mentioned by Manning (1991), is a pair of shallow longitudinal furrows on the telson surface lateral to the median prominence (figs. 146A, 146B).

Acaenosquilla latifrons and *A. brazieri* have widely separated, anti-tropical distributions. *Acaenosquilla latifrons* is recorded only from Japan and Korea, whereas *A. brazieri* is known only from eastern Australia (Manning, 1991; Ahyong, 2001).

Especially compared with Japanese *A. latifrons*, the preserved coloration of the Korean specimen is similar to that of Japanese specimens. According to the description of Komai (1927), all of the thoracic somites and the fifth abdominal somite have broad transverse bands and there are two pairs of dark patches on the dorsal surface of the telson. The present specimen also has this coloration. In Japan, *A. latifrons* has been recorded from Nagasaki (western Kyushu) (Yamaguchi and Baba, 1993) and the present specimens from Korean waters was collected from Jeju Island for the first time. This record represents a significant northward range of *A. latifrons*.

Tetrasquillids have been collected from the shore down to depths of 510–590 m. Among these, species of *Acaenosquilla* are usually collected from depths as shallow as 36 m (Ahyong, 2001). The Korean specimen of *A. latifrons* was collected from Jeju Island at less than 20 m depth.

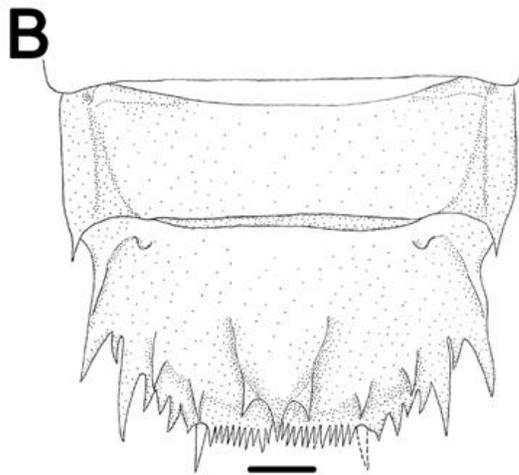


Fig. 146. *Acaenosquilla latifrons*, female, TL 34 mm, MADBK 600501_001

Superfamily Squilloidea Latreille, 1802 갯가재 상과

Family Squillidae Latreille, 1802 갯가재 과

*Genus *Levisquilla* Manning, 1977 무늬갯가재 속

***3. *Levisquilla inermis* (Manning, 1965) 민무늬갯가재**

(Figs. 147–148)

Squilla inermis Manning, 1965: 255–257, fig. 2; 1977: 422.

Squilla lata: Komai, 1927: 310, pl. 14, figs. 1, 1b [not *S. lata* Brooks, 1886].

Levisquilla inermis: Manning, 1995: 24, 209–210; Ahyong, 2001: 271, fig. 132; Ahyong et al., 2008: 131, figs. 104–105; Ahyong, 2012b: 248; Ariyama et al., 2014: 35–37, fig. 6; Hwang et al., 2019: in press.

Material examined

NIBRIV0000150629, female (TL 25 mm), Seosaeng-myeon, Ulju-gun, Ulsan, South Korea, 35°20'24.4"N, 129°19'13.4"E, coll. J.S Hong, 21 October 1998; NIBRIV0000837750, female (TL 13.5 mm), Seosaeng-myeon, Ulju-gun, Ulsan, South Korea, 35°20'24.4"N, 129°19'13.4"E, coll. S.J Song, 24 October 2006; MADBK 600202_001, male (TL 18.5 mm), Seosaeng-myeon, Ulju-gun, Ulsan, South Korea, 35°20'24.4"N, 129°19'13.4"E, coll. S.J Song, 22 May 2007. MADBK 600202_002, female (TL 18.5 mm), Hwanggi-dong, Gwangyang, Jeollnam-do, South Korea, 34°53'31.3"N, 127°39'57.7"E, coll. S.J Song, 18 November 2003.

Distribution. Japan, Taiwan, Vietnam, Australia (Manning, 1995; Ahyong, 2001; Ahyong et al., 2008), and now from Korea.

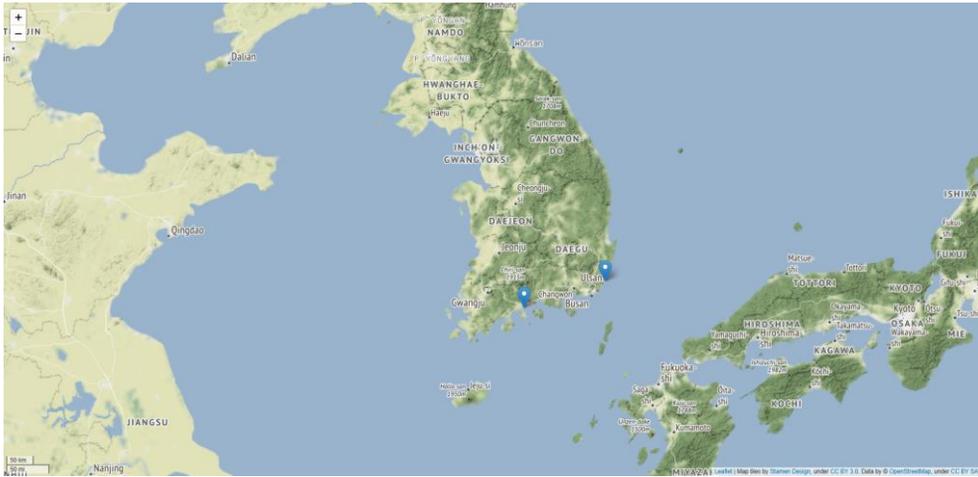


Fig. 147. Distribution of *Levisquilla inermis* (Manning, 1965) in Korea.

Remarks. *Levisquilla inermis* is distinguished from other congeners by the absence of supplementary mid-dorsal carinae on the telson (Fig. 148B) and absence of the postanal carina. The Korean specimens agree well with published accounts (Manning, 1965; Ah Yong, 2001; Ah Yong et al., 2008) except that the lateral process of thoracic somite 5 is less prominently recurved anteriorly, probably a reflection of their smaller size (TL 25 mm or less) (Fig. 148) than previously figured specimens (all with TL 29 mm or greater) (e.g., Ah Yong, 2001: Fig. 132).

According to Ah Yong (2001), *L. inermis* shows allometric changes in the shape of the distal movable spine on the outer margin of the proximal uropodal exopod segment, ranging from spinular in the smallest specimen to spatulate in larger specimens. A single specimen (TL 29.9 mm) reported from Japan (Ariyama et al., 2014, Fig. 6C) also has a spatulate distal spine. The Korean specimens reflect these allometric changes; the spine is most prominently spinular in the smallest specimen (TL 13.5 mm) and becomes spatulate in the larger specimens (> TL 18.5 mm). The largest specimen examined (TL 25 mm) has a distinctly spatulate, and slightly more curved distal spine compared to smaller specimens. The present specimens from Korean waters represent a significant northward range of *L. inermis*.

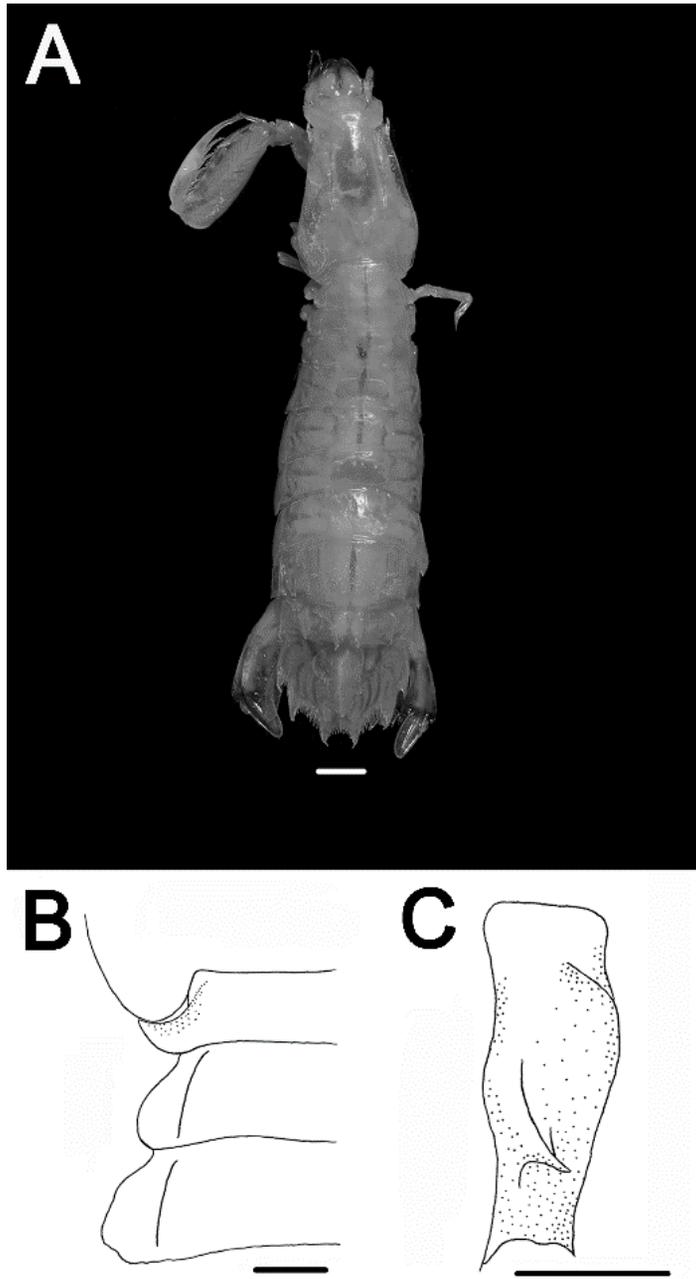


Fig. 148. *Levisquilla inermis*, female, TL 25 mm, NIBRIV0000150629. A, dorsal view; B, left thoracic somites 5–7, dorsal view; C, thoracic somite 5, right lateral view. Scale bars: A = 2.0 mm, B–C = 1.0 mm.

*4. *Levisquilla jurichi* (Makarov, 1979a) 잔무늬갯가재

(Figs. 149–150)

Clorida jurichi Makarov, 1979a: 40, fig. 1.

Levisquilla jurichi: Manning, 1995: 25, 209–210; Ahyong, 1997: fig. 1A, 3K; Ahyong, 2001: 271–274, fig. 133; Ahyong & Naiyanetr, 2002: 299; Ahyong, 2016: 464–465, fig. 4F; Hwang et al., 2019: in press.

Material examined

MADBK 600205_001, female, (TL 13 mm), Junggye-ri, Byeonsan-myeon, Buan-gun, Jeollabuk-do, South Korea, 35°39'00.0"N, 126°27'22.3"E, coll. S.-K Lee, 4 September 2017.

Distribution. Andaman Sea, Vietnam, Singapore, New Caledonia, Australia (Ahyong, 2001, 2016), and now from Korea.

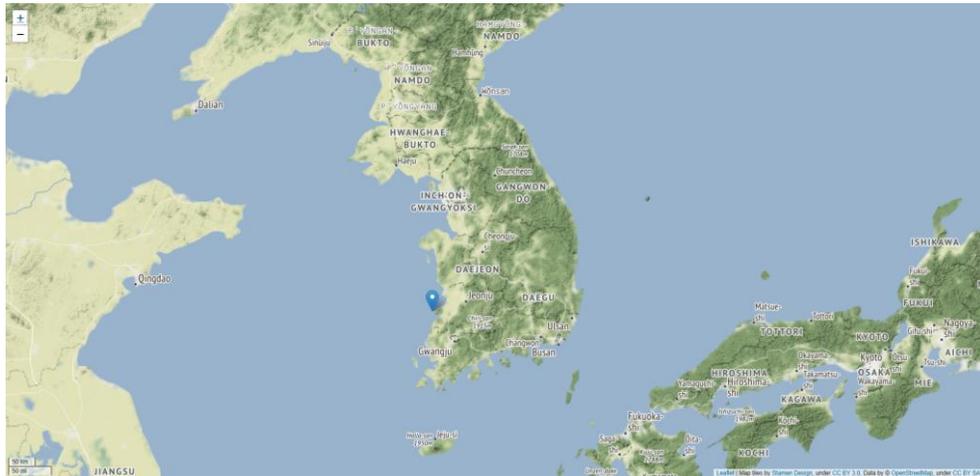


Fig. 149. Distribution of *Levisquilla jurichi* (Makarov, 1979a) in Korea.

Remarks. The genus *Levisquilla* Manning, 1977 includes three species. *Levisquilla jurichi* differs from *L. inermis* reported above by the presence of supplementary carina on the dorsolateral surface of the telson (smooth in *L. inermis*), and can be

distinguished from *L. minor* by the presence of one instead of two lobes between the terminal spines of the protopod of uropod.

Levisquilla jurichi has three to five submedian denticles on either side of the midline and numerous supplementary longitudinal carinae on the telson. The Korean specimen differs slightly from Ahyong's (2001) account of the species in having six submedian denticles as a result of the innermost denticles having multifid apices (a juvenile feature commonly observed in squilloids) and fewer supplementary longitudinal carinae on the telson (Figs. 148A, 148B) than in a TL 51 mm specimen figured by Ahyong (2001: fig. 133). According to Ahyong (2001), the primary diagnostic characters of *L. jurichi* are well developed even in TL 11–12 mm juveniles, although the mid-dorsal carinae on the telson are fewer in number than those of larger specimens. Considering the small size of the Korean specimen (TL 13 mm), the observed differences may be attributable to its immaturity.

The present record from Korean waters represents a northward range extension of *L. jurichi*.

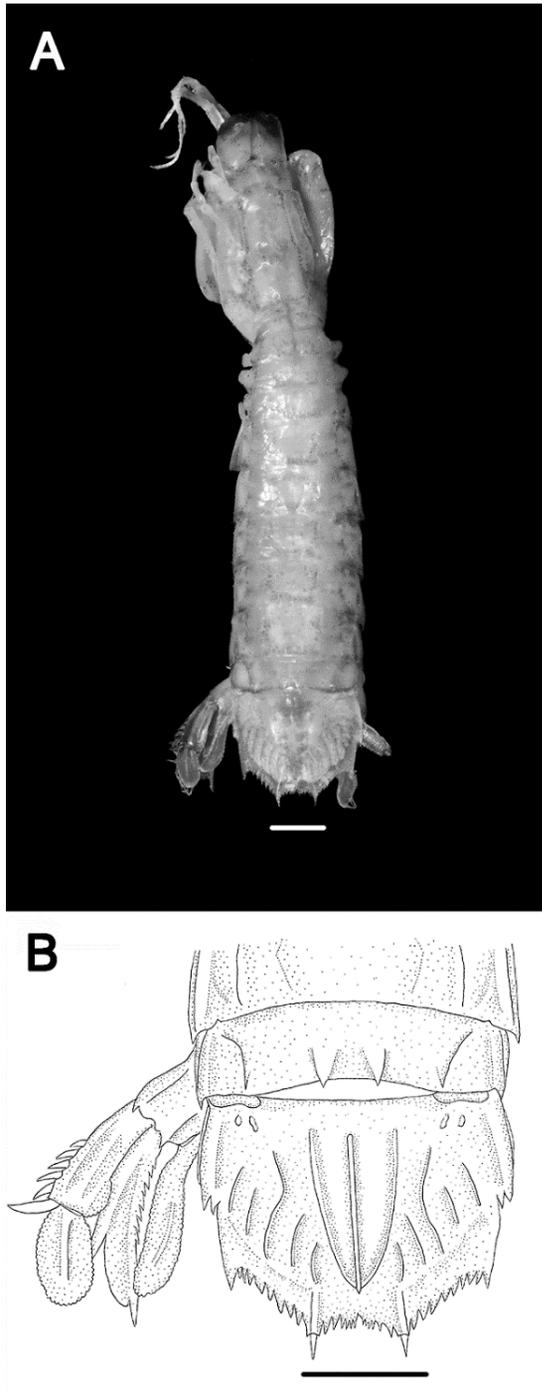


Fig. 150. *Levisquilla jurichi* (Makarov, 1979a) (female, TL 13 mm, MADBK 600205_001). A, dorsal view; B, telson, in dorsal view. Scale bars: A = 1.15 mm, B–C = 1.0 mm.

*Genus *Anchisquilla* Manning, 1968 잔돌기갯가재 속

*5. *Anchisquilla fasciata* (de Haan, 1844) 잔돌기갯가재

(Figs. 151–152)

Squilla fasciata de Haan, 1844: pl. 51, fig. 4.

Anchisquilla fasciata: Manning, 1968: 120, 127; 1977: 420; 1991: 8; 1995: 166, 169, pl. 29, figs. 98–100; Yamaguchi & Baba, 1993: 181–182, fig. 12; Ah Yong & Naiyanetr, 2002: 289–290; Ah Yong et al., 2008: 69–70, fig. 48, 49; Ah Yong, 2012b: 248; Ah Yong & Kumar, 2018: 385–386; Hwang et al., 2019: in press.

Material examined.

NIBRIV000071695, female (TL 27 mm), Gwangyang port, Gwangyang-si, Jeollanam-do, South Korea, 34°54'30.3"N, 127°41'02.1"E, coll. J.S Hong, 1 November 2006; MADBK 600204_001, male (TL 50 mm), Gwangyang port, Gwangyang-si, Jeollanam-do, South Korea, 34°54'30.3"N, 127°41'02.1"E, 1 August 2007.

Distribution. Western Indian Ocean to India, Philippines, Vietnam, Taiwan, Japan (Ah Yong et al., 2008), and now from Korea.

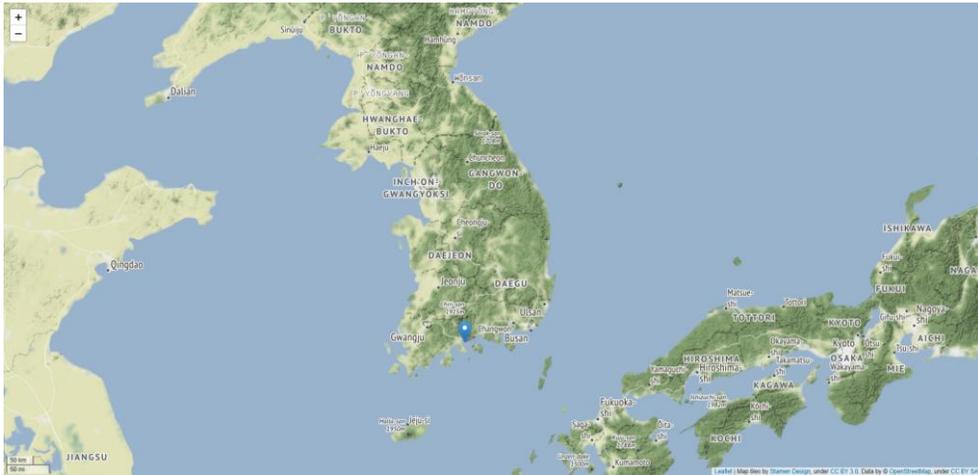


Fig. 151. Distribution of *Anchisquilla fasciata* (de Haan, 1844) in Korea.

Remarks. *Anchisquilla fasciata* is morphologically close to *A. fasciaticauda* Liu & Wang, 1998 and *A. chani* Ah Yong, 2001, but is distinguished from the two species by the presence of an accessory median carina and a blunt prelateral lobe on the telson (fig. 149A), respectively. *Anchisquilla subfasciata* (Tate, 1883) also closely resembles *A. fasciata* but differs in having more numerous carinae flanking the postanal carinae on the telson (four or more rather than one or two; Ah Yong, 2008).

Anchisquilla fasciata and *A. subfasciata* have clearly separated distributions. *Anchisquilla fasciata* is known from the Western Indian Ocean to the Philippines, Vietnam, Taiwan, Korea, and Japan (Ah Yong, 2001; Ah Yong et al., 2008, present study), whereas *A. subfasciata* is recorded only from Australia (Ah Yong, 2008). The Korean specimens morphologically agree with the material from other areas including Japan and Taiwan, although the postanal carina is interrupted (figs. 149B, C), rather than entire, and is almost connected with a pair of the most proximal carinae among the two pairs of carinae flanking the postanal carina.

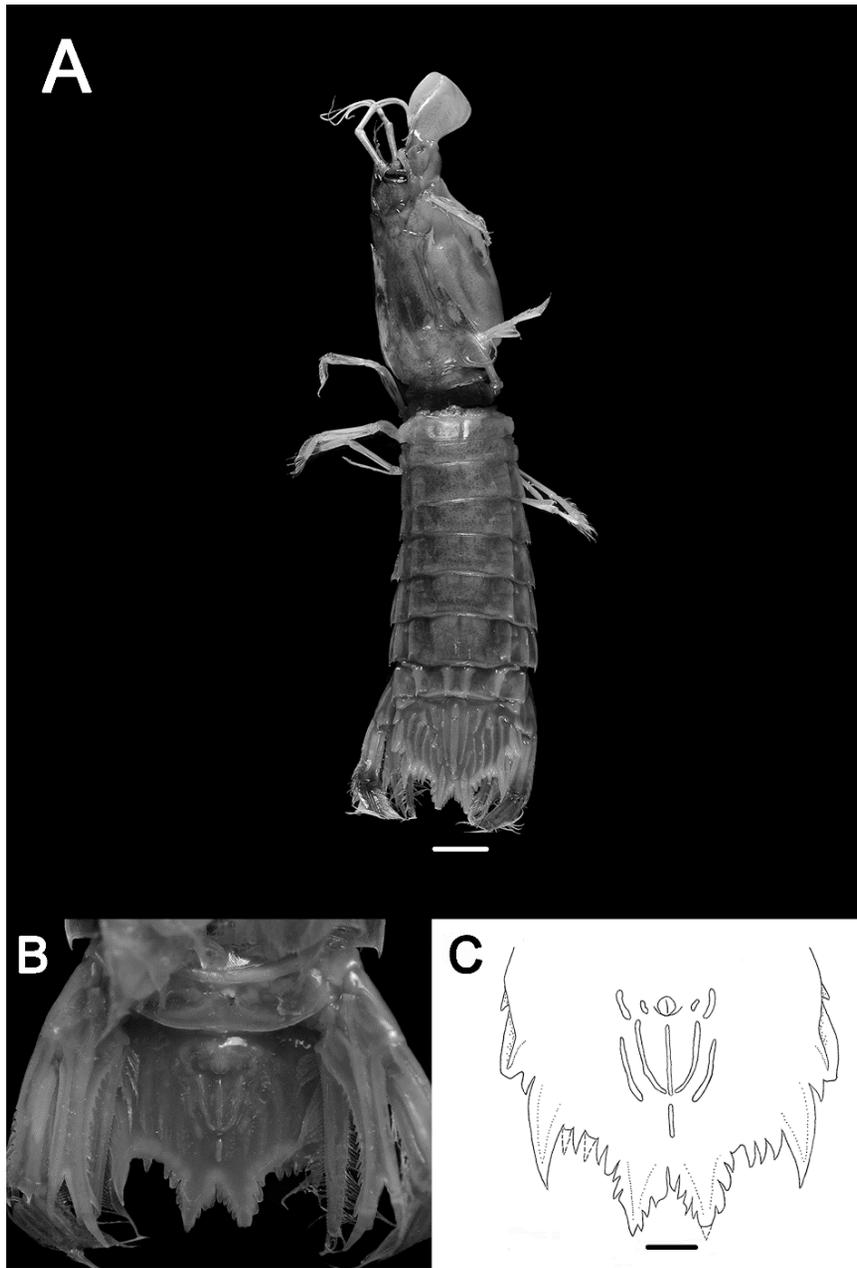


Fig. 152. *Anchisquilla fasciata*, female, TL 27 mm, MADBK 600204_001. A, dorsal view; B, C, telson, ventral view. Scale bars: A= 2.5 mm, C =1.0 mm.

*Genus *Cloridopsis* Manning, 1968 민물갯가재 속

*6. *Cloridopsis scorpio* (Latreille in Latreille et al., 1828) 민물갯가재
(Figs. 153–154)

Squilla scorpio Latreille in Latreille et al., 1828: 472; Lee & Wu, 1966: 48.

Cloridopsis scorpio: Manning, 1995: 24, 196; Ahyong et al., 1999: 42–46, fig. 4;
Ahyong et al., 2008: 94, fig. 70; Ahyong, 2012b: 248; Ahyong, 2016: 460, 464,
fig. 4D; Hwang et al., 2019: in press.

Material examined. MADBK 600203_001, female (TL 74.5 mm), Ho-ri, Palbong-
myeon, Seosan-si, Chungcheongnam-do, South Korea, 36°55'24.2"N,
126°19'26.3"E, commercial fishing trawlers, 20 October 2011.

Distribution. Western Indian Ocean to Malaysia, Indonesia, Vietnam, China, Japan
(Ahyong et al., 1999), and now from Korea.

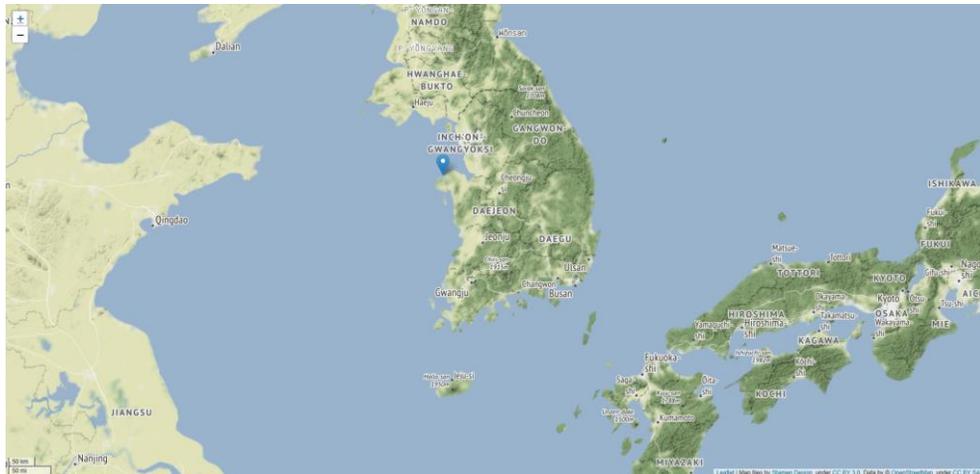


Fig. 153. Distribution of *Cloridopsis scorpio* (Latreille in Latreille et al., 1828) in Korea.

Remarks. Of the species of *Cloridopsis* Manning, 1968, *C. scorpio* is morphologically similar to *C. terrareginensis* (Stephenson, 1953), known from Australia and Papua New Guinea, in having five teeth on the dactylus of the raptorial claw and a dorsal black patch on the lateral process of thoracic somite 5 (Fig. 151A). *Cloridopsis scorpio*, however, can be easily distinguished from *C. terrareginensis* by the absence of a mandibular palp.

Intraspecific variation in *C. scorpio* has been reported in the length and apex of rostral plate and the lobe of the lateral process of thoracic somite 5 (Ahyong et al., 1999). Rostral plate length varies from short to elongate with a broadly rounded to relatively narrow apex, and the form of the lateral process of thoracic somite 5 varies from an anterolaterally directed angular lobe to anteriorly directed spine. In the Korean specimen, the rostral plate is elongated with a broadly rounded apex and the lateral process of thoracic somite 5 is anterolaterally directed (Fig. 151B, C) which is within the reported range of variation in *C. scorpio* (see Ahyong et al., 1999). The preserved coloration of the Korean specimen retains a similar color pattern to that reported by Lee & Wu (1966) and figured by Ahyong (2016: fig. 4D) including a row of dark spots flanking the median carina of the telson.

Species of *Cloridopsis* favour shallow inshore waters with substantial terrigenous influence (Ahyong, 2001). The Korean specimen was also collected from an estuarine region, which has terrigenous influence and relatively low salinity. Evidently, species of *Cloridopsis* tolerate or are even well adapted to relatively low salinities.

The present record extends the known geographical range of *C. scorpio* northeastward.

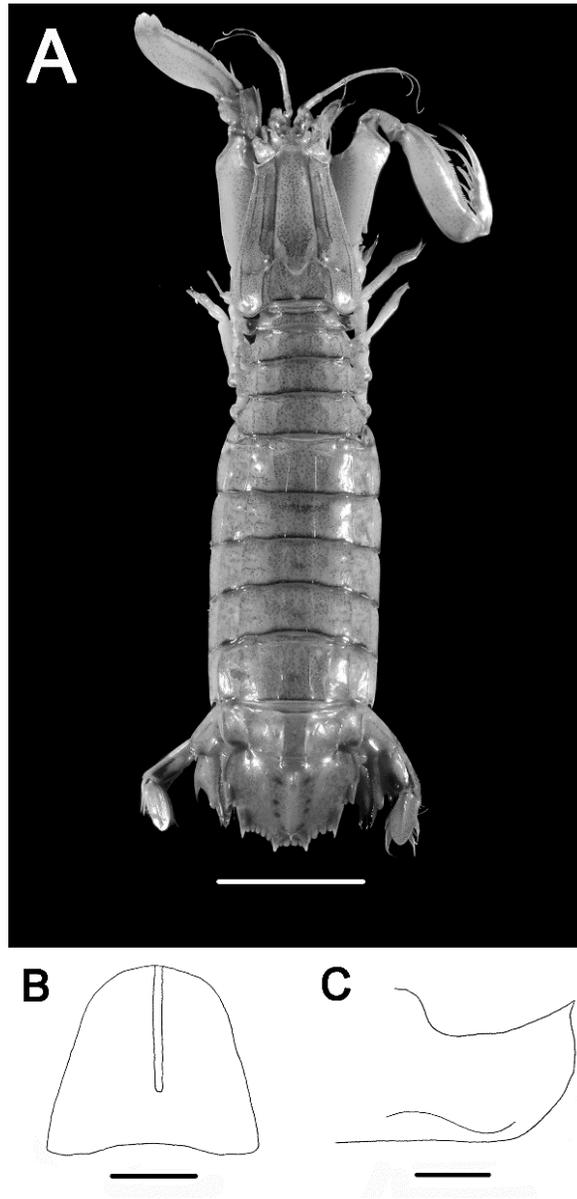


Fig. 154. *Cloridopsis scorpio*, female, TL 74.5 mm, MADBK600203_001. A, dorsal view; B, rostral plate; C, right lateral process of thoracic somite 5. Scale bars: A = 15 mm, B–C = 1.0 mm.

7. *Kempella mikado* (Kemp & Chopra, 1921) 큰점박이갯가재

(Fig. 155)

Squilla mikado Kemp and Chopra, 1921: 301, fig. 2; Manning, 1965: 257–259, 262, fig. a.

Squilla zanzibarica Chopra, 1939: 143–148, figs. 2, 4.

Kempina mikado: Manning, 1978: 40, fig. 23a–c; 1995: 24, 208; Moosa, 1986: 400–402, fig. 10; Ahyong, 2001: 267, fig. 130.

Kempella mikado: Low and Ahyong, 2010: 68; Kang et al., 2016: 235–237, fig. 2a–d; Hwang et al., 2019: in press.

Diagnosis. Raptorial claw dactylus with 6 teeth. Rostral plate with median carina. Carapace with anterolateral spines; median carina distinct, uninterrupted at base of anterior bifurcation, brache of anterior bifurcation distinct, opening anterior to dorsal pit; posterolateral margin angular. Thoracic somite 6 with bilobed lateral processes; anterior lobe broad, trapezoid, with acute apex; posterior lobe triangular. Telson as long as wide, bearing a couple of three pairs of primary teeth; with 14–15 spiniform submedian denticles and 6 intermediate denticles. Uropod with slender endopod; protopod crenulated on inner margin, terminating in 2 spines; proximal segment of exopod with 10–11 movable spines on outer margin.

Distribution. Australia (south to the vicinity of Sydney, New South Wales), Japan, Philippines, New Caledonia, Vietnam, Taiwan (Ahyong et al., 2009), and Korea (Kang et al., 2016).

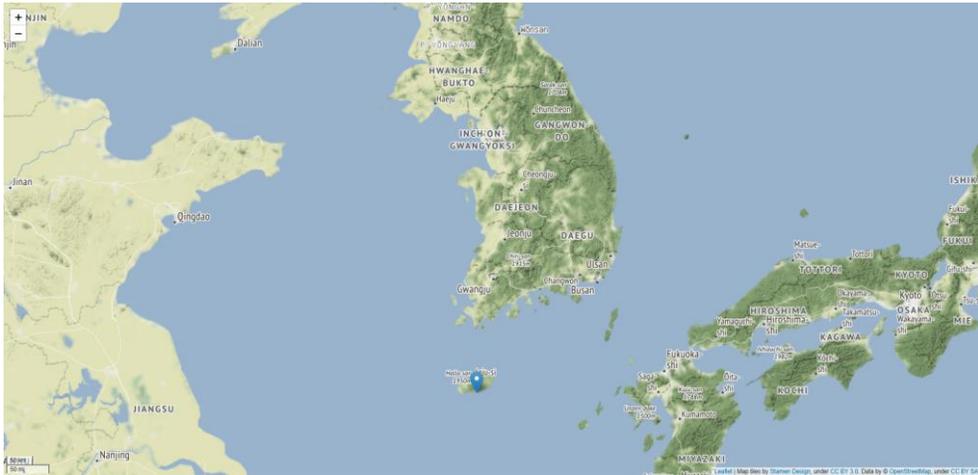


Fig. 155. Distribution of *Kempella mikado* (Kemp & Chopra, 1921) in Korea.

Remarks. Among *Kempella* species, *Kempella mikado* can be easily distinguished from its only congener, *K. stridulans* in having a median carina on the rostral plate and large, dark submedian patches on Abdominal somite 5.

Up to date, *K. mikado* (Kemp & Chopra, 1921) has been reported from Australia, Japan, Philippines, New Caledonia, Vietnam, Taiwan, and Korea (Ahyong et al., 2009; Kang et al., 2016). The record from Korean waters represents a northward range extension of *K. mikado*.

Genus *Oratosquilla* Manning, 1968 갯가재 속

8. *Oratosquilla oratoria* (De Haan, 1844) 갯가재 (Figs. 156–157)

Squilla oratoria de Haan, 1844 (atlas): pl. 51, fig. 2 [type locality: Japan]; 1849: 223; Komai, 1927: 315, 344, 346; Lee & Wu, 1966: 50–51, tab. 1.

Squilla affinis Berthold, 1845: 46; Fukuda, 1909: 169, pl. 4: fig 2; 1910, 150–151; Balss, 1910a: 9; 1910b: 3; Fukuda, 1913: 72.

Oratosquilla oratoria: Manning, 1971: 6–8, fig. 2; Hamano & Matsuura, 1987: 23; Hamano et al., 1994: 5; Hu & Tao, 1996: 207, plate 66: 4, 7; Liu & Wang, 1999: 579;

Moosa, 2000: 447; Ahyong, 2001: 283–285, fig. 138; Ahyong et al., 2008: 146–148: figs. 115–117; Hwang et al., 2019: in press.

Material examined.

Sorae Port, 69, Poguro-ro, Namdong-gu, Incheon (37°21'47.9"N 126°36'41.3"E): 10 females (85–108 mm), 12 males (128–150 mm), commercial fishing trawlers, 25 April 2018.

Suldo Port, Yeomsan-myeon, Yeonggwang-gun, Jeollanam-do (35°12'44.4"N 126°22'32.0"E): 11 females (110–130 mm), 12 males (15–79 mm), commercial fishing trawlers, 20 June 2009.

Gyodongnam 2-gil, Yeosu-si, Jeollanam-do (34°44'18.0"N 127°43'54.3"E): 18 females (100–125 mm), 5 males (77–95 mm), commercial fishing trawlers, 18 June 2010.

Diagnosis. Eye (Fig. 157) large, bilobed, broader than and set obliquely on stalk. Ocular scales separate. Antennular somite dorsal processes with blunt apices. Rostral plate (Fig. 157) broader than long; apex truncate to rounded. Carapace (Fig. 157) with anterolateral spine; median carina distinct, not interrupted at base of anterior bifurcation; branches of anterior bifurcation distinct, opening anterior to dorsal pit; posterolateral margin rounded. Mandibular palp 3-segmented. Maxillipeds 1–4 with epipod. Raptorial claw (Fig. 157) dactylus with 6 teeth, outer margin without basal notch; carpus dorsal carina bi- or tri-tuberculate; merus outer inferodistal angle with spine. Pleopod endopod in adult with posterior endite; hook process blunt distally. Thoracic somites 6–8 (Fig. 157) with distinct submedian and intermediate carinae. Thoracic somites 5–6 (Fig. 157) lateral processes distinctly bilobed. Thoracic somite 7 lateral process with anterior lobe triangular, apex sharp to blunt. Abdominal somites 1–6 (Fig. 157) with carinae. Telson (Fig. 157) submedian teeth with fixed apices; prelateral lobe present, as long as or longer than margin of lateral tooth; dorsolateral surface with curved rows of shallow pits; without longitudinal carinae; ventral surface with short postanal carina. Uropodal exopod proximal segment outer margin with 7–9 movable spines.

Distribution. Southeastern Australia, China, Hong Kong, Japan, Southern Russia, Vietnam, and Korea (Manning, 1995; Ah Yong, 2001; Hwang et al., 2019).

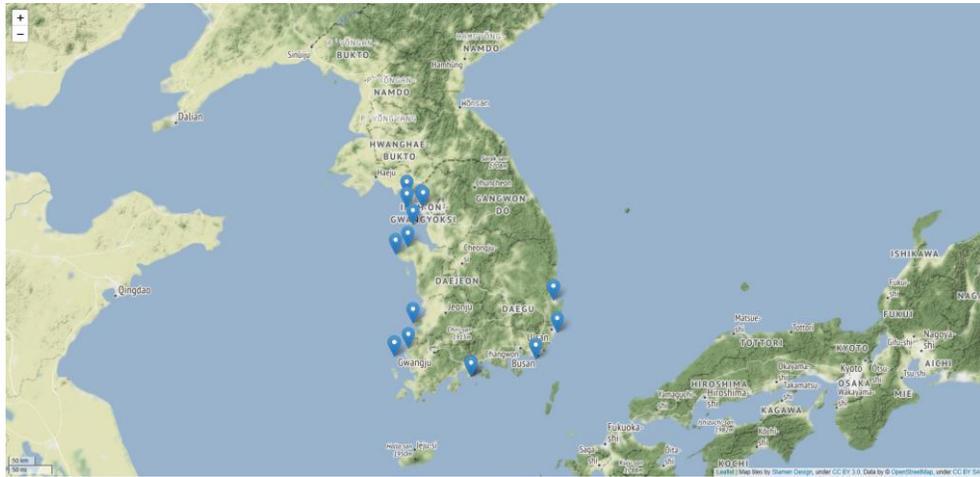


Fig. 156. Distribution of *Oratosquilla oratoria* (De Haan, 1844) in Korea.

Remarks. *Oratosquilla oratoria* is an abundant species in East Asia, including Korea. This species supports important fisheries especially in Japan, where it is popularly known as Shako. Around 5000 tons of *O. oratoria* are harvested annually in Japan. As a result of its fishery importance, *O. oratoria* is one of the best studied stomatopods in the world, and most aspects of its fishery biology have been studied in detail (Komai, 1920, 1924; Hamano, 1988, 1990; Hamano *et al.*, 1995; Hamano & Matsuura, 1984, 1986; Ah Yong, 2001; Hamano, 2005). In Japanese populations of *O. oratoria*, mating typically takes place between April and September (peaking in June) (Hamano *et al.*, 1987) and it has a similar cycle in case of Korea population. Estimated lifespan after settlement is 3.0–3.5 years (Hamano *et al.*, 1987). The alpheid shrimp, *Athanas squilliphilus* Hayashi, 2002, was discovered to live commensally with *O. oratoria* in Japan (Hayashi, 2002).

Among *Oratosquilla* species, this species differs from congeners by the combination of the armed outer inferodistal margin of the merus of the raptorial claw and unarmed submedian carinae on abdominal somite 4. The Korean specimens agree well with published accounts (Ah Yong, 2001; 2012) except those following

characteristics: In some Korean specimens, 1) the apex of the rostral plate is usually truncate but is occasionally rounded, 2) the anterior lobe of thoracic somite 7 varies from blunt to sharp, and 3) the median carina of carapace is sometimes faint. These features, like the case of *O. fabricii*, are found to be less developed before reaching 30 mm. The Korean specimens reflect these allometric changes; the apex of the rostral plate is rounded in the smallest specimen (TL 15 mm) and become truncate (TL 30 mm). The largest specimen examined (TL 150 mm) has the truncate apex of the rostral plate and it has a similar in case of the anterior lobe of thoracic somite 7. In the case of the faint median carina of the carapace, the sample should be observed in a relatively dry condition. Although if it is faint, it should be interpreted that it exists if it is observed in a dry condition.



Fig. 157. *Orotosquilla oratoria*, male. Whole animal, 150 mm, MADBK600103001. Scale bar = 10 mm.

9. *Squilloides leptosquilla* (Brooks, 1886) 사니갯가재 (Fig. 158)

Squilla leptosquilla Brooks, 1886: 30–34, Pl. 1, figs. 1, 2.

Squilloides leptosquilla: Takeda, 1982: 227, fig. 674; Miyake, 1982: 167, fig. 2; Moosa, 1986: 410–411, Pl. 1, figs. D, E; Hamano, 1995: 151, Pl. 80–5; Ahyong, 2001: 310–312, fig. 150; 2002: 382; Kang et al., 2016: 235–237, fig. 2a–d; Hwang et al., 2019: in press.

Diagnosis. Eye small; cornea strongly bilobed, set obliquely on stalk. Ocular scales separate. Antennular somite dorsal processes trianguloid; apices acute, directed anterolaterally. Mandibular palp absent. Maxillipeds 1–4 each with epipod. Carapace with anterolateral angles spine, with intermediate carinae and anterior portion of lateral carinae; median carina without anterior bifurcation. Raptorial claw dactylus with 4 teeth; carpus dorsal carina undivided; merus without outer inferodistal spine. Pleopod endopod in adult with posterior endite; hook process with distal point. Thoracic somite 5 lateral process single; ventral spine stout, directed anteroventrally. Thoracic somites 6–7 lateral process single, broadly rounded anteriorly, acute posteriorly. Telson trianguloid; submedian teeth with fixed apices; prelateral lobe absent; dorsolateral surface without supplementary carinae. Uropodal protopod with slender spine anterior to endopod articulation; inner margin of protopod crenulate; exopod proximal segment outer margin with 7–9 movable spines.

Distribution. Australia (Ahyong, 2001), Indo-Australian region from the Philippines (Brooks, 1886; Moosa, 1986), Indonesia (Hansen, 1926), the Andaman Islands (Kemp, 1913), and Korea.

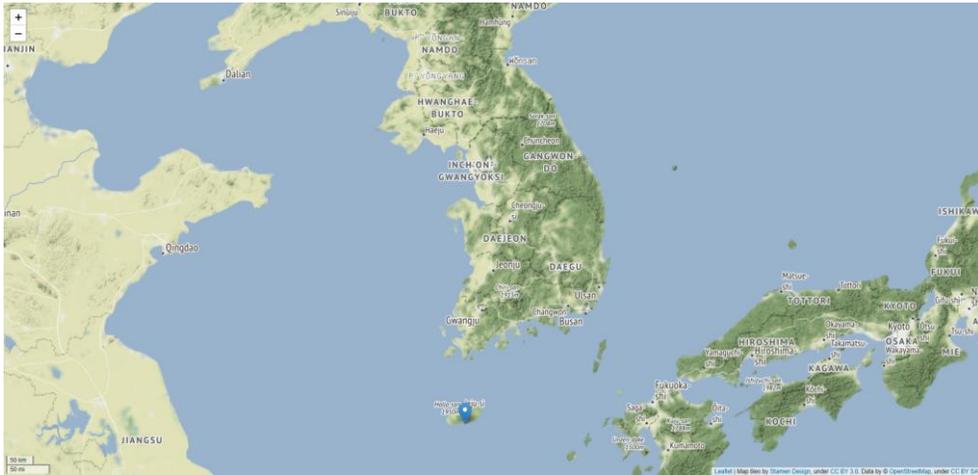


Fig. 158. Distribution of *Squilloides leptosquilla* (Brooks, 1886) in Korea.

Remarks. The *Squilloides* Manning, 1968 includes two species and the species belonging to the genus can be easily distinguished from other congeners by the combination of following characteristics: (1) the presence of median carina on carapace, (2) the absence of median carina on abdominal somite 1–5, (3) the presence of sharp lateral process of thoracic somite 6–7, (4) the presence of epipod of maxilliped 4, and (5) 4 teeth of raptorial claw. Among them, *S. leptosquilla* differs from *S. tenuispinis* by the presence of the intermediate carinae on the carapace (absence in *S. tenuispinis*).

Up to date, *S. leptosquilla* has been reported from Australia (Ahyong, 2001), Indo-Australian region from the Philippines (Brooks, 1886; Moosa, 1986), Indonesia (Hansen, 1926), the Andaman Islands (Kemp, 1913), and Korea (Kang et al., 2016). The record from Korean waters represents a northward range extension of *S. leptosquilla*.

Superfamily Gonodactyloidea Giesbrecht, 1910 가위갯가재 상과

Family Gonodactylidae Giesbrecht, 1910 흑돌기갯가재 과

Genus *Gonodactylaceus* Manning, 1995 흑돌기갯가재 속

10. *Gonodactylaceus falcatus* (Forskål, 1775) 흑돌기갯가재

(Figs. 159–161)

Cancer falcatus Forskål, 1775: 96.

Gonodactylus mutatus: Manning, 1978: 7, figs. 4, 5, 11.

Gonodactylaceus gravieri: Manning, 1995: 42, fig. 13.

Gonodactylaceus falcatus: Manning, 1995: 19; Ahyong, 2001: 35, fig. 17; Hwang et al., 2019: in press.

Material examined.

Korea, Jeju Island, Seogwipo-si, Seogwipo-dong, near Munseom Island, by SCUBA diving: 1♂, TL 32mm, 21 July 1993 (MADBK600103001), no further data; 1♂, TL 61.5mm, 11 March 2009 (NIBRIV0000316631), coll., T Park, HJ Kil.

Diagnosis. Eye (Fig. 160) subcylindrical; cornea narrower than stalk dorsally. Rostral plate (Fig. 160) not sharply trispinous, with blunt, rounded, anterolateral corner. Abdominal somites 1–5 (Fig. 160) without fine transverse grooves. Abdominal somite 6 with short median carinule. Telson (Fig. 160) as broad as long, bearing a couple of three pairs of primary teeth (submedian, intermediate, and lateral), with 10–11 submedian denticles and 2 spiniform intermediate denticles. Dorsal surface (Fig. 160) bearing median carina and four pairs of longitudinal carinae (submedian interrupted, accessory median, intermediate and marginal uninterrupted). Median and accessory carinae bearing each posterior spine.

Submedian, intermediate, and marginal carinae extending to posterior margin of each primary tooth. Knob (Fig. 160) present and bilobed. Ventral surface bearing low carina on each submedian tooth and postanal carina. Uropod (Fig. 160) with exopod having 11–12 movable spines on proximal segment. Protopod bearing one lobe between terminal spines; outer terminal one longer than inner. Endopod bearing a row of marginal setae on outer margin.

Distribution. Japan, Indonesia, Australia, New Caledonia, French Polynesia, Hawaii, and Korea (Jeju Island).

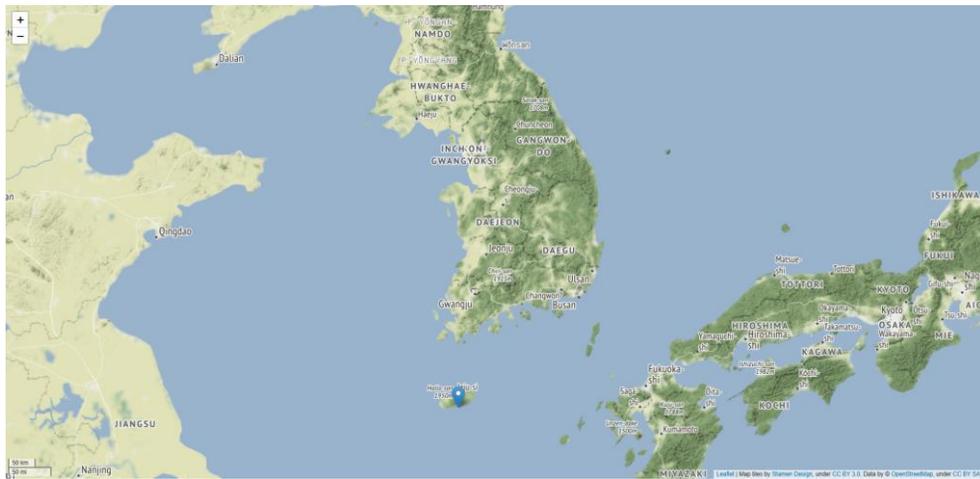


Fig. 159. Distribution of *Gonodactylaceus falcatus* (Forskål, 1775) in Korea

Remarks. Among the known species of *Gonodactylaceus*, *G. falcatus* is morphologically similar to *G. glabrous* (Brooks, 1886) in having following characteristics: 1) the absence of transverse grooves from the first to the fifth abdominal somites, 2) the presence of a lobe between terminal spines of uropodal protopod, and 3) the presence of bilobed knob on the telson. However, *G. falcatus* can be easily distinguished from its congeners by the shape of anterolateral corner of the rostral plate. The shape is rounded and blunt in *G. falcatus*, whereas it is distinctively angular in *G. glabrous*. The Korean specimens generally agree well with those characteristics. Additionally, the presence of the median carinule on the sixth abdominal somite is variable in *G. falcatus* (Ahyong, 2001). Out of the

specimens examined by Ahyong, the proportion of specimens that bear the median carinule was 55%. The median carinule is present in 52 out of 85 males and 60 out of 118 females. Korean two male specimens have a faint median carinule.

Up to date, *G. falcatus* (Forskål, 1775) has been reported from Japan, Indonesia, Australia, New Caledonia, French Polynesia, and Hawaii (Ahyong, 2001). Through the present study, its geographical distribution has been expanded northward.



Fig. 160. *Gonodactylaceus falcatus*, male. Whole animal, 32 mm, MADBK600103001.

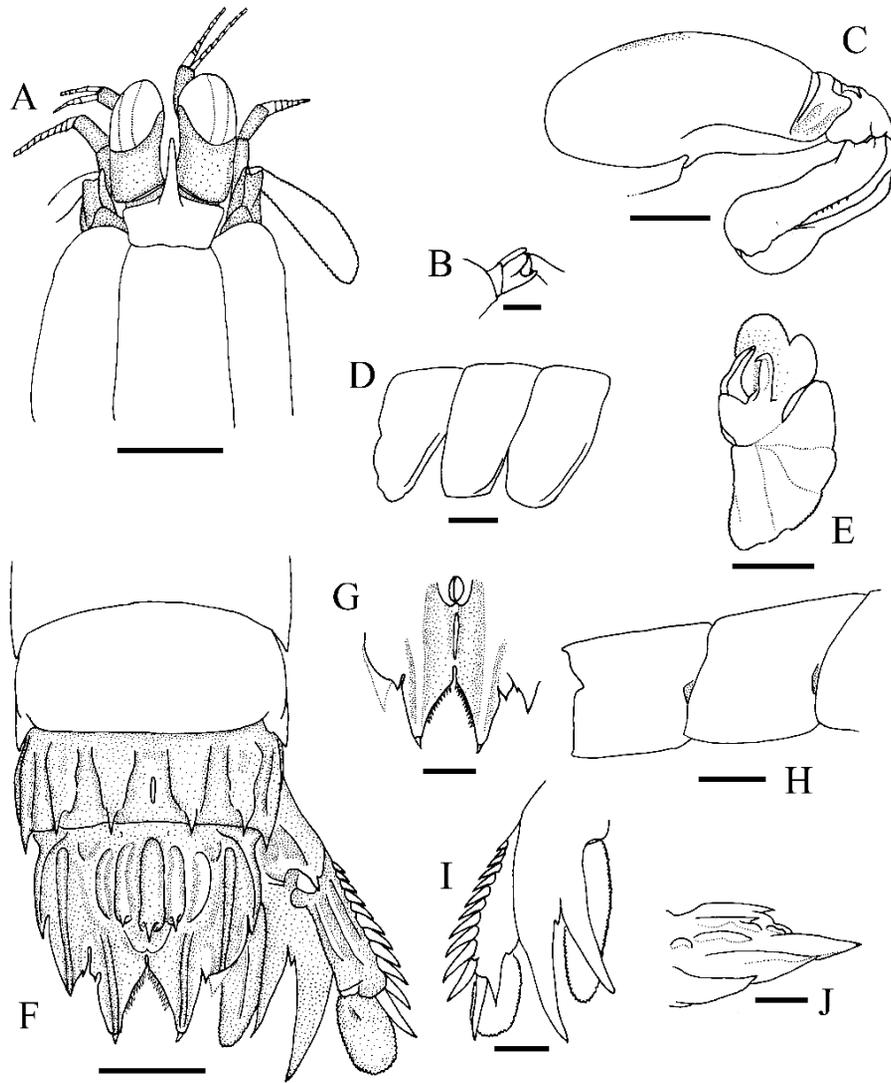


Fig. 161. *Gonodactylaceus falcatus*, male. A, Anterior cephalon; B, Antennal protopod; C, Raptorial claw; D, Lateral margins of sixth to eighth thoracic somites; E, Endopod of first pleopod; F, Fourth to sixth abdominal somites, telson, and uropod; G, Telson, ventral view; H, Fourth to fifth abdominal somites, lateral view; I, Uropod, right ventral view; J, Telson, left lateral view. Scale bars: A–D, F–I=10 mm, E=20 mm.

Family Takuidae Manning, 1995 가위갯가재 과

Genus *Taku* Manning, 1995 가위갯가재 속

11. *Taku spinosocarinatus* (Fukuda, 1909) 가위갯가재 (Figs. 162–163)

Gonodactylus spinosocarinatus Fukuda, 1909: 54–56, pl. 5, figs 2, 2a [type locality: Nakamoto, Kuroshima Island, Taketomi Town, Okinawa Prefecture, by neotype designation, Ah Yong, 2001]; Fukuda, 1910: 143–145, pl. 4 figs 2, 2a; Serène, 1952: 14–16, figs. 28–32; Serène, 1954: 6, 7, 10, 11, fig. 13–10.

Gonodactylus spinosocarinatus: Kemp, 1913: 173–174; Komai, 1927: 340–341.

Gonodactylus strigatus Hansen, 1926: 31, pl. 2, fig. 2 [type locality: near Saleyer, Sulawesi, Indonesia]; Serène, 1949: 225–231.

Mesacturus spinosocarinatus: Manning, 1969: 151, 153; Hamano, 1987: 209; Hamano, 1988: 28, fig. 13c–e.

Mesacturoides spinosocarinatus: Manning, 1978: 3.

Taku spinosocarinatus: Manning, 1995: 10, 11, 21, 120–121, figs. 9j, 65, 66, pl. 23; Moosa, 2000: 427, tab. 1; Ah Yong & Davie, 2002: 86 [unnumbered fig.]; Schram & Müller, 2004: 85 [part]; Hamano, 2005: 13, 38–39, fig. 2–9e–g; Āuriš, 2007: 126; Yeh & Hsueh, 2010: 370–372, fig. 1; Ah Yong, 2012b: 247; Ah Yong et al., 2018b: 451–459, fig. 3; Hwang et al., 2019: in press.

Material examined. (see 23–25 pages in this dissertation).

Diagnosis. Eye (Fig. 163) elongate; cornea subglobular. Ocular scales (Fig. 163) separate, rounded to subtruncate. Rostral plate (Fig. 163) with anterior margins of basal portion straight to faintly concave, almost transverse. Carapace (Fig. 163) anterolateral angles broadly rounded, extending anteriorly beyond base of rostral plate. Mandibular palp 2-segmented. Maxilliped 1–5 with epipod. Telson (Fig. 163) wider than long, without accessory median carinae; submedian primary teeth well

formed, widely separated, with movable spines; submedian denticles present; intermediate and lateral teeth indistinct, indicated by shallow notch in telson margin; dorsal surface with broad, low median carina flanked by 4 or 5 low, curved, appressed longitudinal carinae (median, accessory medians present or absent, submedian, intermediate, lateral, marginal), occupying almost entire dorsal surface except surface of submedian teeth; median carina more than twice width of submedian, intermediate and lateral carinae; marginal carina distinctly narrower than lateral carina. Uropodal endopod (Fig. 163) laminar, held horizontally, margins with single row of setae; lacking dorsal or ventral setae. Uropodal protopod proximal dorsal surface with 2–4 (usually 3) small spines.

Distribution. Japan, Taiwan, Vietnam, northern Indonesia, and Korea (Ahyong et al., 2018).

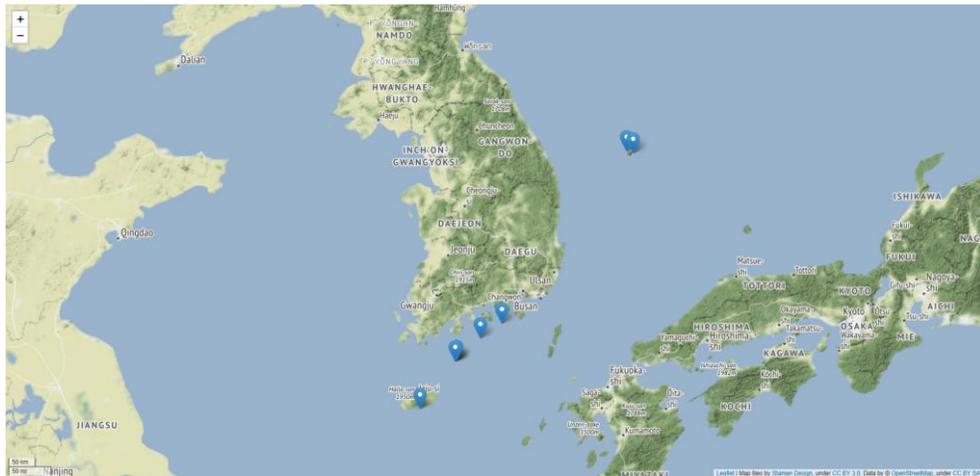


Fig. 162. Distribution of *Taku spinosocarinatus* (Fukuda, 1909) in Korea.

Habitat. Coral reef from preformed cavities in rubble and reef rock including mollusc tubes; intertidal to 35 m (Ahyong et al., 2018).

Remarks. *Taku spinosocarinatus* can be easily distinguished from its only congener, *T. pruvotae* by the absence of the accessory median carinae on the telson, which are

well-developed by about TL 15 mm in the latter species; the deep, spinule-lined grooves demarcating the accessory medians, evident in *T. pruvotae*, are absent in *T. spinosocarinatus*.

Allometric variation in *T. spinosocarinatus* is largely evident in the increasing degree of dorsal telson spinulation and general reduction in the number of minute setae on the inner margin of the uropodal endopod: usually 3 or 4 in the smallest specimens, usually 1 or 2 in the largest specimens, although in some specimens, the pattern may be reversed. The telson carinae of *T. spinosocarinatus* are unarmed at TL 10 mm, but by TL 12 mm the margins of the median and inner margins of the submedian carinae have spinules in addition to a few scattered spinules on the intermediate carinae. By about TL 20 mm, the posterior half of the lateral margins of the median carina are slightly excavated and multi-spinulose.

Up to date, *T. spinosocarinatus* has been reported from Japan, Taiwan, Vietnam, northern Indonesia, and Korea. The record from Korean waters represents a northward range extension of this species.



Fig. 163. *Taku spinosocarinatus* (Fukuda, 1909), female, TL 28 mm, MADBK 600101_015.

Family Protosquillidae Manning, 1980 가시꼬리갯가재 과

Genus *Chorisquilla* Manning, 1969 가시꼬리갯가재 속

12. *Chorisquilla orientalis* Hwang, Ah Yong & Kim, 2018 가시꼬리갯가재

(Figs. 164–166)

Protosquilla brooksii: Fukuda, 1910: 140, pl. IV, figs. 1, 1a.

Gonodactylus spinosissimus: Komai, 1927: 342, 343, tab. 1.

Chorisquilla spinosissima: Kim & Rho, 1972: 97.

Gonodactylus chiragra: Cho *et al.*, 2006: 78 [unnumbered fig.].

Chorisquilla sp. : Hamano, 2005: 32, fig. 2–7e. Ah Yong, 2012b: 247; Hwang *et al.*, 2019: in press.

Material examined. (see 47–48 pages in this dissertation).

Diagnosis. Cornea (Figs. 165, 166A) broadened, not bilobed, dorsoventrally flattened. Ocular scales (Figs. 165, 166A) separate, produced laterally. Raptorial claw (Fig. 166B) stout; propodus occlusal margin minutely pectinated, with proximal movable spine. Dactylus outer margin with shallow basal notch. Abdominal somite 4 (Figs. 165, 166G) smooth medially, with shallow lateral corrugation above low marginal carina. Abdominal somite 5 (Figs. 165, 166G) smooth on anterior dorsal half, with deep, irregular, elongated longitudinal pits and grooves on posterior half; lateral surface corrugated, with 2 or 3 longitudinal ridges. Abdominal somite 6 (Figs. 165, 166G) with paired submedian, intermediate, and lateral bosses, each covered with short spinules, lateral boss with posterior spine; anterior margin adjacent to arthrodistal membrane and anterior sclerotized part of arthrodistal membrane between somites 5 and 6 each bearing row of minute spinules. Telson (Figs. 165, 166G) broader than long; submedian primary teeth spiniform, with curved, movable apices, articulating submarginally; 8–12 spiniform submedian

denticles; 2 spiniform intermediate denticles; intermediate teeth triangular, apex blunt or with minute spinule; lateral teeth short, slender, directed posterolaterally, lateral denticle present or absent. Dorsal surface of bosses and marginal carina covered with minute spinules. Median boss inverted triangular. Submedian bosses ovate to pyriform. Small round boss present anterior to each submedian boss. Lateral margin with 8–14 short spines, posteriormost spine set-off from preceding spines by short convex margin, corresponding to lateral primary tooth. Ventral surface (Fig. 166H) smooth, without postanal carina. Uropodal protopod (Figs. 165, 166G) terminating in 2 flattened spines, outer longer; with small lobe between terminal spines; dorsal surface with spine above exopod articulation and a row of 1–3 (usually 2) slender spines proximally, adjacent to articulation with abdominal somite 6. Exopod proximal article with 6–12 (usually 10 or 11) movable spines and fixed distal spine.

Habitat. In Korea, from preformed cavities or holes drilled by mollusks in rock walls; depth 10–25 m. Habitat in Japan not known.

Distribution. Korea and central Japan (Tateyama, Chiba Prefecture, to Misaki, Osaka Prefecture).

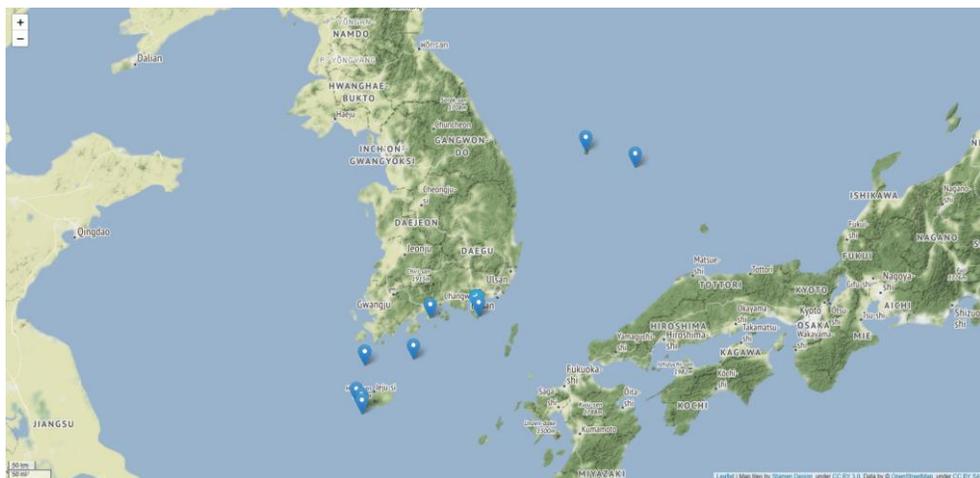


Fig. 164. Distribution of *Chorisquilla orientalis* Hwang, Ahyong & Kim, 2018 in Korea.

Remarks. Previous records of *C. brooksii* from Japan (Fukuda, 1910), reidentified as *C. spinosissima* by Komai (1927), are clearly referable to *C. orientalis* as shown by Fukuda (1910: pl. IV, fig. 1, 1a). Only one species of *Chorisquilla*, *C. spinosissima*, has been reported from Korea (Kim & Rho, 1972). This single report of *C. spinosissima* is not accompanied by figures or descriptive remarks, and the specimen on which the record is based is no longer extant. Extensive surveys in Korean waters over the past three decades, however, have only ever revealed a single species of *Chorisquilla*, that named here as *C. orientalis*. Given the broad morphological similarities between *C. orientalis* and *C. spinosissima*, especially in juveniles with lesser developed telson spination, and Komai's (1927) misidentification of *C. spinosissima* from Japan, we regard the record of Kim & Rho (1972) to be almost certainly based on *C. orientalis*. Similarly, the recent record of *Gonodactylus chiragra* from Korea figured by Cho et al. (2006) is clearly based on *C. orientalis*.



Fig. 165. *Chorisquilla orientalis*. A, male holotype, TL 36 mm, NIBRIV0000160376. B, female paratype, TL 13 mm, MADBK 600301_003.

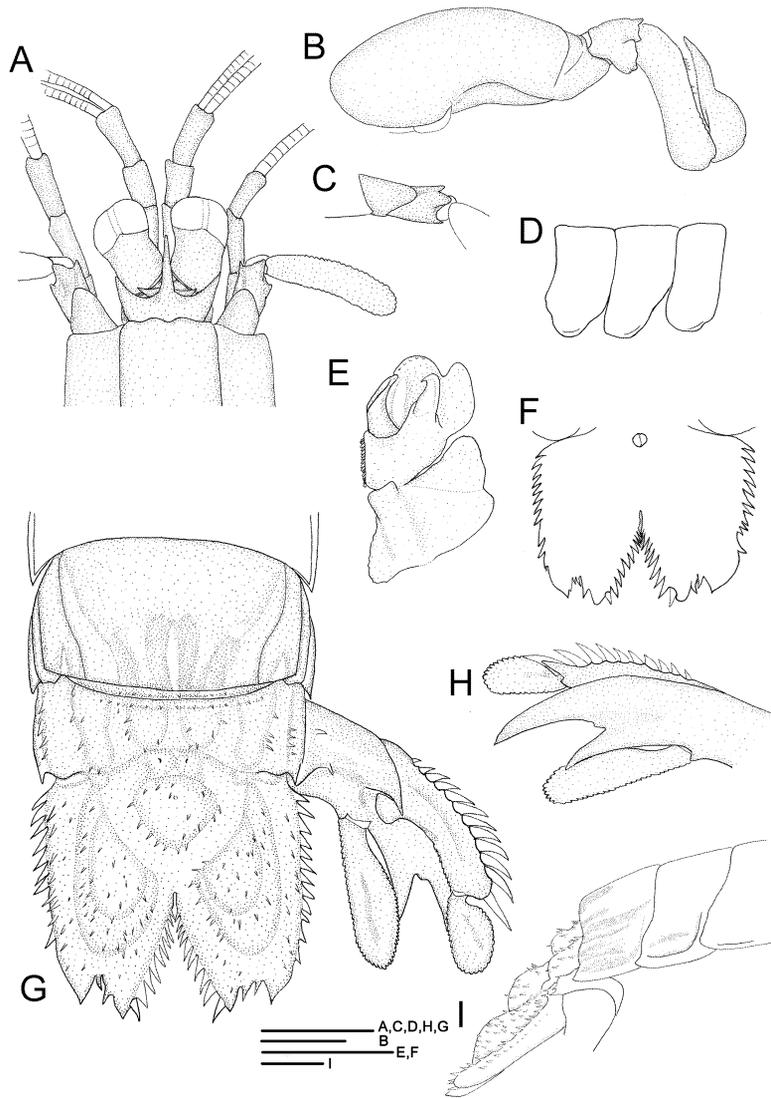


Fig. 166. *Chorisquilla orientalis*, male holotype, TL 36 mm, South Korea, NIBRIV0000160376. A, anterior cephalothorax; B, raptorial claw; C, antennal protopod; D, thoracic somites 6–8, right lateral view; E, right male pleopod 1 endopod; F, telson, ventral view; G, abdominal somites 4–6, telson, and uropod; H, right uropod, ventral; I, abdominal somites 3–5 and telson, right lateral view. Scale bars: A–I = 1.0 mm.

Family Odontodactylidae Manning, 1980

Genus *Odontodactylus* Bigelow, 1893

13. *Odontodactylus japonicus* (de Haan, 1844) (Fig. 167)

Gonodactylus japonicus de Haan, 1844, pl. 51: fig. 7 [type locality: Japan].

Odontodactylus japonicus: Manning, 1965: 260; 1967: 7–10, fig. 2; Yamaguchi & Baba, 1993: 176–178, fig. 9; Manning, 1995: 20, 82; Ahyong & Norrington, 1997: 103; Ahyong, 2001: 81–83, fig. 39; Hwang et al., 2019: in press.

Diagnosis. Eye subglobular. Ocular scales oblique, appressed medially. Antennal scale with anterior margin smooth, without setae. Rostral plate triangular, but appearing trapezoid in dorsal view; lateral margin sinuous; apex deflexed. Raptorial claw dactylus with 8 teeth on inner margin; proximal margin strongly inflated; without basal notch. Abdominal somites 1–5 posterolateral angles rounded; Abdominal somite 5 without posterolateral spine. Telson mid-dorsal surface with distinct median carina and 4 longitudinal carinae either side of midline (double accessory median, anterior submedian, carina of inner intermediate denticle) in addition to carinae of primary teeth. Uropodal exopod proximal longer than distal segment; outer margin with 10–12 movable spines, distalmost evenly tapering to spatulate with blunt apex; distal segment longer than proximal segment length.

Distribution. Australia, Japan, and Korea (Manning, 1967; Ahyong, 2001; Hwang et al., 2019).

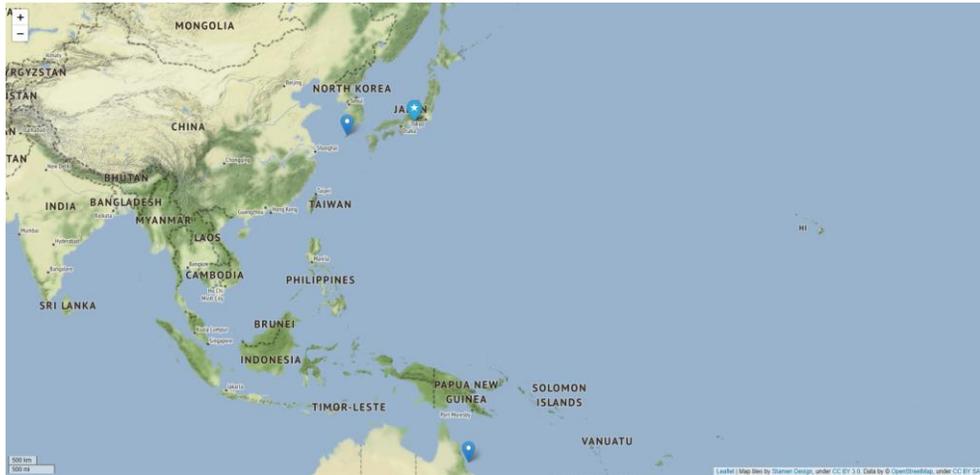


Fig. 167. Distribution of *Odontodactylus japonicus* (de Haan, 1844). Legend: star = type locality; circle = distribution in worldwide.

Remarks. Among *Odontodactylus* species, *O. japonicus* is morphologically similar to *O. scyllarus* and *O. hawaiiensis* in having the medially appressed ocular scales and double accessory median carinae either side of median carina on the dorsal surface of telson. *O. japonicus*, however, can be easily distinguished from two species by the presence of longitudinal carina extending anteriorly from inner intermediate denticles and by the absence of posterolateral spine on abdominal somite 5.

Odontodactylus japonicus from Korea is known only from the record of Komai (1927). This single report of *O. japonicus* is not accompanied by figures or descriptive remarks, and the specimen on which the record is based is no longer extant. So further exploration is required.

Superfamily Parasquilloidea Manning, 1995 돌기갯가재 상과

Family Parasquillidae Manning, 1995 돌기갯가재 과

Genus *Faughnia* Serène, 1962 돌기갯가재 속

14. *Faughnia formosae* Manning & Chan, 1997 다섯돌기갯가재

(Figs. 168–170)

Pseudosquilla empusa: Komai, 1927: 325, 346, fig. 1; Dong et al., 1983: 90, fig. 3 [not *Squilla empusa* de Haan, 1844].

Faughnia formosae Manning and Chan, 1997: 546–551, figs. 1–4; Moosa, 2000: 422; Ah Yong & Naiyanetr, 2002: 289; Hwang et al., 2013: 245–248, figs. 1–2; Hwang et al., 2019: in press.

Material examined. Korea: 1 male, Jeju Island, Seogwipo-si, Daejeong-eup, Hamori, Moseulpo port, 10 Sep 2006, by fishing net.

Description. Body (Fig. 169) approximately cylindrical; dorsal surface overall pitted and smooth; articulation compressed.

Eye (Fig. 170A) not reaching to end of first segment of antennular peduncle. Cornea asymmetrically bilobed, outer margin longer than inner.

Carapace (Fig. 169, 170A) with indistinct reflected marginal carina; anterolateral angles rounded, not produced anteriorly.

Rostral plate (Fig. 169, 170A) without long apical spine, width 2.6 times longer than median length. Raptorial claw (Fig. 169, 170B) stout; ischio-meral articulation terminal; dorsal margin of carpus with 2 blunt teeth; occlusal margin of propodus with 3 movable spine and a series of dense pectinations; dactylus slender, bearing 3 teeth on inner margin.

Sternal keel of eighth thoracic somite (Fig. 170C) rounded.

Lateral processes of sixth to eighth thoracic somites (Fig. 169, 170D) broadly rounded, with low ridge; that of seventh slightly wider than sixth.

Endopod of first male pleopod (Fig. 170E) bearing posterior endite.

Telson (Fig. 170F) as long as broad, with 3 pairs of primary teeth (submedian, intermediate, lateral); with 2 spiniform intermediate denticles, 1 spiniform lateral denticle. Dorsal surface with median carina and 5 pairs of longitudinal carinae (accessory median, anterior submedian, and lateral slightly interrupted, anterior intermediate and marginal uninterrupted) in addition to carinae of all primary teeth extending onto surface of telson. Ventral surface of telson smooth, without postanal carina. Posterolateral angles of fourth to sixth abdominal somites (Fig. 169G) bearing low lateral, marginal carinae, except for submedian; sixth somite with spinule produced ventrolaterally.

Uropod (Fig. 170H) with exopod having 8 movable spines; protopod bearing well-developed spinules, outermost largest, flanked proximally by 4 smaller spinules as well as some denticulation on inner margin.

Distribution. Japan, Taiwan, Philippines, Thailand, and Korea (Jeju Island).

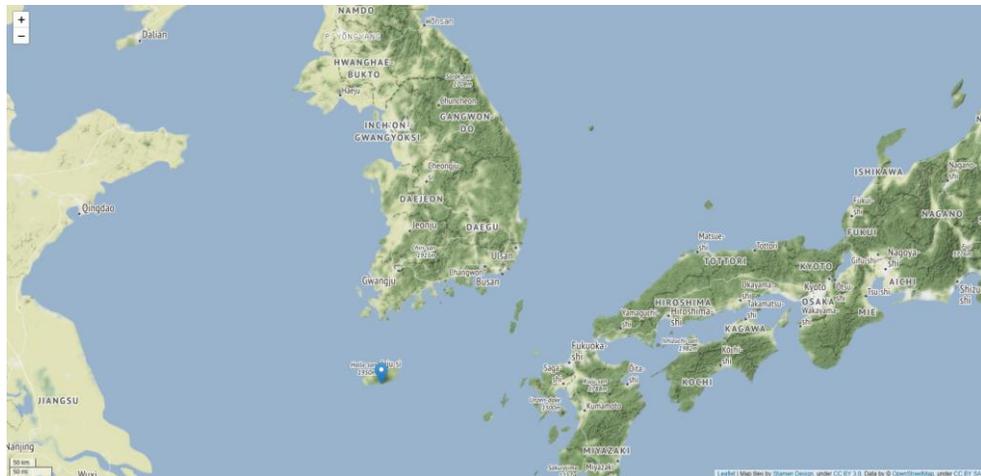


Fig. 168. Distribution of *Faughnia formosae* Manning & Chan, 1997 in Korea.

Remarks. The present species, *Faughnia formosae* is the first record from Korean waters. According to the original description of Manning and Chan (1997), *F. formosae* is easily distinguished from allied species by the following characteristics: 1) five pairs of carinae on the telson, and 2) well developed spinules on the inner margin of the uropodal protopod. The present specimen agrees well with the original description, except that the width of the rostral plate was 2.6 times as long as the median length in the present specimen, whereas width was only ‘more than twice median length’ in the original description.



Fig. 169. *Faughnia formosae* Manning and Chan, 1997, male.
Whole animal, 132 mm.

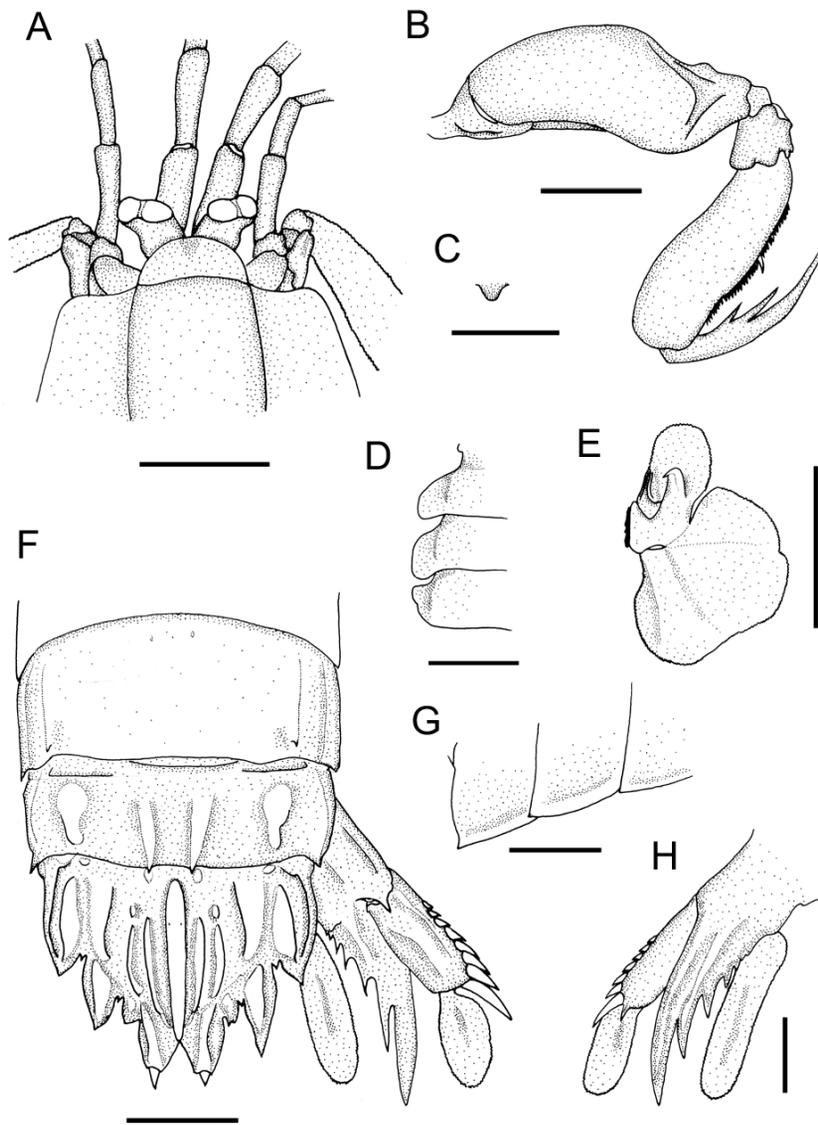


Fig. 170. *Faughnia formosae* Manning and Chan, 1997, male. A, Anterior cephalon; B, Raptorial claw; C, Sternal keel of eighth thoracic somite, right lateral; D, Lateral processes of sixth to eighth thoracic somites; E, Endopod of first male pleopod; F, Fifth to sixth abdominal somites, telson, and uropod; G, Posterolateral angles of fourth to sixth abdominal somites; H, Uropod, right ventral. Scale bars: A, B, D–H=10 mm, C=20 mm.

DISCUSSION

Prior to the present study, eight stomatopod species were recorded from Korea but the results of the present study increase the stomatopod fauna to 14 species in seven families and four superfamilies. The known Korean stomatopod fauna is significantly smaller than that of Japan (68 species in 12 families and six superfamilies; Ahyong, 2012b) and China (104 species in 12 families and six superfamilies; Wang & Liu, 2008). Not surprisingly, given the immediate geographic proximity of the two regions, all known species of Korean stomatopods also occur in Japan. Thirteen of 14 Korean species also occur in Chinese waters, with the exception of the protosquillid, *Chorisquilla orientalis*, which is currently known only from Korea and Japan. Most species of Korean stomatopods are known from only single or a few specimens, and *Odontodactylus japonicus* in Korea is known only from the record of Komai (1927); further exploration is required. Although the Korean stomatopod fauna is expected to remain smaller than those of Japan and China, both of which occupy much larger geographic areas that extend into tropical latitudes, additional species of Stomatopoda will probably be discovered in Korea when benthic habitats are sampled more intensively. To assist identification, a key to the species of Korean Stomatopoda is given below. Among Korean stomatopod species, if additional taxonomic studies about corresponding species are required, detailed descriptions of the Korean specimen of corresponding species were made for providing information on Korean species.

CONCLUSION

Through this study, systematic studies on the major groups of stomatopods were carried out on 68 species of 14 genera under 5 families based on examination of identification key characters requiring taxonomic revision and molecular taxonomic study using mitochondrial COI gene sequences. As a result, the key for the respective genus was updated, and some aspects of morphological terminology which had ambiguous definition and the characteristics to which this terminology will be applied were clarified. And it revealed that *T. pruvotae*, *Chorisquilla orientalis*, *Gonodactylaceus mutatus*, *Gonodactylaceus insularis*, and *G. siamensis* were respectively valid species and geographically separated.

As the first group using the telson tooth characteristics as the main identification key, 17 species of 2 genera under 2 families were covered. It turned out that genus *Taku* which was considered monotypic, contains two geographically discrete species (*T. spinosocarinatus* sensu stricto from Korea to Indonesia and *T. pruvotae* ranging from New Caledonia to Australia). A species previously known as *Chorisquilla spinosissima* in Korea was identified as new species, *Chorisquilla orientalis*. Also, *C. mehtae*, which had not been adequately illustrated, was redescribed.

As the second group using the rostral plate characteristics as the main identification key, 14 species of 2 genera belonging to the family Gonodactylidae were covered. *Gonodactylaceus falcatus* from throughout its range using morphological and molecular data was newly identified as four geographically discrete species (*G. falcatus* ranging from the Red Sea and the Persian Gulf, *G. siamensis* ranging from Thailand to Indonesia and Hawaii, *G. mutatus* ranging from the Maldiv Islands to Sri Lanka, and *G. insularis* ranging from the oceanic margins of the western Pacific to the central western). Through the present study, it is proposed morphological characters that can be used as new identification keys.

As the third group using the carina characteristics as the main identification key, 36 species of 10 genera under 3 families were covered. As a result, the keys considering allometric variations for all species of 7 genera (*Oratosquilla*,

Levisquilla, *Anchisquilla*, *Cloridopsis*, *Miyakella*, *Squilloides*, and *Kempella*) belonging to Squillids were updated. Additional taxonomic key characters were proposed to improve the accuracy of morphological classification for *Faughnia* species belonging to Parasquillids, *Acaenosquilla* belonging to Tetrasquillids and *Acanthosquilla* belonging to Nannosquillids.

Lastly, the systematic study of Korean stomatopod fauna was conducted. In the early stages of this study, only 2 species have previously been recorded in Korean waters: *Oratosquilla oratoria* (De Haan, 1844), *Taku spinosocarinatus* (Fukuda, 1909). As a result, 14 species of 13 genera belonging to the 7 families of 4 superfamilies were identified. This present study resulted in discovery 6 first records of species (*Levisquilla inermis* (Manning, 1965), *Levisquilla jurichi* (Makarov, 1979a), *Anchisquilla fasciata* (de Haan, 1844), *Cloridopsis scorpio* (Latreille, 1828), *Acanthosquilla multifasciata* (Wood-Mason, 1895), and *Acaenosquilla latifrons* (de Haan, 1844)). The superfamily Lysiosquilloidea is also reported for the first time from Korean waters. Diagnosis, distribution in Korea, and comparisons between Taiwan and Japan species of each species were made. Also, a checklist and a key for the Korean stomatopods were updated.

REFERENCE

- Ahyong, S.T., 1997. A phylogenetic analysis of the Stomatopoda (Crustacea: Malacostraca). *Journal of Crustacean Biology*, 17: 695–715.
- Ahyong, S.T., 2001. Revision of the Australian stomatopod Crustacea. *Records of the Australian Museum, Supplement* 26: 1–326.
- Ahyong, S.T., 2002. Stomatopoda (Crustacea) from the Marquesas Islands: results of MUSORSTOM 9. *Zoosystema* 24(2): 347–372.
- Ahyong, S.T., 2004. New species and new records of stomatopod Crustacea from the Philippines. *Zootaxa* 793: 1–28.
- Ahyong, S.T., 2005. Phylogenetic analysis of the Squilloidea (Crustacea: Stomatopoda). *Invertebrate Systematics* 19(3): 189–208.
- Ahyong, S.T., 2007. Shallow water Stomatopoda of New Caledonia (0–100 m). In: *Compendium of Marine Species from New Caledonia* (C.E. Payri & B. Richer de Forges, eds.). pp. 333–335. *Documents Scientifiques et Techniques*. IRD Nouméa, Nouméa, New Caledonia.
- Ahyong, S.T., 2008. Stomatopod Crustacea from the Dampier Archipelago, Western Australia. *Records of the Western Australian Museum, Supplement*, 73: 41–55.
- Ahyong, S.T., 2010. A new genus and two new species of mantis shrimp from the Western Pacific (Stomatopoda: Gonodactyloidea: Protosquillidae). *Journal of Crustacean Biology*, 30 (1): 141–145.
- Ahyong, S.T., 2012a. The marine fauna of New Zealand: mantis shrimps (Crustacea: Stomatopoda). *NIWA Biodiversity Memoir*, 125: 1–111.
- Ahyong, S.T., 2012b. Stomatopod Crustacea of the KUMEJIMA 2009 Expedition, Japan. *Zootaxa*, 3367: 232–251.

- Ahyong, S.T., 2016. Results of the Comprehensive Marine Biodiversity Survey International Workshops 2012 and 2013: Stomatopod Crustacea. Raffles Bulletin of Zoology, Supplement, 34: 455–469.
- Ahyong, S.T., Chan T.Y., Liao Y.C., 2008. A catalog of the mantis shrimps (Stomatopoda) of Taiwan. National Taiwan Ocean University, Keelung, Taiwan R.O.C. :1–191.
- Ahyong, S.T., Chu K.H., Chan T.Y., Chen Q.C., 1999. Stomatopoda of the Zhujiang estuary between Hong Kong and Macau. Crustaceana, 72 (1): 37–54.
- Ahyong, S.T. & Davie, P.J.F., 2002. Hoplocarida: 31–90. In: Crustacea: Malacostraca: Phyllocarida, Hoplocarida, Eucarida (Part 1) (P.J.F. Davie, ed.), pp. 31–90. Zoological Catalogue of Australia. CSIRO Publishing, Melbourne.
- Ahyong, S.T. & Erdmann, M.V., 2003. The stomatopod Crustacea of Guam. Micronesica, 35–36, 315–352.
- Ahyong, S.T. & Harling, C. 2000. The phylogeny of the stomatopod Crustacea. Australian Journal of Zoology, 48(6): 607–642.
- Ahyong, S. T., Hwang, H.-S. & Kim, W., 2018. Review of the mantis shrimp genus *Taku* Manning, 1995 (Stomatopoda: Gonodactyloidea: Takuidae). Journal of Crustacean Biology, 38(4): 451–459.
- Ahyong, S. T. & Jarman, S. N., 2009. Stomatopod interrelationship: preliminary results based on analysis of three molecular loci. Arthropod Systematics and Phylogeny, 67: 91–98.
- Ahyong, S. T. & Low M. E. Y., 2013. *Miyakella* nom. nov., a replacement name for *Miyakea* Manning, 1995(Crustacea: Stomatopoda: Squillidae), preoccupied by *Miyakea* Marumo, 1933 (Insecta: Lepidoptera: Crambidae). Zootaxa. 3616(1): 99–100.

- Ahyong, S.T. & Naiyanetr, P., 2002. Stomatopod Crustaceans from Phuket and the Andaman Sea. *Phuket Marine Biological Centre Special Publication*, 23: 281–312.
- Ahyong, S.T., & S.F. Norrington, 1997. Stomatopod Crustacea in the Macleay Museum, University of Sydney. *Proceedings of the Linnean Society of New South Wales* 118: 97–110.
- Ahyong, S.T., & A.B. Kumar, 2018. First records of seven species of mantis shrimp from India (Crustacea: Stomatopoda), *Zootaxa* 4370 (4), pp. 381–394
- Ariyama, H., Omi H., Tsujimura H., Wada T., Kashio S., 2014. Three rare mantis shrimps collected from Osaka Bay, Japan. *Bulletin of the Osaka Museum of Natural history*, 68: 27–39.
- Alcock, A., 1894. On the results of the deepsea dredging during the season 1890–91 (concluded). Natural history notes from H.M. Marine Survey Steamer “Investigator,” Commander R.F. Hoskyn, R.N., late commanding, series 2, no. 1. *The Annals and Magazine of Natural History*, series 6, 13: 400–411.
- Alexander, W.B., 1916a. On a stomatopod new to Australia, with a list of the Western Australian species of the order. *Journal and Proceedings of the Royal Society of Western Australia* 1: 8–9.
- Balss, H., 1921. Results of Dr. E. Mjobergs Swedish Expeditions to Australia 1910–13, XXIX. Stomatopoda, Macrura, Paguridea und Galatheidea. *Kungl. Svenska Vetenskapsakademiens Hanflingar* 61(10): 1–24.
- Berthold, A.A., 1827. Latreille’s *Natürliche Familien des Thierreichs*, aus dem Franzöischen met Ammerkungen und Zusätzen. Weimer: 606.
- Berthold, A.A., 1845. Ueber verschiedene neue oder seltene Reptilien aus Neugranada und Crustaceen aus China. *Gesellschaft der Wissenschaften zu Göttingen, Nachrichten* 1845: 37–48.

- Blumstein, R., 1974. Stomatopod crustaceans from the Gulf of Tonkin with the description of new species. *Crustaceana* 26(2): 112–126.
- Borradaile, L.A., 1898. On some Crustaceans from the South Pacific—Part I: Stomatopoda. *Proceedings of the Zoological Society of London* 1898: 32–38, pls. 5–6.
- Borradaile, L.A., 1907. Stomatopoda from the western Indian Ocean. The Percy Sladen Trust Expedition to the Indian Ocean in 1905, under the leadership of J. Stanley Gardiner. *Transactions of the Linnean Society of London* (2, Zoology) 12: 209–216, pl. 22.
- Brooks, W.K., 1886. Report on the Stomatopoda collected by H.M.S Challenger during the years 1873-76. *The voyage of the H.M.S. Challenger, Zoology*, 16: 1–116, pls. 1–16.
- Caldwell, R.L. & Dingle, H., 1976. Stomatopods. *Scientific American*, 234 (1): 80–89.
- Cannon, L.R.G., G.B. Gordon & P. Campbell, 1987. Community patterns revealed by trawling in the inter-reef regions of the Great Barrier Reef. *Memoirs of the Queensland Museum* 25(1): 45–70.
- Cho, S.H., Lee, J.E., Son, M.H. & Kim, M.H., 2006. Marine Invertebrates on the Artificial Reefs in Jeju Island I – Invertebrates. National Institute of Fisheries Science, Jeju Fisheries Research Institute, Jeju, 78 pp.
- Chopra, B., 1939. Stomatopoda. *John Murray Expedition Scientific Reports*, 6(3): 137–181, figs. 1–13.
- Debelius, H., 1999. *Crustacea Guide of the World*. Frankfurt: IKAN.
- De Man, J.G. 1887. Bericht über die von Herrn Dr. G. Brock im indischen Archipel gesammelten Dekapoden und Stomatopoden. *Archiv für Naturgeschichte*, 53 (I): 571–583.

- Man, J.G. de, 1888 (1887–1888). Bericht über die von Herrn Dr. J. Brock im indischen Archipel gesammelten Decapoden und Stomatopoden. *Archiv für Naturgeschichte* 53(I, 2): 215–288, pls. 7–10 (issued 1887); 53(I, 3): 289–600, pls. 11–22a (issued 1888, fide Clark et al., 1990).
- Debelius, H., 1999. *Crustacea Guide of the World*. Frankfurt: IKAN.
- De Man, J.G. 1898. Bericht über die von Herrn Schiffscapitän Storm zu Atjeh, an den westlichen Küsten von Malakka, Borneo and Celebes sowie in der Java-See gesammelten Decapoden und Stomatopoden, sechster (schluss-) Theil. *Zoologische Jahrbücher, Abtheilung für Systematik, Geographie und Biologie der Thiere* 10: 677–708, pls. 28–38.
- De Man, J.G. 1902. Die von Herrn fProfessor Kükenthal im Indischen Archipel gesammelten Dekapoden und Stomatopoden (in) Kükenthal, W., *Ergebnisse einer zoologischen Forschungsreise in den Molukken und Borneo*. *Abhandlungen der Senckenbergischen naturforschenden Gesellschaft* 25: 467–929, pls. 19–27.
- Dong Y.M., Chen Y.S., Huang L.Q., 1983. Report on the stomatopods of the East China Sea. *Donghai Marine Science*, 1: 82–98.
- Đuriš, Z., 2007. Mantis Shrimps (Crustacea: Stomatopoda) of Nhatrang Bay. In: *Benthic Fauna of the Bay of Nhatrang, Southern Vietnam* (À.N. Sysoev & Y.I. Kantor, eds.), pp. 124–159. KMK Scientific Press, Moscow.
- Edgar, R.C., 2004. MUSCLE: multiple sequence alignment with high accuracy and high throughput. *Nucleic Acids Research*, 32: 1792–1797.
- Erdmann, M.V., & R.L. Caldwell, 1997. Stomatopod Crustaceans as bioindicators of marine pollution stress on coral reefs. *Proceedings of the 8th International Coral Reef Symposium* 2: 1521–1526.
- Erdmann, M.V., & O. Sisovann, 1998. Distribution and abundance of reef-flat stomatopods in Teluk Jakarta and Kepulauan Seribu. In *Proceedings of*

Coral Reef Evaluation Workshop, Pulau Seribu, Indonesia, Study 10, ed. S. Soemodiharjo, UNESCO.

- Fabricius, J.C., 1781. *Species Insectorum Exhibentes Eorum Differentias Specificas, Synonyma Auctorum, Loca Natalia, Metamorphosin Adiectis, Observationibus, Descriptionibus* 1: vii+552. Hamburgii et Kilonii.
- Folmer, O., Black, M., Hoeh, W. Lutz, R. & Vrijenhoek. R., 1994. DNA primers for amplification of mitochondrial cytochrome c oxidase subunit I from diverse metazoan invertebrates. *Molecular Marine Biology and Biotechnology*, 3: 294–299.
- Forskål, P., 1775. *Descriptiones Animalium, Avium, Amphibiorum, Piscium, Insectorum, Vermium*, pp. 19 + xxxii + 164. Hauniae (Copenhagen).
- Fukuda, T., 1909. Japanese Stomatopoda (continued). *Dobutsugaku Zasshi*, 21 (244): 54–62. (In Japanese)
- Fukuda, T., 1910. Report on the Japanese Stomatopoda with descriptions of two species. *Annotations Zoologicae Japonenses*, 7(3): 139–152, pl. 4.
- Ghosh, H.C., & R.B. Manning, 1988. Types of stomatopod crustaceans in the Zoological Survey of India. *Proceedings of the Biological Society of Washington* 101(3): 653–661.
- Giesbrecht, W., 1910. Stomatopoden, Erster Theil. *Fauna und Flora des Golfes von Neapel Monographie* 33: i–vii, 1–239, pls. 1–11.
- Ghosh, H.C., 1990. Stomatopoda: Crustacea. *Fauna of Lakshadweep. State Fauna Series* 2: 199–212.
- Gosliner, T.M., D.W. Behrens & G.C. Williams, 1996. *Coral Reef Animals of the Indo-Pacific*. Monterey, California: Sea Challengers: vi+314.
- Gordon, I., 1935. On two new species of Crustacea from Christmas Island. *Annals and Magazine of Natural History*, series 10, 16: 629–637.

- Graham, K.J., G.W. Liggins, J. Wildfoster & S.J. Kennelly, 1993. Kapala Cruise Report 110: 1–69. NSW Fisheries Research Institute. Graham, K.J., G.W. Liggins, J. Wildfoster & S.J. Kennelly, 1993b. Kapala Cruise Report 112: 1–74. NSW Fisheries Research Institute.
- Gravier, C.H., 1930. Sur une collection de Crustaces (Stomatopodes) reueillis par Mme. Pruvot sur les cotes de la Nouvelle Caledonie. Bulletin du Museum national d’Histoire naturelle, Paris, series 2, 2(2): 214–216.
- Haan, W. de, 1844 (1833–1850). Crustacea. In Fauna Japonica sive descriptio animalium, quae in itinere per Japoniam, jussu et auspiciis superiorum, qui summum in India Batavia Imperium tenent, suscepto, annis 1823–1830 collegit, notis observationibus et adumbrationibus, ed. Ph.F. von Siebold, pp.243, illustravit. Lugdunum Batavorum: A. Arnz.
- Hale, H. M., 1924. Notes on Australian Crustacea, No. 1. Family Squillidae. Records of the South Australian Museum Adelaide 2: 491–502.
- Hale, H. M., 1927. The Crustaceans of South Australia, part I, Handbook of the flora and fauna of South Australia, Adelaide: 201.
- Hamano, T., 1987. Biology of Stomatopoda–3. Stomatopods from Japan–1. History of taxonomy and species list. Aquabiology, 9(3): 208–211.
- Hamano, T., 1988. Biology of Stomatopoda–7. Stomatopods from Japan–5. Gonodactylidae and Odontodactylidae. Aquabiology, 10(1): 28–32.
- Hamano, T., 2005. Biology of stomatopod crustaceans and stock management of the Japanese mantis shrimp *Oratosquilla oratoria*. Japan Fisheries Resource Conservation Association, Tokyo, 210 pp. [In Japanese]
- Hansen, H.J., 1926. The stomatopoda of the Siboga Expedition. *Siboga-Expeditie, monographe*, 35: 1–48.
- Heard, R., & R.B. Manning, 1990. *Caecopilumnus crassipes* (Tesch, 1918) (Decapoda, Brachyura, Pilumnidae) and *Acanthosquilla multifasciata*

- (Wood-Mason, 1895) (Stomatopoda, Nannosquillidae), new to the Hawaiian Islands. *Crustaceana*, 59 (1): 105–107.
- Holthuis, L.B., 1941. The Stomatopoda of the Snellius Expedition. *Biological Results of the Snellius Expedition XII. Temminckia* 6: 241–294.
- Holthuis, L.B., 1959. Stomatopod Crustacea of Suriname. *Studies on the Fauna of Suriname and other Guyanas* 10: 173–191.
- Holthuis, L.B., 1967. Fam. Lysiosquillidae et Bathysquillidae. Stomatopoda I. In *Crustaceorum Catalogus*, eds. H.E. Gruner & L.B. Holthuis, Den Haag: W. Junk, 1: 1–8.
- Hong S.Y., Park K.Y., Park C.W., Han C.H., Suh H.L., Yun S.G., Song C.B., Jo S.G., Lim H.S., Kang Y.S., Kim D.J., Ma C.W., Son M.H., Cha H.K., Kim K.B., Choi S.D., Park K.Y., Oh C.W., Kim D.N., Shon H.S., Kim J.N., Choi J.H., Kim M.H., Choi I.Y., 2006. Marine Invertebrates in Korean Coasts. Academy Publishing Company, Seoul, pp. 1–479.
- Hughes, R. N., 1977. The Biota of Reef-Flats and Limestone Cliffs near Jeddah, Saudi Arabia. *Journal Natural History* 11: 77–96.
- Hwang, H.S., S.K. Lee, M. Kim, W. Kim, 2013. First report of the mantid shrimp *Faughnia formosae* (Stomatopoda: Parasquillidae) from Korea. *Animal Systematics, Evolution and Diversity*, 29(3): 245–248.
- Hwang, H.S., Park, T. & Kim, W., 2018a. New record of a gonodactylid species, *Gonodactylaceus falcatus* (Crustacea: Stomatopoda: Gonodactylidae) from Korea. *Animal Systematics, Evolution and Diversity*, 34(2): 114–118.
- Hwang, H.S., S.T. Ah Yong, & Kim W., 2018b. A new species of *Chorisquilla* Manning, 1969 (Stomatopoda: Protosquillidae) from Korea and Japan with redescription of *C. mehtae* Erdmann & Manning, 1998. *Zootaxa*, 4483(2): 365–374.

- Hwang, H.S., S.T. Ahyong, & Kim W., 2019. First records of six species of mantis shrimp from Korea with a key to the Korean stomatopoda. *Crustaceana*: in press.
- Jones, D., & G. Morgan, 1994. *A Field Guide to Crustaceans of Australian Waters*. Australia: Reed.
- Jurich, B., 1904. Die Stomatopoden der Deutsche Tiefsee-Expedition. *Wissenschaftliche Ergebnisse der deutschen Tiefsee-Expedition auf dem Dampfer "Valdivia" 1898–1899*, 7: 361–408, pls. 25–30.
- Kang, J.H., S.H. Lee, H.S. Ko, 2016. First report of two species of mantid shrimps (Stomatopoda: Squilloidea: Squillidae) from Korean waters. *Animal Systematics, Evolution and Diversity*, 32(3): 234–239.
- Kemp, S., 1911. Preliminary descriptions of new species and varieties of Crustacea Stomatopoda in the Indian Museum. *Records of the Indian Museum* 6(2): 93–100.
- Kemp, S., 1913. An account of the Crustacea Stomatopoda of the Indo-Pacific region, based on the collection in the Indian Museum. *Memoirs of the Indian Museum*, 4: 1–217.
- Kemp, S & B. Chopra, 1921. Notes on Stomatopoda. *Records of the Indian Museum*, 22: 297–311.
- Kim, H.S. & B.J. Rho. 1972. The seashore marine fauna of Chuja Islands, Korea. In: *A report on the floral and faunal survey of Chuja Island* (Office of Cultural Properties, Korea Ministry of Culture and Information, ed.), pp. 67–108. Office of Cultural Properties, Korea Ministry of Culture and Information, Seoul.
- Kimura, M., 1980. A simple method for estimating evolutionary rates of base substitutions through comparative studies of nucleotide sequences. *Journal of Molecular Evolution*, 16: 111–120.

- Kinzie, R.A. III, 1968. The ecology of the replacement of *Pseudosquilla ciliata* (Fabricius) by *Gonodactylus falcatus* (Forskål) (Crustacea: Stomatopoda) recently introduced into the Hawaiian Islands. *Pacific Science* 22(4): 465–475.
- Komai, T., 1927. Stomatopoda of Japan and adjacent localities. *Memoirs of the College of Science, Kyoto Imperial University (B)*, 3(3): 307–354, figs. 1–2, pls. 13–14.
- Lanchester, W.F., 1903. Stomatopoda, with an account of the varieties of *Gonodactylus chiragra*. *Marine Crustaceans VIII*. In *The fauna and geography of the Maldive and Laccadive Archipelagoes: being the account of the work carried on and of the collections made by an expedition during the years 1899 and 1900*, ed. J.S. Gardiner, vol. 1, pp. 444–459.
- Latreille, P.A., 1802. *Histoire naturelle, générale et particulière, des Crustacés et des Insectes* Paris: F. Dufart, 3: 467.
- Latreille, P.A., 1817. *Nouveau dictionnaire d'histoire naturelle, appliquée aux arts, à l'agriculture, à l'économie rurale et domestique, à la médecine, etc.*, 10: 1–404. (Déterville, Paris).
- Latreille, P.A., Le Peletier, A.-L.-M., Serville, J.-G.-A. & Guérin, F.-E. (Eds.) 1825–1828. *Encyclopédie Méthodique. Histoire Naturelle. Entomologie, ou Histoire naturelle des Crustacés, des Arachnides et des Insectes*: 832. (Agasse, Paris).
- Lee, S.-C., Wu S. –K., 1966. The stomatopod Crustacea of Taiwan. *Bulletin of the Institute of Zoology, Academia Sinica*, 5: 41–58.
- Liu, J.-Y., & Y. Wang, 1998. On two new species of the Squillidae and Harpiosquillidae (Crustacea Stomatopoda) from the South China Sea. *Oceanologia et Limnologia Sinica* 29(6): 588–592 (Chinese text), 592–596 (English text), figs. 1–2.

- Low M. E. Y. & Low Ahyong, S. T., 2010. *Kempella* nom. nov., a replacement name for *Kempina* Manning, 1978 (Crustacea: Stomatopoda: Squillidae), preoccupied by *Kempina* Roewer, 1911, a junior synonym of *Zaleptus* Thorell, 1877 (Arachnida: Opiliones: Sclerosomatidae), *Zootaxa* 2642(1): 68.
- Linnaeus, C., 1758. *Systema Naturae per Regna Tria Naturae, Secundum Classes, Ordines, Genera, Species, cum Characteribus, Differentiis, Synonymis Locis*. Edition 10, (1): iii+824. Holmiae.
- Makarov, R.R., 1979a. A collection of stomatopod crustaceans of the genus *Clorida* Eydoux & Souleyet, 1842, from Tonkin Bay, Vietnam. *Crustaceana*, 37 (1): 39–56.
- Makarov, R.R., 1979b. Mantis shrimps (Crustacea: Hoplocarida: Stomatopoda) in collection of expeditions of the research vessel “Akademic Kripovich”. *Biological Moraya, Vladivostok* 3: 14–23.
- Man, J.G. de, 1887. Bericht über die von Herrn Dr. G. Brock im indischen Archipel gesammelten Dekapoden und Stomatopoden. *Archiv für Naturgeschichte*, 53 (I), 571–583.
- Man, J.G. de, 1888 (1887–1888). Bericht über die von Herrn Dr. J. Brock im indischen Archipel gesammelten Decapoden und Stomatopoden. *Archiv für Naturgeschichte* 53(I, 2): 215–288, pls. 7–10 (issued 1887); 53(I, 3): 289–600, pls. 11–22a (issued 1888, fide Clark et al., 1990).
- Manning, R.B., 1963b. Preliminary revision of the genera *Pseudosquilla* and *Lysiosquilla* with descriptions of six new genera. *Bulletin of Marine Science of the Gulf and Caribbean* 13(2): 308–328.
- Manning, R.B., 1965. Stomatopoda from the collection of His Majesty. The Emperor of Japan. *Crustaceana*, 9(3): 249–262, pls. 11–12.

- Manning, R.B., 1966. Notes on some Australian and New Zealand stomatopod Crustacea, with an account of the species collected by the Fisheries Investigation Ship *Endeavour*. *Records of the Australian Museum* 27(4): 79–137, figs. 1–10.
- Manning, R.B., 1967. Stomatopoda in the Vanderbilt Marine Museum. *Crustaceana* 12(1): 101–106.
- Manning, R.B., 1968. A revision of the family Squillidae (Crustacea, Stomatopoda), with the description of eight new genera. *Bulletin of Marine Science*, 18 (1): 105–142.
- Manning, R.B., 1969. Notes on the *Gonodactylus* section of the family Gonodactylidae (Crustacea, Stomatopoda), with descriptions of four new genera and a new species. *Proceedings of the Biological Society of Washington*, 82: 143–166.
- Manning, R.B., 1970. Some stomatopod crustaceans from Tuléar, Madagascar. *Bulletin du Muséum national d'Histoire naturelle, Paris, series 2*, 41(6): 1429–1441 (dated 1969, published 1970).
- Manning, R.B., 1971a. Two new species of *Gonodactylus* (Crustacea, Stomatopoda) from Eniwetok Atoll, Pacific Ocean. *Proceedings of the Biological Society of Washington* 84: 73–80.
- Manning, R.B., 1971b. Keys to the species of *Oratosquilla* (Crustacea: Stomatopoda), with descriptions of two new species. *Smithsonian Contributions to Zoology* 71: 1–16.
- Manning, R.B., 1975. *Gonodactylus botti*, a new stomatopod crustacean from Indonesia. *Senckenbergiana Biologica* 56(4/6): 289–291.
- Manning, R.B., 1977. Preliminary accounts of five new genera of stomatopod crustaceans. *Proceedings of the Biological Society of Washington*, 90 (2): 420–423.

- Manning, R.B., 1978. A new genus of stomatopod crustacean from the Indo-West Pacific region. *Proceedings of the Biological Society of Washington*, 91(1): 1–4.
- Manning, R.B., 1980. The superfamilies, families, and genera of recent stomatopod Crustacea, with diagnoses of six new families. *Proceedings of the Biological Society of Washington*, 93: 362–372.
- Manning, R.B., 1981. First record of *Kempina zanzibarica* (Chopra, 1939) from the Red sea, with notes on *Lenisquilla gilesi* (Kemp, 1911) (Crustacea: Stomatopoda). *Senckenbergiana Biologica*, 61(3/4): 297–303.
- Manning, R.B., 1990. Stomatopod Crustacea from the Persian Gulf, with the description of a new *Manningia*. *Steenstrupia* 16(6): 93–108.
- Manning, R.B., 1991. Stomatopod Crustacea collected by the Galathea Expedition, 1950-1952, with a list of Stomatopoda known from depths below 400 meters. *Smithsonian Contributions to Zoology*, 521: 1–18.
- Manning, R.B., 1995. Stomatopod Crustacea of Vietnam: the legacy of Raoul Serène. *Crustacean Research*, Special No. 4: 1–339.
- Manning, R.B., & D.K. Camp, 1993. Erythroscilloidea, a new superfamily and Tetrasquillidae, a new family of stomatopod crustaceans. *Proceedings of the Biological Society of Washington*, 106 (1): 85–91.
- Manning R.B., & T.Y. Chan, 1997. The genus *Faughnia* from Taiwan, with the description of a new species (Stomatopoda: Parasquillidae). *Journal of Crustacean Biology*, 17: 546–554.
- Manning, R.B. & Erdmann, M.V., 1998. Preliminary descriptions of nine new stomatopod Crustaceans from coral reef habitats in Indonesia and Australia. *Raffles Bulletin of Zoology*, 46 (2), 615–626.
- Manning, R.B., & R. Heard, 1997. Stomatopod Crustaceans from the Carolinas and Georgia, Southeastern United States. *Gulf Research Reports* 9(4): 303–320.

- Manning, R.B., & Ch. Lewinsohn, 1981. Selection of a Neotype for *Cancer falcatus* Forskål, 1775 (Stomatopoda). *Crustaceana* 41(3): 314–316.
- Manning, R.B., & Ch. Lewinsohn, 1986. Notes on some stomatopod Crustacea from the Sinai Peninsula, Red Sea. *Smithsonian Contributions to Zoology* 433: 1–19.
- Manning, R.B., & R.R. Makarov, 1978. A new species of *Faughnia* from the western Indian Ocean (Crustacea, Stomatopoda). *Bulletin du Muséum national d'Histoire naturelle, Paris, series 3, 520 (Zoologie 356)*: 517–523.
- Manning, R.B., & M.L. Reaka, 1981a. *Gonodactylus aloha*, a new stomatopod crustacean from the Hawaiian Islands. *Journal of Crustacean Biology* 1(2): 190–200.
- Manning, R.B., & M.L. Reaka, 1981b. *Gonodactylus siamensis*, a new stomatopod crustacean from Thailand. *Proceedings of the Biological Society of Washington* 94(2): 479–482.
- Manning, R.B., & M.L. Reaka, 1982. *Gonodactylus insularis*, a new stomatopod crustacean from Enewetak Atoll, Pacific Ocean. *Proceedings of the Biological Society of Washington* 95(2): 347–351.
- McNeill, F.A., 1968. Crustacea, Decapoda & Stomatopoda. Scientific reports of the Great Barrier Reef Expedition 1928–29 7(1): 1–98, pl. 1, 2. London: British Museum (Natural History).
- Miers, E.J., 1875. On some new or undescribed species of Crustacea from the Samoa Islands. *Annals and Magazine of Natural History, series 4, 16*: 341–344.
- Miers, E.J., 1880. On the Squillidae. *Annals and Magazine of Natural History, 5*: 1–30, 108–127. Moosa, M.K., 1986. Stomatopod Crustacea. Résultats du Campagnes MUSORSTOM I & II Philippines, 2. *Mémoires du Muséum national d'Histoire naturelle, Paris, series A, Zoologie 133*: 367–414 (dated 1985, printed 1986).

- Milne Edwards, H., 1837. Histoire naturelle des Crustacés, comprenant l'anatomie, la physiologie et la classification de ces animaux 2: 1–532. Atlas: 32pp, pls. 1–14, 14 bis, 15–25 bis, 26–42. Paris: Roret.
- Moosa, M.K., 1974. On a new and rare species of Stomatopoda (Crustacea) from Indonesian waters. *Treubia* 28(3): 73–82.
- Moosa, M.K., 1982. *Faughnia serenei*, new species, a stomatopod from the South China Sea. *Journal of Crustacean Biology* 2(4): 600–604.
- Moosa, M.K., 1986. Stomatopod Crustacea. Résultats du Campagnes MUSORSTOM I & II Philippines, 2. Mémoires du Muséum national d'Histoire naturelle, Paris, series A, Zoologie 133: 367–414 (dated 1985, printed 1986).
- Moosa, M.K., 1973. The stomatopod Crustacea collected by the Mariel King memorial expedition in Malaku waters. *Marine Research in Indonesia* 13: 1–30.
- Moosa, M.K., 1989. Some stomatopods (Crustacea: Stomatopoda) from Japanese waters, with description of a new species. *Bulletin of the National Science Museum, Tokyo, series A (Zoology)* 15(4): 223–229.
- Moosa, M.K., 1991. The Stomatopoda of New Caledonia and Chesterfield Islands. In *Le benthos des fonds meubles des lagons de Nouvelle-Calédonie*, ed. Richer de Forges, Paris: Editions de l'ORSTOM, 1: 149–219.
- Moosa, M.K. 2000. Marine Biodiversity of the South China Sea: a checklist of stomatopod Crustacea. *Raffles Bulletin of Zoology, Supplement* 8: 405–457.
- Moosa, M.K., & R. Cleva, 1984b. Stomatopod Crustacea collected by the mission Corindon II in the Makassar Strait, Indonesia. *Marine Research in Indonesia* 24: 73–82.

- Moosa, M.K., & M.V. Erdmann, 1994. A survey of the distribution of Stomatopod Crustacea in the Spermonde Archipelago. Proceedings of the International Symposium on Marine Research in the Spermonde Archipelago, pp. 74–92.
- Naiyanetr, P., 1980. Stomatopoda of Thailand. Chulalongkorn University, Bangkok, pp. 1–95, 35 pls.
- Naiyanetr, P., 1989. *Siamosquilla hyllebergi*, a new genus and new species of stomatopod crustacean from Thailand. In: Ferrero, E. A. (Eds.), Biology of Stomatopods. Selected Symposia and Monographs. U.Z.I. Vol. 3. Mucchi, Modena, pp. 281–284.
- Naiyanetr, P., 1995. *Acanthosquilla sirindhorn* n. sp. a new mantis shrimp from Thailand. Crustaceana 68: 409–417.
- Nobili, G., 1899. Contribuzioni alla conoscenza della fauna carcinologica della Papuasias, della Molucche e dell’Australia. Annali del Museo Civico di Storia Naturale Giacomo Doria, Genoa, 40 (= series 2, 20): 230–282 (1–53 on separate).
- Nobili, G., 1903. Contributo alla fauna carcinologica di Borneo. Bollettino dei Musei di Zoologia ed Anatomia comparata della R. Università di Torino 18(447): 27–32.
- Nobili, G., 1906. Fauna Carcinologique de la Mer Rouge. Decapodes et Stomatopodes. Annales des Sciences Naturelles, Zoologie et Paléontologie (9)4: 1–347, pls. 1–11.
- Odhner, T., 1923. Indopazifische Stomatopoden. Göteborgs kungl. Vetenskaps och Vitterhets-Sä mhalles Handlingar 27(4): 1–16, pl. 1.
- Pfeffer, G., 1888. Übersicht der von Herrn Dr. F. Stuhlmann in Ägypten, auf Sansibar und dem gegenüberliegenden Festlande gesammelten Reptilien, Amphibien, Fische, Mollusken und Krebse. Mitteilungen aus dem Hamburgischen zoologische Museum und Institut, 6, 28–35.

- Pocock, R.I., 1893. Report upon the stomatopod crustaceans obtained by P. W. Bassett-Smith, Esq., Surgeon R. N., during the cruise, in the Australian and China seas, of H.M.S. "Penguin," Commander W. U. Moore. *Annals and Magazine of Natural History*, series 6, 11: 473–479, pl. 20B.
- Porter, M. L., Zhang Y., Desai S., Caldwell R. L., Cronin T. W. 2009. Molecular diversity of visual pigments in Stomatopoda (Crustacea). *Visual neuroscience*, 26: 255–265.
- Roxas, H.A., & E. Estampador, 1930. Stomatopoda of the Philippines. *Natural and Applied Science Bulletin, University of the Philippines* 1(1): 93–131.
- Schram, F.R. & Müller, H.G. 2004. *Catalog and Bibliography of the Fossil and Recent Stomatopoda*. Backhuys Publishers, Leiden.
- Serène, R., 1949. Observations sur le *Gonodactylus strigatus* Hansen (Crustacé Stomatopode). *Bulletin de la Société Zoologique de France*, 74 (4–5): 225–231.
- Serène, R., 1950. Deux nouvelles especes Indo Pacifiques de Stomatopodes. *Bulletin du Museum national d'Histoire naturelle, Paris*, series 2, 22(5): 571–572.
- Serène, R., 1952. Étude d'une collection de Stomatopodes de l'Australian Museum du Sydney. *Records of the Australian Museum*, 23(1): 1–24, pls. 1–3.
- Serène, R., 1962. Révision du genre *Pseudosquilla* (Stomatopoda) et définition de genres nouveaux. *Bulletin de l'Institut océanographique, Monaco* 1241: 1–27.
- Stephenson, W., 1952. Faunistic records from Queensland. Part I— General Introduction. Part II—Adult Stomatopoda (Crustacea). *Zoology Papers of the University of Queensland* I (1): 1–15.
- Stephenson, W., 1953. Three new Stomatopoda (Crustacea) from eastern Australia. *Australian Journal of Marine and Freshwater Research*, 4 (1): 201–218.

- Stephenson, W., 1962. Some interesting Stomatopoda—mostly from Western Australia. *Journal of the Royal Society of Western Australia* 45(2): 33–43.
- Stephenson, W., & F. McNeill, 1955. The Australian Stomatopoda (Crustacea) in the collections of the Australian Museum, with a check list and key to the known Australian species. *Records of the Australian Museum* 23(5): 239–265.
- Sun, X., & S. Yang, 1998. Studies on stomatopod Crustacea from Nansha Islands, China. Part 1, Protosquillidae and Pseudosquillidae, with descriptions of a new genus and two new species. *Studies on marine fauna and flora and biogeography of the Nansha Islands and neighbouring waters*. Vol. 3: 142–155.
- Tamura, K., Dudley, J., Nei, M., Kumar, S. 2007. MEGA4: molecular evolutionary genetics analysis (MEGA) software version 4.0. *Molecular Biology and Evolution*, 24: 1596–1599.
- Tang, R.W.K., Yau, C., & Ng, W.C., 2010. Identification of stomatopod larvae (Crustacea: Stomatopoda) from Hong Kong waters using DNA barcodes. *Molecular Ecology Resources*, 10: 439–448.
- Tate, R., 1883. Descriptions of some new species of *Squilla* from South Australia. *Transactions and Proceedings of the Royal Society of South Australia*, 6: 48–53, pl. 2.
- Tirmizi, N.M., & Q.B. Kazmi, 1984. A handbook on the Pakistani mantis shrimp *Oratosquilla*. Centre of Excellence in Marine Biology Publication 4. University of Karachi, Pakistan. Pp, i–vi, 1–101.
- Tiwari, K.K., & S. Biswas, 1952. On two new species of the genus *Squilla* Fabr., with notes on other stomatopods in the collections of the Zoological Survey of India. *Records of the Indian Museum* 49(3–4): 349–363, figs. 1–5.

- The Korean Society of Systematic Zoology, 1997. List of animals in Korea (excluding insects). Academy Publishing Co., Seoul: 1–489.
- Tweedie, M.W.F., 1950. The fauna of the Cocos-Keeling Islands, Brachyura and Stomatopoda. *Bulletin of the Raffles Museum, Singapore* 22: 102–148.
- Schram, F. R., S. T. Ah Yong, S. N. Patek, P. A. Green, M. V. Rosario, M. J. Bok, T. W. Cronin, K. S. Mead Vetter, R. L. Caldwell, G. Scholtz, K. D. Feller & P. Abello, 2013. Subclass Hoplocarida Calman, 1904: order Stomatopoda Latreille, 1817. In: J. C von Vauper Klein, M. Charmantier-daures & F.R. Schram (eds.), *Treatise on Zoology - Anatomy, Taxonomy, Biology. The Crustacea*, revised and updated, as well as extended from the *Traite de Zoologie*, 4 (A): 179–355. (Koninklijke Brill N. V., Leiden).
- Wang, Y. L., & Liu, J. Y., 2008. Order Stomatopoda. In: Liu, J. Y. (ed.) *Check list of Marine Biota of China Seas*: 654–660. Science Press, Beijing.
- White, A., 1847. List of the Species of Crustacea in the Collection of the British Museum, London, pp. viii+143.
- Wood-Mason, J., 1875. (On some new species of stomatopod Crustacea). *Proceedings of the Asiatic Society of Bengal* 1875: 231–232.
- Wood-Mason, J. & A. Alcock., 1891. Natural History Notes from H. M. Indian Survey Steamer “Investigator” Nr. 21. Note on the results of the last seasons Deep Sea dredging. *The Annals and magazine of natural history* (6)7: 271–272.
- Wood-Mason, J., 1895. Figures and descriptions of nine species of Squillidae from the collection in the Indian Museum. *Calcutta*: 1–11.
- Yamaguchi, T., & K. Baba, 1993. Crustacean specimens collected in Japan by Ph.F. von Siebold and H. Bürger and held by the Nationaal Natuurhistorisch Museum in Leiden and other museums. In Ph.F. von Siebold and Natural

History of Japan Crustacea, ed. T. Yamaguchi. Kumamoto: The Carcinological Society of Japan. Shimoda Printing.

Yeh, T.-C. & Hsueh, P.-W., 2010. *Taku spinosocarinatus* (Fukuda, 1909): first record of a takuid stomatopod from Taiwan. *Crustaceana*, 83: 369–373.

국문 초록

인도-서태평양 해역에 서식하는 구각류 중 분류학적 개정이 필요한 형태학적 형질(꼬리마디, 이마판, 마루)를 종 동정시 사용하는 주요 그룹들을 대상으로 계통분류학적 연구를 수행하였다. 형태학적 형질 비교를 위해 한국 표본들은 1991년부터 2019년까지 조간대와 조하대에서 수집되었으며 해외 표본들은 전세계 14개의 박물관으로부터 대여하여 관찰하였다. 분자학적 형질 비교를 위해 미토콘드리아 COI 유전자를 이용하였다. 제 1 장에서는 꼬리마디의 형질을 주요형태학적 형질로 사용하는 *Taku* 속와 *Chorisquilla* 속의 분류학적 연구를 수행하였다. 그 결과, 단형속이었던 *Taku* 속에서는 *T. spinosocarinatus* 와 동물이명처리되었던 *T. pruvotae* 와 구분하여 동물이명처리를 제거하여 재기재하였고, *Chorisquilla* 속에서는 국내에서 *C. spinosissima* 로 알려져 있던 종을 재동정하여 신종 *C. orientalis* 로 기재하고 주요 형태학적 형질에 대한 기재가 부족했던 *C. mehtae* 에 대해 재기재하였다. 2 장에서는 이마판의 형질을 주요형태학적 형질로 사용하는 *Gonodactylaceus* 속과 *Gonodactylus* 속의 분류학적 연구를 수행하였다. 특히 *Gonodactylaceus falcatus* 를 4 종(*G. falcatus*, *G. siamensis*, *G. mutatus*, *G. insularis*) 으로 재동정하여 기재하였다. 3 장에서는 마루의 형질을 주요형태학적 형질로 사용하는 Squillidae 과의 7 개의 속(*Oratosquilla*, *Levisquilla*, *Anchisquilla*, *Cloridopsis*, *Miyakella*, *Squilloides*, *Kempella*), Parasquillidae 과의 *Faughnia* 속과 Tetrasquillidae 과의 *Acaenosquilla* 속과 Nannosquillidae 과의 *Acanthosquilla* 속의 분류학적 연구를 수행하였다. 4 장에서는 기존의 연구가 미진했던 한국산 구각류의 계통분류학적 연구를 수행하여, 6 종의 미기록종 (Squillioidea 상과에 속하는 *Levisquilla inermis* (Manning, 1965), *Levisquilla jurichi*

(Makarov, 1979), *Anchisquilla fasciata* (de Haan, 1844), 그리고 *Cloridopsis scorpio* (Latreille, 1828)와 국내에 처음으로 보고되는 Lysiosquilloidea 상과에 속하는 *Acaenosquilla latifrons* (de Haan, 1844)와 *Acanthosquilla multifasciata* (Wood-Mason, 1895))을 발굴하였고 4 상과, 7 과내 총 13 속, 14 종으로 구성되어 있음을 확인하였다. 본 연구를 통해 다루어진 모든 속의 검색표와 종목록을 최신화하였다.

주요어: 구각류, 사마귀 새우, DNA 바코딩, 계통분류학, 분류학, 한국 동물상

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감사의 글

학위논문을 완성하기까지 부족한 저를 제자로 맞아주시고 모든 것을 할 수 있도록 아낌없는 지원과 가르침을 주신 김원 교수님과 구혜영 교수님께 진심으로 감사드립니다. 저의 부족한 논문의 심사를 맡아 주시고 세심하게 지도해주신 이건수 교수님, 정말 꼼꼼하고 상세하게 조언해주신 임영운 교수님, 논문의 전반적인 내용과 구성에 큰 도움이 된 조언해주신 정종우 교수님, 형태분류에 대해 섬세하게 조언해주신 송성준 박사님, 용어와 정의에 대해 설명해주시고 심사해주신 노현수 박사님께 감사드립니다. 많은 질문에 항상 스스로 연구할 수 있는 자세와 방향에 대해 제시해주신 호주박물관의 Shane T. Ahyong 박사님께도 진심으로 감사드립니다.

대학원 생활 동안 많은 조언을 해주셨던 이상규 박사님, 김성민 박사님, 신명화 박사님, 강승현 박사님께 감사드립니다. 샘플도 구해 주시고 계통분류학에 대해 많은 조언해주셨던 박태서박사님께도 감사드립니다. 함께 채집도 다니고 학위과정을 함께 했던 정지범 박사와 박진호 박사에게도 고맙다고 말하고 싶습니다. 석사기간동안 늘 동무였던 미진이, 지훈이, 상희오빠, 루월언니, 박사기간동안 늘 함께 의논하고 조언하며 힘냈던 우리 콩이 현경이, 정말 잘 될 거라 생각하는 희수, 진협이, 다민이에게도 고맙다는 말 하고 싶습니다. 그리고 함께 예심발표했던 창호오빠, 정말 감사하게 생각하는 미개척 생물분류군 전문인력 양성사업으로 알게 된 이화여대의 지선씨, 이번에 함께 박사학위 취득하게 된 단국대의 김성현박사에게도 고마움을 전합니다.

그리고 늘 저를 이해해주고 응원해줬던 친구 주리와 공부하며 힘들다고 짜증도 많이 내고 심술낼 때도 도와주시고 응원해준 우리 엄마, 아빠, 수승이, 그리고 어머님, 아버님, 은화언니에게도 정말 고맙고, 많은 힘이 되었다고 전하고 싶습니다. 끝으로, 포기하고 싶을 때마다 늘 나의 편이 되어주고 잘 될 거라고 응원해준 남편 이재문과 저의 가장 큰 보물인 사랑하는 아들 이우혁에게 이 논문을 바칩니다. 모두모두 진심으로 감사합니다.