



The Marine Fauna of New Zealand:

Mantis Shrimps (Crustacea: Stomatopoda)

Shane T. Ahyong

NIWA Biodiversity Memoir 125

COVER PHOTO

Pariliacantha georgeorum gen. et sp. nov., male paratype, TL 65 mm (AM P87901), Deliverance Cove, Castlepoint.

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NATIONAL INSTITUTE OF
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Australian Museum, 6 College St, Sydney
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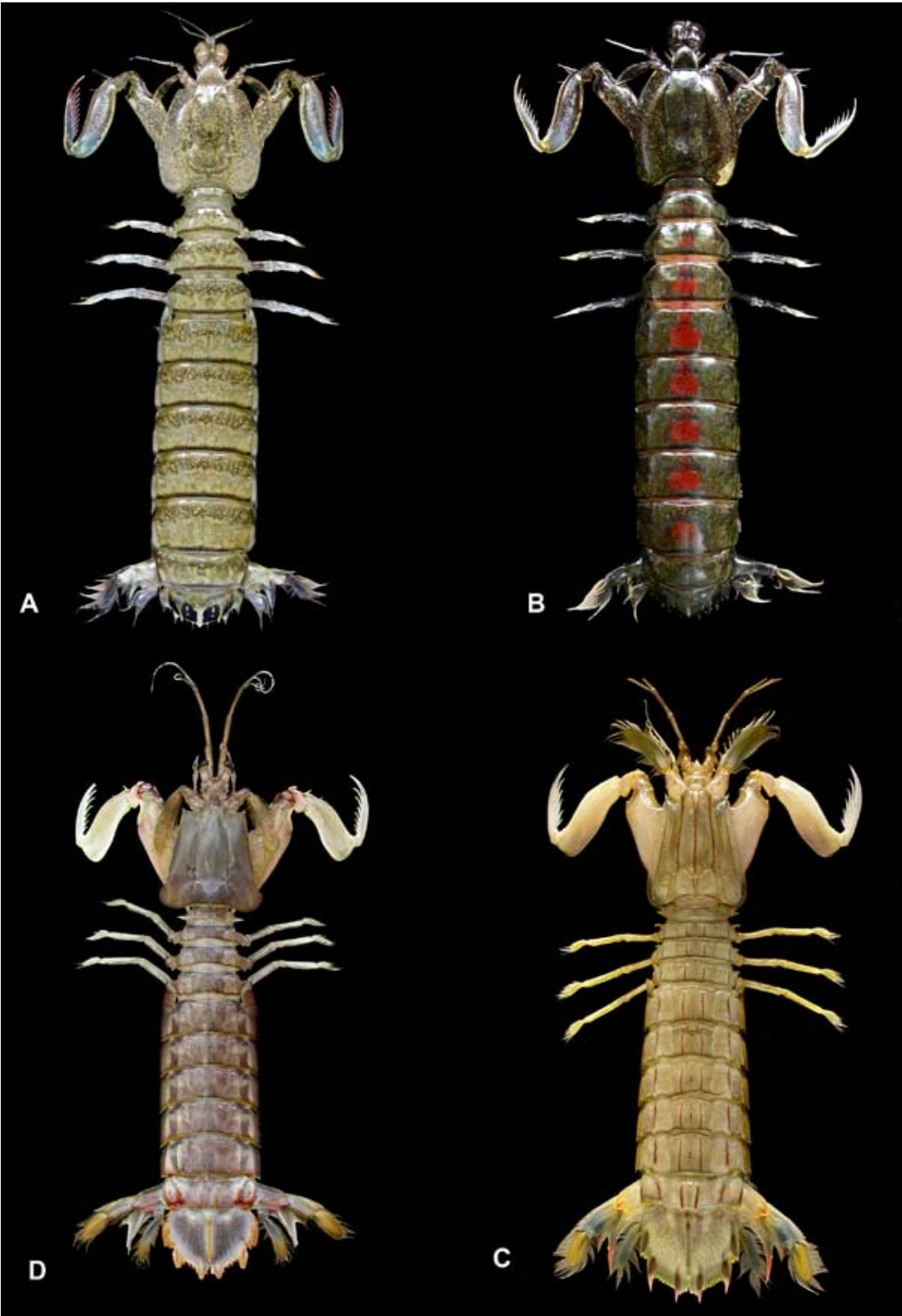
CONTENTS

ABSTRACT	6
INTRODUCTION	7
MATERIALS AND METHODS	7
CHECKLIST OF NEW ZEALAND STOMATOPODA	13
SYSTEMATICS	14
BATHYSQUILLOIDEA Manning, 1967	14
BATHYSQUILLIDAE Manning, 1967	14
<i>Bathysquilla</i> Manning, 1963	14
<i>Bathysquilla microps</i> (Manning, 1961)	14
GONODACTYLOIDEA Giesbrecht, 1910	18
GONODACTYLIDAE Giesbrecht, 1910	18
<i>Gonodactylaceus</i> Manning, 1995	19
<i>Gonodactylaceus falcatus</i> (Forskål, 1775)	19
<i>Gonodactylellus</i> Manning, 1995	23
<i>Gonodactylellus osheai</i> sp. nov.	23
<i>Gonodactylellus viridis</i> (Serène, 1954)	25
<i>Gonodactylus</i> Berthold, 1827	29
<i>Gonodactylus platysoma</i> Wood-Mason, 1895	29
HEMISQUILLIDAE Manning, 1980	32
<i>Hemisquilla</i> Hansen, 1895	32
<i>Hemisquilla australiensis</i> Stephenson, 1967	33
ODONTODACTYLIDAE Manning, 1980	36
<i>Odontodactylus</i> Bigelow, 1893	36
<i>Odontodactylus hawaiiensis</i> Manning, 1967	36
<i>Odontodactylus scyllarus</i> (Linnaeus, 1758)	39
PROTOSQUILLIDAE Manning, 1980	42
<i>Haptosquilla</i> Manning, 1969	43
<i>Haptosquilla helleri</i> sp. nov.	43
LYSIOSQUILLOIDEA Giesbrecht, 1910	46
TETRASQUILLIDAE Manning & Camp, 1993	46
<i>Colubrisquilla</i> gen. nov.	47
<i>Colubrisquilla dempsey</i> gen. et sp. nov.	48
<i>Heterosquilla</i> Manning, 1963	51
<i>Heterosquilla koning</i> sp. nov.	52
<i>Heterosquilla laevis</i> (Hutton, 1879)	55
<i>Heterosquilla tricarinata</i> (Claus, 1871)	60
<i>Heterosquilla tridentata</i> (Thomson, 1882)	66
<i>Heterosquilla trifida</i> sp. nov.	70
<i>Pariliacantha</i> gen. nov.	73
<i>Pariliacantha georgeorum</i> gen. et sp. nov.	74
SQUILLOIDEA Latreille, 1802	78
SQUILLIDAE Latreille, 1802	78
<i>Anchisquilloides</i> Manning, 1977	79
<i>Anchisquilloides mcneilli</i> (Stephenson, 1953)	79
<i>Oratosquilla</i> Manning, 1968	85
<i>Oratosquilla fabricii</i> (Holthuis, 1941)	86
<i>Oratosquilla oratoria</i> (De Haan, 1844)	89
<i>Pterygosquilla</i> Hilgendorf, 1890	92
<i>Pterygosquilla schizodontia</i> (Richardson, 1953)	93
DISCUSSION	99
ACKNOWLEDGMENTS	101
REFERENCES	102
SPECIES INDEX	109



Frontispiece 1: A, *Bathysquilla microps* (Manning, 1961), male, TL 226 mm, east of East Cape (NIWA 23989); B, *Hemisquilla australiensis* Stephenson, 1967, male TL 136 mm, Norfolk Ridge (AM P66302); C, *Odontodactylus hawaiiensis* Manning, 1967, female, TL 98 mm, Norfolk Ridge (AM P65970); D, *Pariliacantha georgeorum* gen. et sp. nov., male, TL 48 mm, Plimmerton (NIWA 68024).

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Frontispiece 2: A, *Heterosquilla tricarinata* (Claus, 1871), male, TL 68 mm, Whitianga (AM P87887); B, *Heterosquilla tricarinata* (Claus, 1871), female, TL 55 mm, Pepe Stream, Tairua (AM P87888); C, *Oratosquilla oratoria* (De Haan, 1844), male, TL 135 mm, Kaipara Harbour (NIWA-MITS 69606); D, *Pterygosquilla schizodontia* (Richardson, 1953), male, TL 120 mm, Wellington Harbour (AM P87906).
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Shane T. Ahyong

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Australian Museum, 6 College St, Sydney
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ABSTRACT

Twenty species in 13 genera and seven families of stomatopod Crustacea are now known from New Zealand, more than doubling the most recent estimate. Four superfamilies are represented: Bathysquilloidea, Gonodactyloidea, Lysiosquilloidea and Squilloidea. Bathysquilloidea is represented in New Zealand by one genus and species (*Bathysquilla microps*). Gonodactyloidea is represented by four families, six genera and eight species, of which two are new to science (*Gonodactylellus osheai* sp. nov., *Haptosquilla helleri* sp. nov.). Lysiosquilloidea is represented by one family, seven species and three genera, of which two genera and four species are new to science (*Pariliacantha georgeorum* gen. et sp. nov., *Colubrisquilla dempsey* gen. et sp. nov., *Heterosquilla koning* sp. nov., *Heterosquilla trifida* sp. nov.), and *Heterosquilla laevis* is removed from the synonymy of *H. tricarinata*. Squilloidea is represented by one family, three genera and four species. Five previously described species are new records for New Zealand. The New Zealand Stomatopoda comprises a widespread tropical component (nine species or 45%; mostly gonodactyloids) and a temperate-water component of which eight species (40%) are endemic, one is introduced (5%), and two (10%) are shared with eastern Australia. Most new taxa are endemic to New Zealand, except for *Haptosquilla helleri*, which also ranges to Tonga and the South China Sea. The tropical component comprises widespread tropical Indo-West Pacific species that occur along the Norfolk and Kermadec Ridges south to northern New Zealand. The endemic New Zealand stomatopods are dominated by tetrasquillid lysiosquilloids: the Southern Hemisphere genus *Heterosquilla* and the two new endemic genera *Colubrisquilla* and *Pariliacantha*. Notably, five of the eight known species of *Heterosquilla* are New Zealand endemics. Three species of *Heterosquilla* (*H. laevis*, *H. koning*, *H. tricarinata*) range throughout New Zealand, from Northland south to at least Stewart Island and east to the Chatham Islands. Temperate-water species occurring only around the North Island are *Pariliacantha georgeorum* and *Hemisquilla australiensis*. *Anchisquilloides mcneilli* and *Heterosquilla trifida* are also primarily North Island species but range to the northern tip of the South Island. *Colubrisquilla dempsey* is known only from localities between East Cape and the Chatham Rise. The introduced squilloid *Oratosquilla oratoria* is currently restricted to northern North Island localities (Kaipara and Hokianga). Only *H. tridentata* is apparently restricted to the South Island. The squilloid *Pterygosquilla schizodontia* is common around the South Island, but occasionally occurs as far north as East Cape. Five species occur on the Chatham Rise (*Colubrisquilla dempsey*, *Heterosquilla koning*, *Heterosquilla tricarinata*, *Heterosquilla laevis*, *P. schizodontia*) and three range south as far as the Auckland Islands (*H. laevis*, *H. tridentata*, *P. schizodontia*).

Keywords: Crustacea, Stomatopoda, mantis shrimps, Bathysquillidae, Gonodactylidae, Hemisquillidae, Odontodactylidae, Protosquillidae, Tetrasquillidae, Squillidae, *Colubrisquilla*, *Pariliacantha*, taxonomy, systematics, new genera, new species, biodiversity, New Zealand, Australia, Tasman Sea.

INTRODUCTION

The mantis shrimps (order Stomatopoda) are an exclusively predatory lineage of malacostracan crustaceans. Characteristic are their triflagellate antennules, second maxilliped modified as large powerful raptorial appendages and highly specialised eyes, which may be the most complex of any invertebrate. The last three segments of the second maxilliped fold against each other forming a raptorial claw reminiscent of the fore-legs of the praying mantis insect, hence the common name, mantis shrimp. Stomatopods capture prey by 'spearing' or 'smashing', depending on whether the dactyl is extended or held folded during the strike, which is one of the fastest known animal movements. The two methods of prey capture distinguish two broad functional groups – the 'smashers' and the 'spears' (Caldwell & Dingle 1976). More than 450 species are known in seven superfamilies and 17 families (Ahyong 2001). A number of species are fished commercially, especially *Squilla mantis* (Linnaeus, 1758) in the Mediterranean Sea and *Oratosquilla oratoria* (De Haan, 1844) in East Asia, with artisanal fisheries targeting various squillids and lysiosquillids in many parts of the Indo-Pacific.

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. New Zealand spans subtropical/warm temperate through to subantarctic waters, and stomatopods occur throughout this range. The New Zealand stomatopod fauna is revised herein.

WORLD STUDIES

The taxonomy of the Stomatopoda has been extensively studied over the past four decades. The Atlantic species were largely revised by Manning (1969b, 1977a). The eastern Pacific stomatopods were studied by Schmitt (1940) and Hendrickx & Salgado-Barragán (1991). Currently, about 160 Atlanto-East Pacific stomatopods are known. The Indo-West Pacific region, however, contains the largest proportion of world stomatopods (67%). The first major work on the Indo-West Pacific stomatopods recognised 139 species worldwide, and 98 from the Indo-West Pacific (Kemp 1913). Moosa (1986, 1991) made major studies of the Philippine and New Caledonian stomatopods, and Manning (1995) revised the Vietnamese fauna. Ahyong (2001) revised the Australian fauna, recognising 146 species; and

Hamano (2005) and Ahyong (in press) listed 68 species of Stomatopoda from Japan. Seventy-two species are recorded from New Caledonia (Moosa 1991; Ahyong 2007), 63 species from Taiwan (Ahyong *et al.* 2008) and at least 104 species from the China Seas (Wang & Liu 2008). Currently, almost 330 species are known from the Indo-West Pacific region, with new species regularly discovered (e.g. Ahyong 2010a, in press).

PREVIOUS NEW ZEALAND STUDIES

White (1847) listed the first species of stomatopod from New Zealand under the name *Coronis tricarinata*, a nomen nudum. The name *Coronis tricarinata* was validated by Claus (1871) in his work on stomatopod larvae but went unnoticed for almost a century. Heller (1865) reported *Squilla nepa* Latreille, 1828, and *Gonodactylus trispinosus* Dana, 1852, from Auckland, both of which were listed by Miers (1876) as the only two New Zealand stomatopods. Wood-Mason (1875) described *Coronis spinosa* (using specimens believed to originate from both New Zealand and the Andaman Islands) later referring it to *Lysiosquilla* (Wood-Mason 1895). Hector (1877) made the first report of *Squilla armata* H. Milne Edwards, 1837, from New Zealand, and Kirk (1878) described a new species, *Squilla indefensa*, from Kapiti Island and the Chatham Islands. Hutton (1879) described a new species, *Squilla laevis* (not *Squilla laevis* Hess, 1865, now *Belosquilla laevis*) from the Auckland Islands. Miers (1880) synonymised *Squilla indefensa* with *Lysiosquilla spinosa*, but did not comment on Hutton's *Squilla laevis*. In 1882, Thomson described *Squilla tridentata* from Stewart Island. Chilton (1891) reassessed the status of *Squilla laevis* Hutton, *Squilla indefensa* and *Squilla tridentata*, regarding each as synonymous with *Lysiosquilla spinosa*, and listed *Squilla nepa*, *Squilla armata* and *Gonodactylus trispinosus* [as *Protosquilla trispinosa* following Brooks (1886)] from New Zealand.

Chilton (1911a) added *Lysiosquilla brazieri* Miers, 1880, based on specimens from Otaki, New Zealand, and referred Heller's earlier record of *Squilla nepa* to *Squilla affinis* Berthold, 1845. Five species were thus recognised from the region: *Protosquilla trispinosa*, *Lysiosquilla spinosa*, *Lysiosquilla brazieri*, *Squilla armata* and *Squilla affinis*. Subsequently, Richardson (1953) referred New Zealand *Squilla armata* to a new subspecies, *S. a. schizodontia* and Manning (1963b) transferred *Lysiosquilla spinosa* to a new genus, *Heterosquilla*. Manning (1966) showed that *Coronis tricarinata* Claus, 1871, belonged in *Heterosquilla* and was the valid name for the species long known as *Lysiosquilla spinosa* in New

Zealand. Manning (1966) also questioned the records of three species from New Zealand: *Squilla nepa* and *Protosquilla trispinosa* reported by Heller (1865), and *Squilla affinis* reported by Chilton (1911a). Stephenson (1967) described *Hemisquilla ensigera australiensis* as new, based on Australian and New Zealand specimens, and Manning (1968c) resurrected *Pterygosquilla* Hilgendorf, 1890, for *Squilla armata*. Manning (1978b) showed that *Heterosquilla spinosa* and *H. tricarinata* are synonyms. Manning (1991) reported *Odontodactylus brevirostris* (Miers, 1884) from the Kermadec Islands and placed *Lysiosquilla brazieri* in a new genus, *Acaenosquilla*. O'Shea *et al.* (2000) recorded *Bathysquilla microps* (Manning, 1961) from northern New Zealand. Ah Yong (2001) removed *Heterosquilla tridentata* from the synonymy of

H. tricarinata and recognised *Hemisquilla australiensis* as a distinct species. Most recently, *Oratosquilla oratoria* was detected in northern New Zealand as a recent introduction (Ah Yong 2010c).

In summary, the most recent list of New Zealand Stomatopoda (Webber *et al.* 2010) included eight species: *Bathysquilla microps* (Manning, 1961), *Hemisquilla australiensis* Stephenson, 1967, *Odontodactylus brevirostris* (Miers, 1884), *Acaenosquilla brazieri* (Miers, 1880), *Heterosquilla tricarinata* (Claus, 1871), *Heterosquilla tridentata* (Thomson, 1882), *Oratosquilla oratoria* (De Haan, 1844) and *Pterygosquilla schizodontia* (Richardson, 1953). The present study more than doubles the known stomatopod fauna from New Zealand.

MATERIALS AND METHODS

STUDY AREA AND STUDY MATERIAL

The study area spans all localities within the New Zealand Exclusive Economic Zone (EEZ) and Extended Continental Shelf Zone (ECS) from which stomatopods are known, ranging from the Kermadec Islands in the north (~30°S) to the Auckland Islands (~51°S) in the south, Challenger Plateau in the west and the Chatham Rise in the east (Fig. 1). Only species occurring in the New Zealand EEZ and ECS are analysed, but in some cases, specimens of these species from extralimital waters were also included, as in the case of type material, additional specimens that extend known distributions, or material otherwise useful to the present study. In the Systematics section under 'Material examined', type specimens are listed first, followed by New Zealand specimens listed from north to south and generally grouped by administrative/

local government region. Extralimital material is listed last. Specimens are deposited in the NIWA Invertebrate Collection (NIWA) and Marine Invasives Taxonomic Service (NIWA-MITS) at the National Institute of Water and Atmospheric Research, Wellington; Museum of New Zealand Te Papa Tongarewa (NMNZ); Auckland War Memorial Museum, Auckland (AWMM); Australian Museum, Sydney (AM); Canterbury Museum, Christchurch (CM); Muséum national d'Histoire naturelle, Paris (MNHN), National Museum of Natural History, Smithsonian Institution, Washington DC (USNM); Natural History Museum, London (NHM); Naturhistorisches Museum Wien (NHMW); Otago Museum, Dunedin (OM); University Museum of Zoology, Cambridge (MZC); and Western Australian Museum, Perth (WAM).

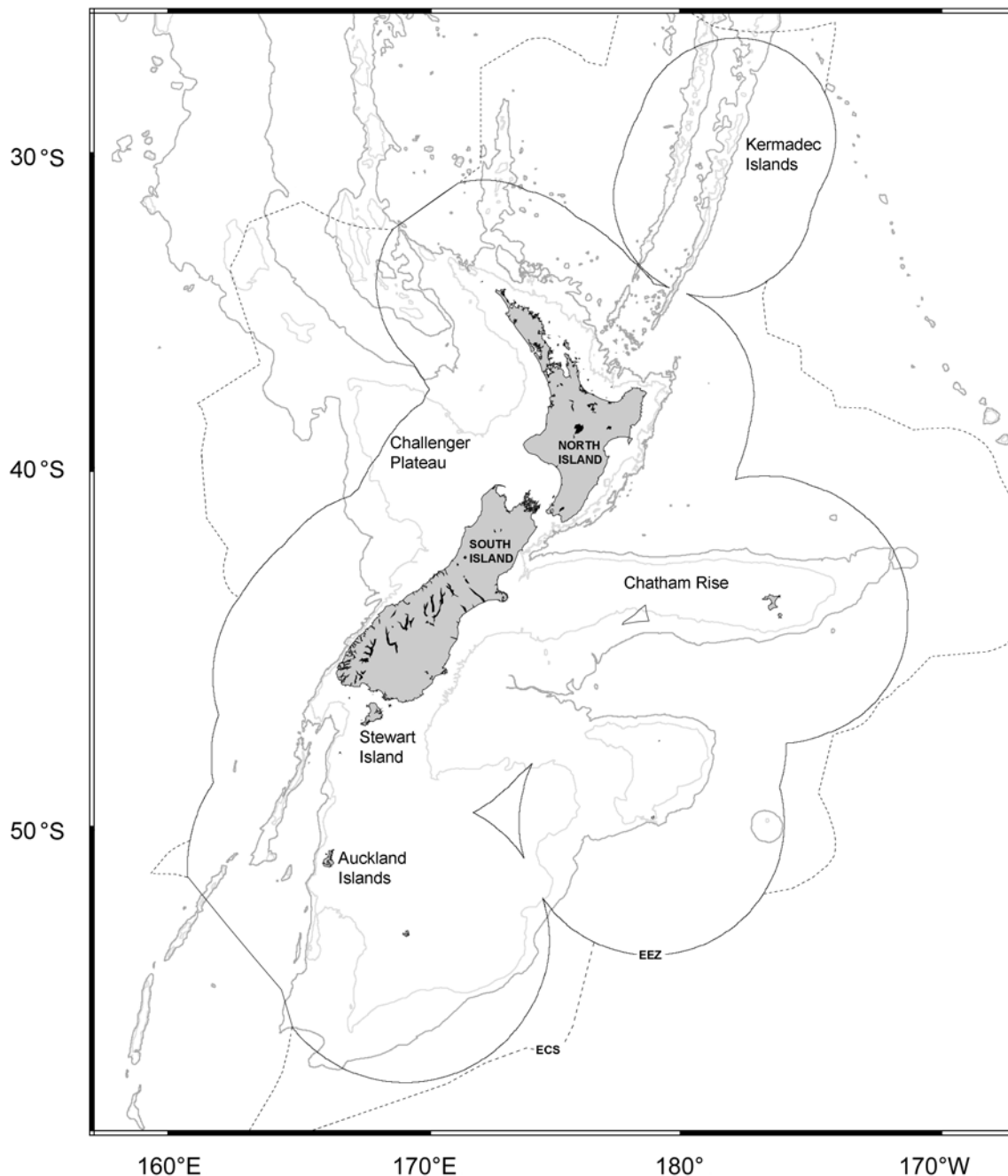


Figure 1. Study area, showing boundaries of the New Zealand Exclusive Economic Zone (EEZ) (solid lines) and Extended Continental Shelf Zone (ECS) (broken lines).

MEASUREMENTS AND TERMINOLOGY

Terminology and size descriptors generally follow Ahyong (2001) and Ahyong *et al.* (2008). General morphology is illustrated in Figs 2–4. Specimens are measured in millimetres (mm). Total length (TL) is measured along the midline from the apex of the rostral plate to the apices of the submedian teeth of the telson. For broken or damaged specimens, carapace

length (CL) is indicated, measured along the midline excluding the rostral plate.

Spination of abdominal carinae, herein used for bathysquilloids and squilloids, follows a standard structure, for instance, submedian 5–6, intermediate (3)4–6, lateral 1–6, marginal 1–5. This indicates that the submedian carinae are posteriorly spined on AS5–6; the intermediate carinae may or may not be spined

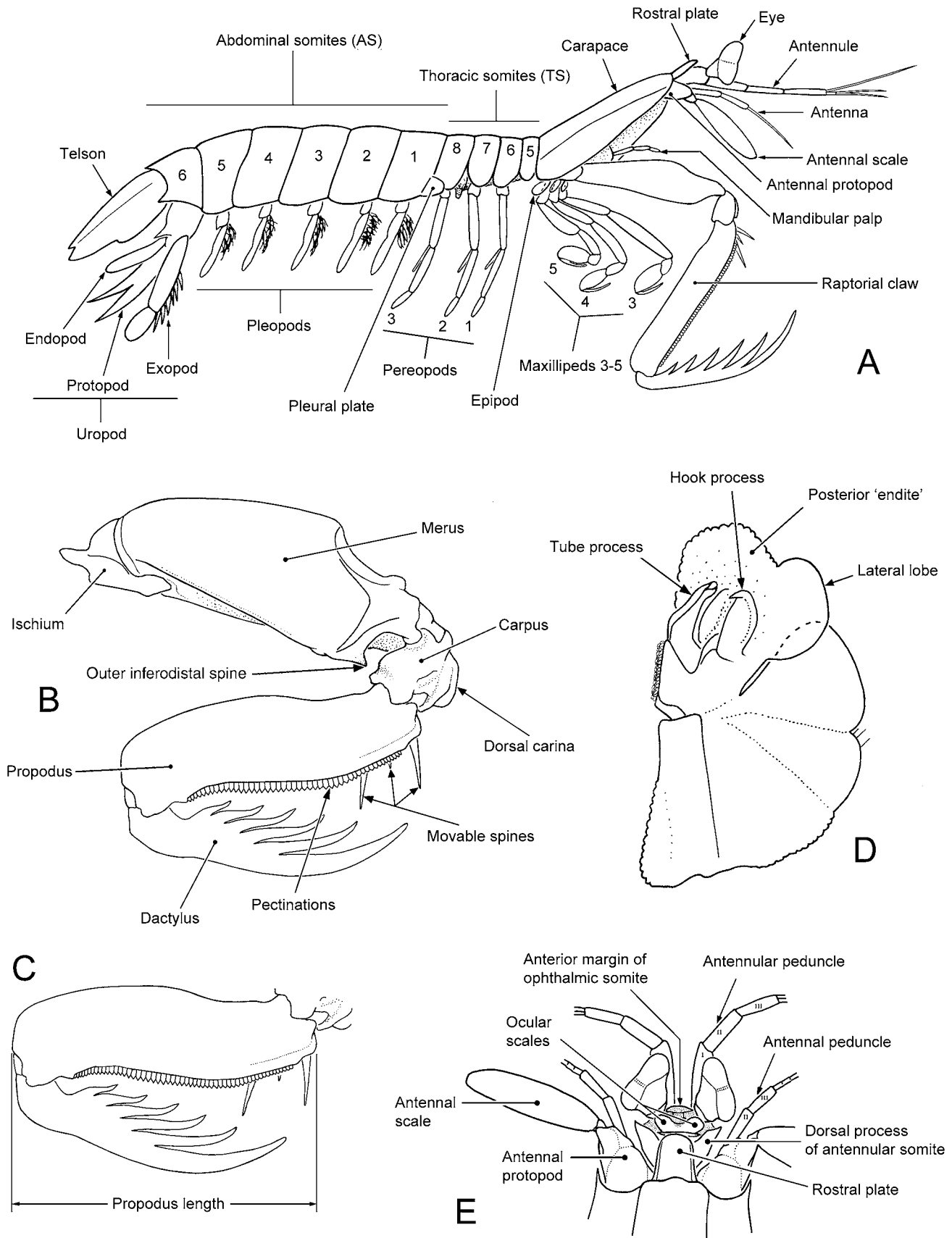


Figure 2. Morphology. A, general; B-C, right raptorial claw; D, right male pleopod 1 endopod, anterior view; E, anterior cephalothorax.

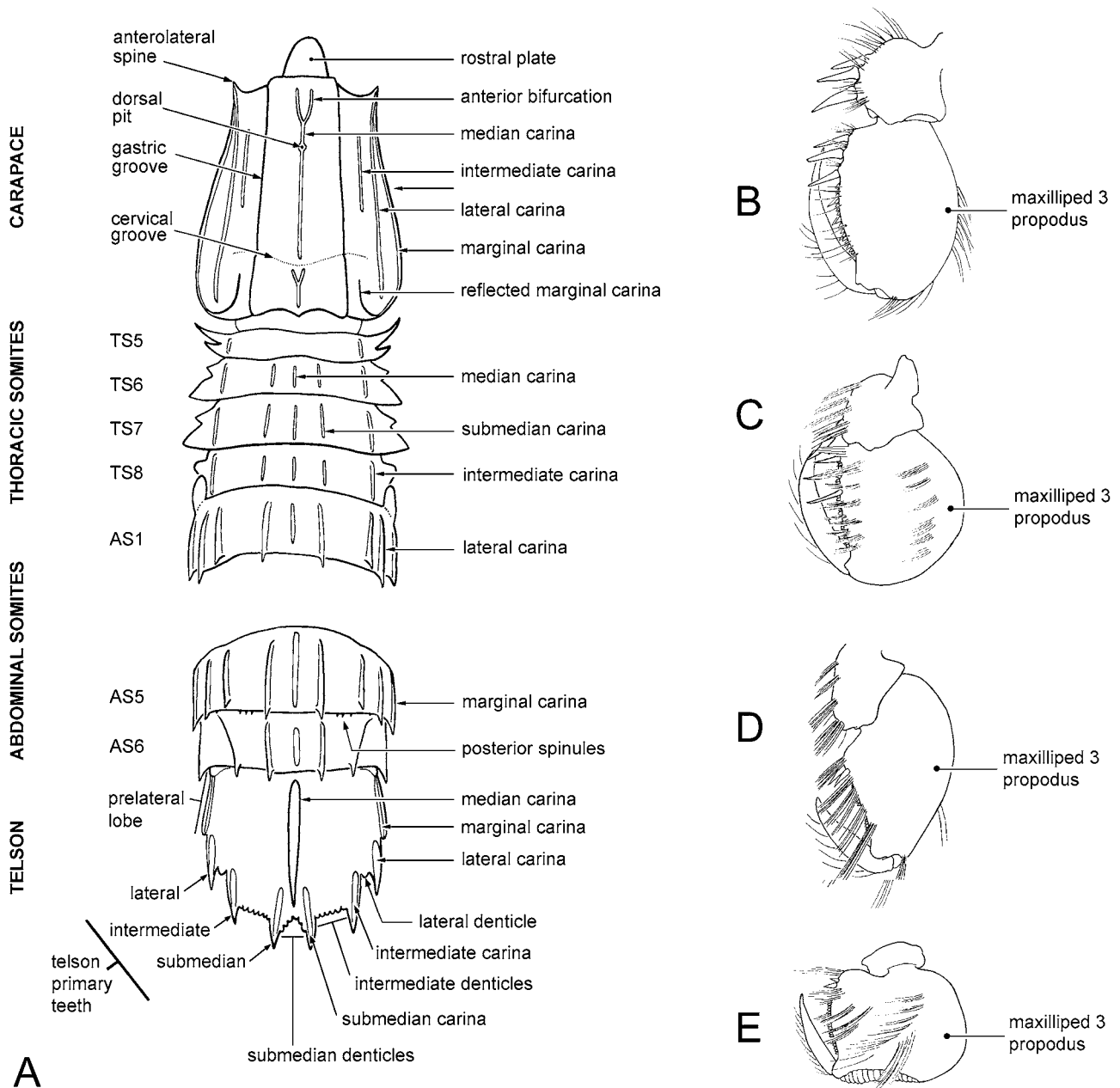


Figure 3. Morphology. A, dorsal carinae; B, maxilliped 3 (Bathysquilloidea); C, maxilliped 3 (Squilloidea); D, maxilliped 3 (Gonodactyloidea); E, maxilliped 3 (Lysiosquilloidea).

on AS3, but are always spined on AS4–6; the lateral carinae are spined on AS1–6; and the marginal carinae are spined on AS1–5.

Relative eye size is a useful taxonomic feature in some species and is measured by the corneal index (CI). The CI is given as $100CL/\text{corneal width}$. The relative length of the raptorial claw, useful among some lysiosquilloids, is measured by the propodal index (PI), given as $100CL/\text{propodus length}$. The relative width of the abdomen in some gonodactyloids is indicated by the abdominal-width carapace-length index (AWCLI),

given as $100(\text{AS5 width})/CL$. Other abbreviations: abdominal somite (AS), and thoracic somite (TS). Rostral plate length is measured along the midline, and rostral plate width is the greatest width.

Distribution maps were produced with the aid of Online Map Creation (www.aquarius.ifm-geomar.de currently www.planiglobe.com).

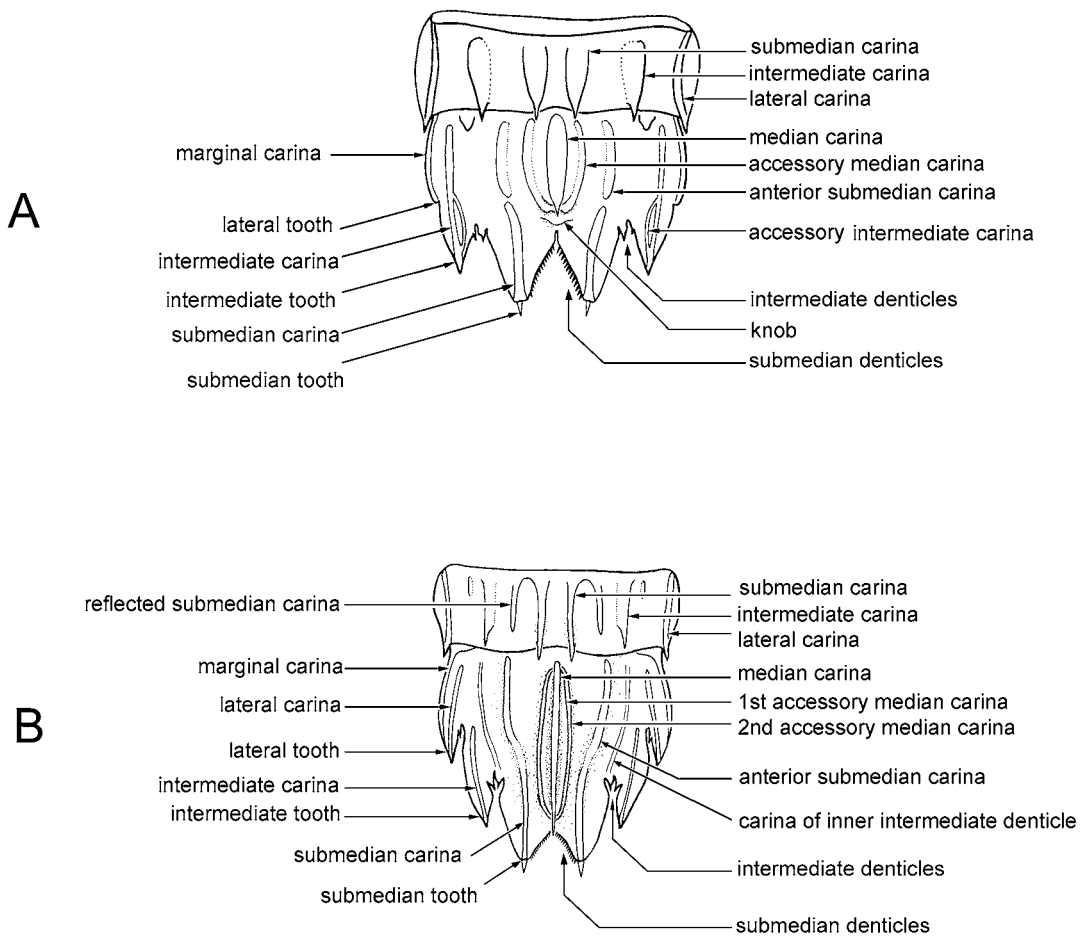


Figure 4. Telson morphology. A, Gonodactylidae; B, Odontodactylidae.

CHECKLIST OF NEW ZEALAND STOMATOPODA

Superfamily BATHYSQUILLOIDEA Manning, 1967

Family BATHYSQUILLIDAE Manning, 1967

Bathysquilla microps (Manning, 1961)

Superfamily GONODACTYLOIDEA Giesbrecht, 1910

Family GONODACTYLIDAE Giesbrecht, 1910

Gonodactylaceus falcatus (Forskål, 1775)*

Gonodactylellus osheai sp. nov.

Gonodactylellus viridis (Serène, 1954)*

Gonodactylus platysoma Wood-Mason, 1895*

Family HEMISQUILLIDAE Manning, 1980

Hemisquilla australiensis Stephenson, 1967

Family ODONTODACTYLIDAE Manning, 1980

Odontodactylus hawaiiensis Manning, 1967*

Odontodactylus scyllarus (Linnaeus, 1758)*

Family PROTOSQUILLIDAE Manning, 1980

Haptosquilla helleri sp. nov.

Superfamily LYSIOSQUILLOIDEA Giesbrecht, 1910

Family TETRASQUILLIDAE Manning & Camp, 1993

Colubrisquilla dempsey gen. et sp. nov.

Heterosquilla koning sp. nov.

Heterosquilla laevis (Hutton, 1879)

Heterosquilla tricarinata (Claus, 1871)

Heterosquilla tridentata (Thomson, 1882)

Heterosquilla trifida sp. nov.

Pariliacantha georgeorum gen. et sp. nov.

Superfamily SQUILLOIDEA Latreille, 1802

Family SQUILLIDAE Latreille, 1802

Anchisquilloides mcneilli (Stephenson, 1953)*

Oratosquilla fabricii (Holthuis, 1941)*

Oratosquilla oratoria (De Haan, 1844)

Pterygosquilla schizodontia (Richardson, 1953)

* new record for New Zealand

SYSTEMATICS

STOMATOPODA

KEY TO NEW ZEALAND SUPERFAMILIES OF THE STOMATOPODA

1. Apices of all primary teeth of telson movable..... **Bathysquilloidea**
– Apices of submedian teeth of telson movable only, or with all primary teeth of telson fixed 2
2. Propodi of maxillipeds 3–4 subquadrate, with distal ribbing..... **Lysiosquilloidea**
– Propodi of maxillipeds 3–4 ovate, without distal ribbing 3
3. Telson with 4 or more intermediate denticles **Squilloidea**
– Telson with 1 or 2 intermediate denticles (rarely with 3) **Gonodactyloidea**

BATHYSQUILLOIDEA Manning, 1967

DIAGNOSIS. Cornea without rows of midband ommatidia; facets, if present, hexagonal. Maxilliped 3–4 propodi ovate, not ribbed or beaded ventrally. Body depressed, articulation compact. Raptorial claw with terminal ischiomerale articulation; propodus occlusal margin with 2 rows of fixed spines and 4 movable spines proximally; dactylus uninflated basally, occlusal margin lined with spines. Telson with distinct median carina; all primary teeth with movable apices; intermediate denticles absent. Uropodal protopod with two primary spines; articulation of exopod segments terminal or distal segment separated from proximal by diaeresis.

COMPOSITION. Bathysquillidae Manning, 1967, Indosquillidae Manning, 1995.

REMARKS. Bathysquilloids are exclusively deepwater species, all of which have reduced or degenerate eyes in which the cornea is reduced in size and lacks a midband of ommatidia. Only Bathysquillidae is represented in New Zealand waters.

BATHYSQUILLIDAE Manning, 1967

Bathysquillidae Manning, 1967b: 238.

DIAGNOSIS. AS5 mid-posterior tergal margin unarmed or at most with minute spinules, without long, posteriorly directed median spine. Telson wider than long, with rugose, tuberculate or granular dorsum. Segments of uropodal exopod fully articulated; distal segment longer than proximal.

COMPOSITION. *Altosquilla* Bruce, 1985; *Bathysquilla* Manning, 1963b.

REMARKS. Only *Bathysquilla* is known from New Zealand.

Bathysquilla Manning, 1963

Bathysquilla Manning, 1963b: 323–324; 1969b: 94–95. [Type species: *Lysiosquilla microps* Manning, 1961, by original designation. Gender: feminine].

DIAGNOSIS. Carapace with cervical groove distinct across dorsum. Male pleopod 1 endopod with lateral lobe on posterior endite. Telson posterior margin with 4 pairs of primary teeth, each with movable apices.

COMPOSITION. *Bathysquilla crassispinosa* (Fukuda, 1909); *B. microps* (Manning, 1961).

REMARKS. One species of *Bathysquilla* is known from New Zealand.

KEY TO SPECIES OF *BATHYSQUILLA*

1. Rostral plate longer than wide, apical spine long, reaching end of antennular peduncle segment 1. Eyes large, cornea pigmented. Posterior margin of AS2–5 without spinules..... *B. crassispinosa*
– Rostral plate wider than long, apical spine short, not reaching midlength of antennular peduncle segment 1. Eyes very small, cornea at most faintly pigmented. Posterior margin of AS2–5 with spinules..... *B. microps*

Bathysquilla microps (Manning, 1961)

(Figs 5, 6, Frontispiece 1A)

Lysiosquilla microps Manning, 1961: 693–696, figs 1–5 [type locality: south-east of Tortugas, Florida Straits, 24°11.0'N, 83°21.5'E].

Bathysquilla microps. – Manning, 1969b: 95–99, figs 26–28.
– Manning & Struhsaker, 1976: 443–408, figs 1, 2.
– Moosa, 1986: 371–373, fig. 1. – Bruce, 1988: 90, figs 1, 5. – Manning *et al.*, 1990: 313–314, fig. 1. – Manning, 1991: 13; 1995: 18. – O'Shea *et al.*, 2000: 36. – Ahyong, 2001: 12–14, fig. 7; 2002b: 349–350, fig. 1. – Webber *et al.*, 2010: 136, 218.

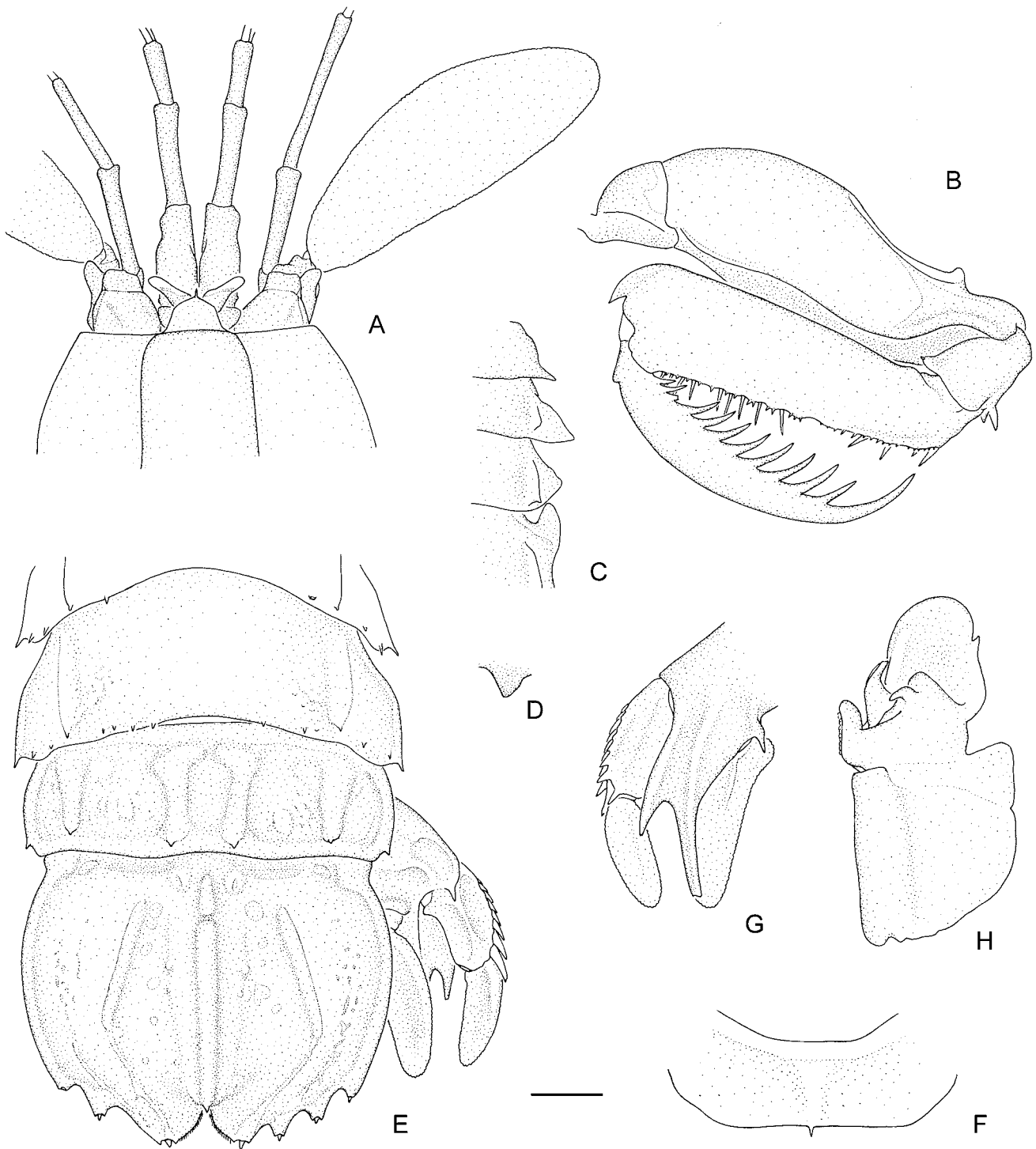


Figure 5. *Bathysquilla microps* (Manning, 1961), male, TL 226 mm, east of East Cape (NIWA 23989). A, anterior cephalothorax; B, right raptorial claw; C, right TS6-8 and AS1 lateral processes, dorsal view; D, TS8 sternal keel, right lateral view; E, AS4-6, telson and right uropod; F, AS6 sternum; G, right uropod, ventral view; H, right pleopod 1 endopod, anterior view. Scale A-C, E-G = 10 mm; D, H = 5 mm.

TYPE MATERIAL. *Holotype*: USNM 104109, male (TL 198 mm), south-east of Tortugas, Florida Straits, 24°11.0'N, 83°21.5'E, 728 m, coll. H. R. Bullis, Jr., 8 Jun 1959.

OTHER MATERIAL EXAMINED. *Gisborne*: NIWA 23989, 1 male (TL 226 mm), east of East Cape, 37°50.0'S, 179°10'E,

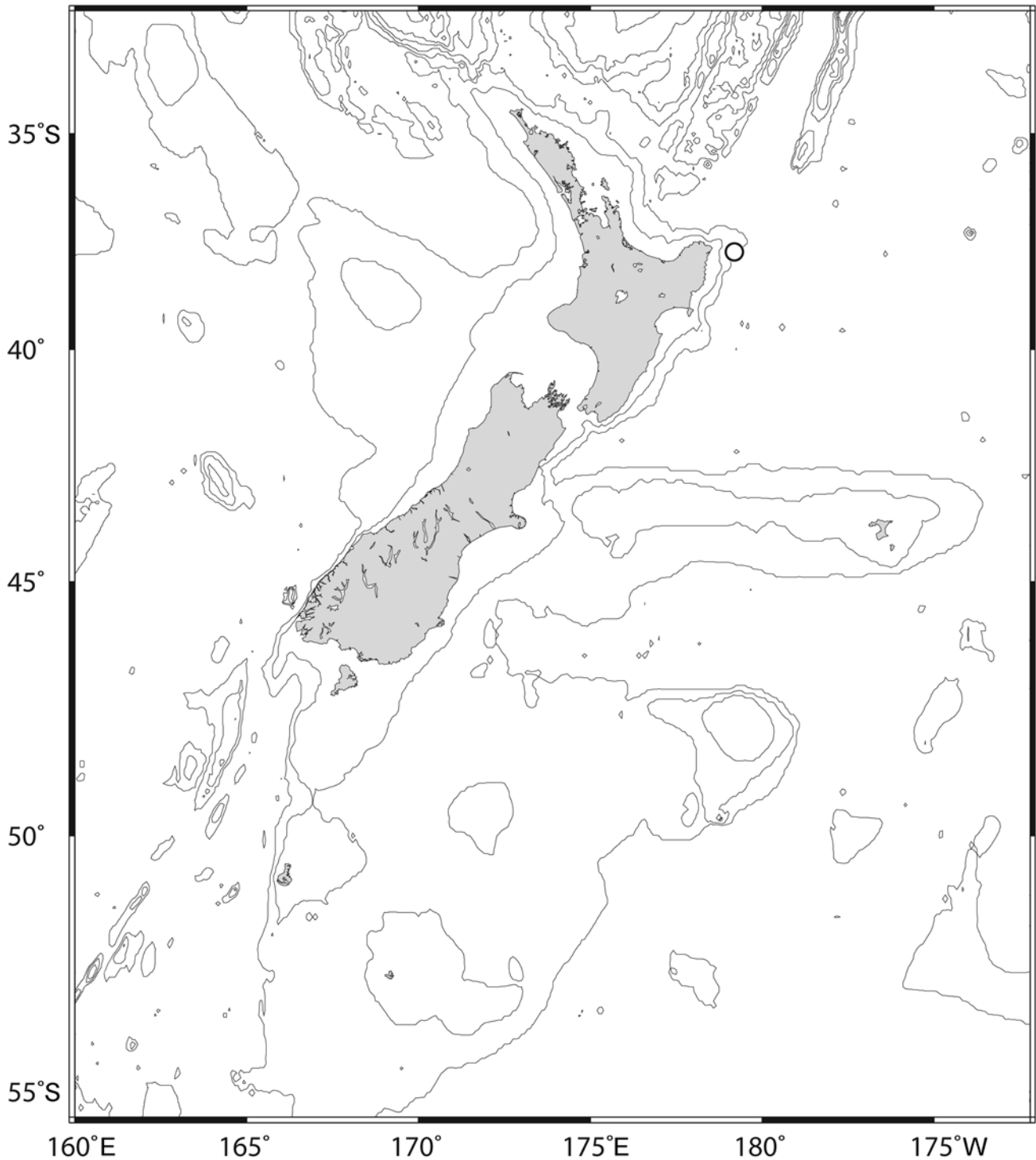


Figure 6. New Zealand distribution of *Bathysquilla microps* (Manning, 1961).

1200 m, FV *Ocean Fresh*, Z10069, coll. D. Wrightson, Dec 1999.

Australia: QM W15314, 1 female (TL 187 mm), Coral Sea, Queensland, 17°49.45'S, 148°39.51'E, 990–1006 m, RV *Franklin*, beam trawl, bottom temperature 5°C, *Cidaris* Expedition, 8 May 1986; AM P52745, 1 female (TL 173 mm), east of Broughton Island, New South

Wales, 32°38'S, 152°54'E, K89-17-02, 814–850 m, coll. K. Graham, 15 Aug 1989; AMP57883, 1 male (TL 109 mm), off Kiama, New South Wales, 34°48–45'S, 151°14–15'E, 730–790 m, trawl, bottom temperature 7.5°C, K89-14-02, coll. K. Graham, 4 Jul 1989.

Tonga: MNHN, 2 females (TL 72–92 mm), north-west of Tongatapu, 20°58'S, 175°16'W, 869–880 m, BOR-

DAU2 stn CP1565, coll. P. Bouchet *et al.*, 9 Jun 2000.

Austral Isles: MNHN, 1 female (TL 86 mm), east of Rapa, 27°37.1'S, 144°15.4'W, 800–850 m, BENTHAUS CP1891, N/O *Alis*, 7 Nov 2002.

DIAGNOSIS. Eye small, inclined laterally, at most faintly pigmented. Rostral plate broader than long; with short apical spine, at most with very shallow median sulcus opening anteriorly. Carapace anterolateral angles obtuse, blunt. Raptorial claw dactylus with 12–15 teeth; carpus dorsal margin with slender, acute distal spine. AS2–4 lower posterior margins with up to 6 spinules. AS5 posterior margin spinulate either side of midline. Telson accessory median carina absent; anterior submedian carina uninterrupted divergent. Uropodal protopod outer margin lacking ventral spine anterior to exopod articulation. Uropodal exopod proximal segment unarmed dorsally excepting dorsal spine above exopod articulation.

DESCRIPTION. Eye small, inclined laterally, at most faintly pigmented. In adults, eye not reaching midlength of antennular peduncle segment 1. Ophthalmic somite anterior margin flattened. Ocular scales obsolete.

Antennular peduncle length 0.92–1.00CL. Antennular somite dorsal processes obsolete. Antennal protopod dorsally unarmed; with 1 ventral papilla. Antennal scale length 2.69–3.68 width, 0.88–1.22CL.

Rostral plate slightly wider than long, subpentagonal, with short median spine; surface smooth, unarmed. Carapace anterolateral angles obtuse, blunt.

Raptorial claw dactylus with 12–15 teeth, outer margin broadly curved, proximal margin with notch. Carpus disto-dorsal margin slender spine, almost perpendicular to carpus surface; posterior margin with minute movable spine. Propodus with 4 movable spines proximally; occlusal margin lateral row of 34–40 minute spines and mesial row of 10–13 slender, upright spines; outer inferodistal margin broadly rounded; distal margin with stout tooth.

Mandibular palp 3-segmented. Maxillipeds 1–5 with epipod. Maxilliped 5 basal segment without ventrally directed spine.

Pereopods 1–3 basal segment unarmed; endopod distal segments elongate, slender. Female gonopore anteriorly with a broad, articulated triangular plate; posteriorly with a transverse median process bearing a pair of short, broad, curved, processes, directed posteroventrally.

Male pleopod 1 endopod with narrow lateral lobe of distal 'endite'.

TS5–6 smooth, non-carinate. TS7 with unarmed intermediate carina. TS8 with posteriorly armed intermediate carina. TS5 lateral process obsolete, lacking ventral spine. TS6 lateral process produced to a short, laterally directed spine. TS7 lateral process triangu-

lar, apex sharp, occasionally bifurcate distally. TS8 lateral process bluntly triangular; sternal keel blunt, angular.

AS1–5 with intermediate and marginal carinae. AS1–4 surface smooth; AS5 surface rugose mesial to intermediate carinae, otherwise smooth. AS6 dorsally rugose; submedian, intermediate and lateral carina blunt, posterior spine minute; without spine or projection anterior to uropodal articulation; sternum posterior margin with median spine. AS1 posterior margins unarmed on either side of midline; AS2–4 with 0–6 spinules; AS5 with 4–8 spinules. Abdominal carinae spined as follows: submedian 6, intermediate (1–3)4–6, lateral 6, marginal 1–5.

Telson flattened, wider than long, surface between carinae smooth to irregular; lateral margins convex; primary teeth triangular, movable apices small, conical; submedian denticles minute, spiniform, 12–24 on either side of midline. Median carina blunt, interrupted proximally; posterior spine small. Anterior submedian carina straight, blunt, divergent posteriorly, unarmed; with low, thin, irregular ridge leading from posterior end of anterior submedian carina to submedian tooth. Post-anal carina long, thin, reaching well beyond midpoint between anal pore and posterior margin of telson.

Uropodal protopod terminal spines slender, ventrally carinate; outer spine shorter than half length of inner spine, margins unarmed; with ventral spine anterior to endopod articulation. Uropodal exopod proximal segment unarmed dorsally; with fixed distal spine and 6–8 movable spines on outer margin, distalmost reaching almost to or slightly beyond midlength of distal exopod segment; outer ventral margin with row of short, fixed spines corresponding to movable spines. Exopod distal segment longer than proximal segment, with blunt laterodorsal carina. Endopod reniform, length 3.38–4.00 times width; blunt laterodorsal carina and short, cristate ventromedial carina.

COLOUR IN LIFE. Dorsal surface almost entirely deep-red. Eye with cornea unpigmented. Antennular peduncle, antennal protopod and peduncle, carpus and distal portion of merus of raptorial claw translucent white.

MEASUREMENTS. Male ($n = 3$) TL 109–226 mm, female ($n = 5$) TL 72–187 mm. The present series includes the largest known specimen of the species.

HABITAT. Soft substrates at depths of 660–1519 m (Manning 1991; Ahlyong 2002b).

REMARKS. *Bathysquilla microps* is the largest and deepest occurring stomatopod in New Zealand waters and is easily recognised in the field by its bright-red body colour. It was first reported from New Zealand based

on the present specimen (O'Shea *et al.* 2000), which is the largest known of the species. The left posterior margin of the telson of the New Zealand specimen is deformed, lacking the second primary tooth, and the distal segment of right antenna is foreshortened, apparently from damage; it otherwise agrees well with previous accounts (Manning 1961; Ah Yong 2001).

Bathysquilla microps can be distinguished from its only congener, *B. crassispinosa* by the short, flat rostral plate (versus longer than wide and dorsally sulcate in *B. crassispinosa*); small, reduced, minimally pigmented eyes (versus large, subglobular, darkly pigmented); spinous rather than unarmed posterior margins of AS2-5; and unarmed lateral margin of the uropodal protopod. *Bathysquilla crassispinosa* ranges from the western Indian Ocean to western margin of the western Pacific, including eastern Australia, and can be expected to occur in deep northern New Zealand waters.

Specimens of *B. microps* collected by the French BORDAU 2 and BENTHAUS expeditions are reported herein to document the presence of the species from Tonga and the Austral Isles, respectively.

DISTRIBUTION. The tropical western Atlantic Ocean and central to western Pacific from French Polynesia, Hawaii and Tonga to the Philippines, eastern Australia and New Zealand.

GONODACTYLOIDEA Giesbrecht, 1910

DIAGNOSIS. Cornea with 6 rows of rectangular ommatidia in the midband. Propodi of maxillipeds 3-4 ovate, not ribbed or beaded ventrally. Body subcylindrical, articulation compact. Raptorial claw with terminal or subterminal ischiomeral articulation; dactylus inflated or not inflated basally. Telson with distinct median carina; submedian teeth with movable apices; at most with 3 intermediate denticles, arising marginally. Uropodal protopod with 1 or 2 primary spines; articulation of exopod segments terminal or subterminal.

COMPOSITION. Alainosquillidae Moosa, 1991; Pseudosquillidae Manning, 1977a; Hemisquillidae Manning, 1980; Odontodactylidae Manning, 1980; Gonodactylidae Giesbrecht, 1910; Protosquillidae Manning, 1980; Takuidae Manning, 1995.

REMARKS. Four families of the Gonodactyloidea are recorded from New Zealand waters, distinguished in the key below. The Gonodactyloidea formerly included all stomatopods having the combination of ovate, unribbed propodi of maxillipeds 3-4, a median carina or boss on the telson and two intermediate denticles on the telson (Manning 1980, 1995). Ah Yong & Harling (2000) however, showed that Parasquillidae and Eurysquillidae, originally placed in Gonodactyloidea, are more

closely related to the Squilloidea and belong in separate superfamilies, Parasquilloidea and Eurysquilloidea. Recent molecular phylogenetic analysis identified further possible polyphyly of the remaining gonodactyloids with Pseudosquillidae and Hemisquillidae placed well outside of the Gonodactyloidea (Ah Yong & Jarman 2009; Porter *et al.* 2010). At present, however, both Pseudosquillidae and Hemisquillidae are retained in the Gonodactyloidea pending further study.

Gonodactyloidea includes the majority of coral reef and rocky shore stomatopods, most notably the 'smashers' of the families Gonodactylidae, Protosquillidae, Odontodactylidae and Takuidae.

KEY TO NEW ZEALAND FAMILIES OF THE GONODACTYLOIDEA

1. Raptorial claw with terminal ischiomeral articulation; dactylus with outer proximal margin thickened but not inflated into distinct, buttressed heel. Uropodal protopod with one prominent terminal spine and at most a minute spinule on outer margin of primary spine **Hemisquillidae**
 - Raptorial claw with subterminal ischiomeral articulation; base of dactylus strongly inflated, forming blunt, buttressed heel. Uropodal protopod terminating in two prominent terminal spines 2
2. Articulation of uropodal exopod segments terminal..... 3
 - Articulation of uropodal exopod segments subterminal..... **Gonodactylidae**
3. Dactylus of raptorial claw with short teeth on inner margin. Antennal protopod with articulated dorsal plate. AS6 articulating with telson. Telson with distinct median carina **Odontodactylidae**
 - Dactylus of raptorial claw without teeth on inner margin. Antennal protopod with fixed dorsal spine. AS6 fused with telson. Telson with low median boss **Protosquillidae**

GONODACTYLIDAE Giesbrecht, 1910

Gonodactylinae Giesbrecht, 1910: 148.
Gonodactylidae. - Manning, 1968c: 137.

DIAGNOSIS. Rostral plate trispinous or with median spine and trapezoid basal portion. Antennal protopod dorsally with fixed, anteriorly directed spine or tooth. Raptorial claw with subterminal ischiomeral articulation; propodus occlusal margin sparsely pectinate; dactylus of raptorial claw without teeth on inner margin, outer basal margin strongly inflated into blunt heel. AS6 articulating with telson. Telson with distinct median carina. Articulation of uropodal exopod segments subterminal. Distal spines on outer margin of

uropodal exopod slender, straight or slightly curved, not strongly recurved anteriorly.

COMPOSITION. *Gonodactylaceus* Manning, 1995; *Gonodactyllellus* Manning, 1995; *Gonodactyloideus* Manning, 1984a; *Gonodactylolus* Manning, 1970; *Gonodactylopsis* Manning, 1969c; *Gonodactylus* Berthold, 1827; *Hoplosquilla* Holthuis, 1964; *Hoplosquilloides* Manning, 1978b; *Neogonodactylus* Manning, 1995.

REMARKS. Three gonodactylid genera are recorded from New Zealand waters: *Gonodactylaceus*, *Gonodactyllellus* and *Gonodactylus*.

KEY TO NEW ZEALAND GENERA OF GONODACTYLIDAE

1. Ocular scales truncate, wider than base of median spine of rostral plate.....*Gonodactylus*
 - Ocular scales rounded or angular, narrower than base of apical spine of rostral plate.....2
2. Uropodal protopod without lobes between terminal spines.....*Gonodactyllellus*
 - Uropodal protopod with 1 or 2 lobes between terminal spines*Gonodactylaceus*

Gonodactylaceus Manning, 1995

Gonodactylaceus Manning, 1995: 42–43. [Type species: *Gonodactylus ternatensis* De Man, 1902, by original designation. Gender: masculine].

DIAGNOSIS. Eye subcylindrical, cornea not broader than stalk in dorsal view. Ocular scales small, narrower than basal width of median spine of rostral plate, rounded dorsally. Rostral plate with slender median spine and short, broad, trapezoid basal portion. Anterolateral margins of carapace convex, extending anteriorly beyond base of rostral plate. Mandibular palp present. Opposable margin of propodus of raptorial claw without proximal movable spine in adults. Telson with 5 mid-dorsal carinae (median, paired anterior submedian, paired anterior intermediate); intermediate carina without accessory longitudinal carina on mesial margin; anus located ventrally; submedian and intermediate teeth prominent; lateral tooth acute, indicated by V-shaped incision in telson margin. Uropodal protopod with one or two proximal lobes between terminal spines; endopod margins fully setose, without spines on inner margin.

COMPOSITION. *Gonodactylaceus falcatus* (Forskål, 1775); *G. graphurus* (Miers, 1875); *G. glabrous* (Brooks, 1886); *G. randalli* (Manning, 1978a); *G. ternatensis* (De Man, 1902).

REMARKS. *Gonodactylaceus* differs from other gonodactylids by the combination of subglobular corneae,

absence of a movable proximal spine on the propodus of the raptorial claw in adults, and the presence of five mid-dorsal carinae on the telson. One species of *Gonodactylaceus* is known from New Zealand waters.

KEY TO SPECIES OF GONODACTYLACEUS

1. AS1–5 with fine transverse grooves crossing dorsum. [Rostral plate with angular anterolateral angles; meral spot on raptorial claw orange in life] ..
.....*G. graphurus*
- AS1–5 smooth, without fine transverse grooves crossing dorsum. [Meral spot on raptorial claw yellow or orange in life]2
2. Rostral plate with blunt, rounded anterolateral corners.....3
 - Rostral plate with angular anterolateral corners ...
.....*G. glabrous*
3. Uropodal endopod with multiple rows of marginal setae, some deflected dorsally*G. randalli*
 - Uropodal endopod with single row of marginal setae, some deflected dorsally.....4
4. Telson with undivided knob, at most with a median depression. AS6 never with median carina. Meral spot of raptorial claw orange in males, yellow in females*G. ternatensis*
 - Telson with bilobed knob. AS6 with or without short median carina. Meral spot of raptorial claw yellow in both sexes*G. falcatus*

Gonodactylaceus falcatus (Forskål, 1775)

(Figs 7, 8)

Cancer falcatus Forskål, 1775: 96 [type locality: Djeddah, Red Sea, by neotype selection (Manning & Lewinsohn 1981)].

Gonodactylus chiragra var. *mutatus* Lanchester, 1903: 450 [type locality: Furnadu Velu, Miladumadulu Atoll, Maldive Islands, 6°00'N, 73°10'E].

Gonodactylus glaber var. *rotundus* Borradaile, 1907: 211–212, pl. 22: fig. 2 [type locality: Coetivy, Seychelles, 7°08'S, 56°16'E, and Zanzibar, 6°10'S, 39°12'E].

Gonodactylus insularis Manning & Reaka, 1982: 347–351, figs. 1, 2 [type locality: Kidrenen Island, Enewetak, 11°22'50"N, 162°10'30"E]. — Moosa 1989: 224.

Gonodactylus aloha Manning & Reaka, 1981a: 190–200, figs. 1–3 [type locality: Oahu, Hawaiian Islands].

Gonodactylus siamensis Manning & Reaka, 1981b: 479–482, fig. 1 [type locality: Sattahip, Gulf of Thailand, 12°40'N 100°52'E].

Gonodactylus takedai Moosa, 1989: 225–226, fig. 1 [type locality: Miyanojima, Chichi-jima, Ogasawara Islands].

Gonodactylaceus gravieri Manning, 1995: 42, 43, 46–48, fig. 13 [type locality: Poulo Condore, Vietnam].

Gonodactylaceus falcatus. — Ah Yong, 2001: 35–38, fig. 17.

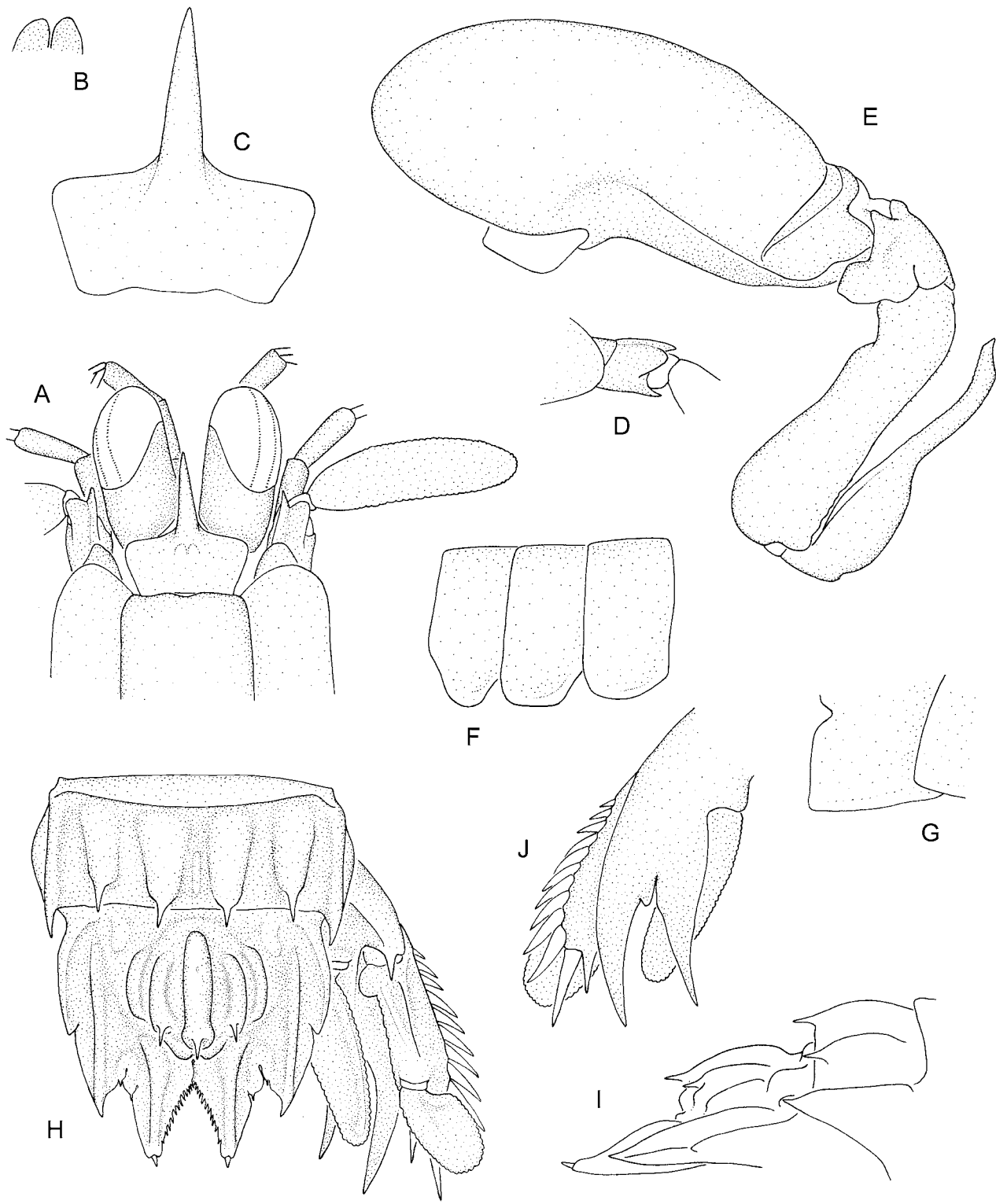


Figure 7. *Gonodactylaceus falcatus* (Forskål, 1775), female, TL 30 mm, south of Three Kings Islands (NIWA 23968). A, anterior cephalothorax; B, ocular scales; C, rostral plate; D, right antennal protopod, lateral view; E, right rap-torial claw; F, TS6–8, right lateral view; G, AS4–5, right lower lateral view; H, AS6, telson and right uropod; I, AS6 and telson, right lateral view; J, right uropod, ventral view. Scale A, D–I = 2.5 mm, B–C = 1.2 mm.

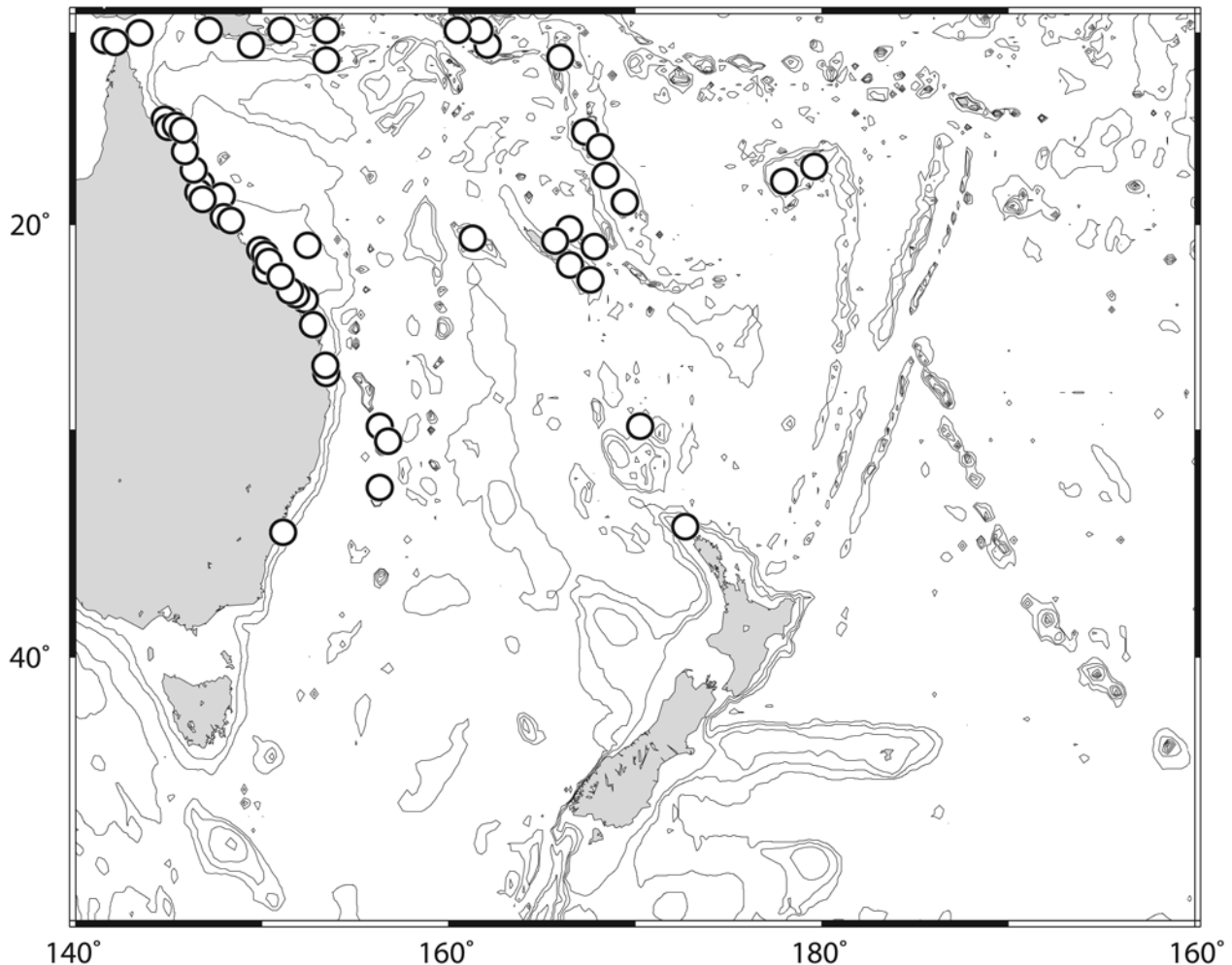


Figure 8. South-western Pacific distribution of *Gonodactylaceus falcatus* (Forskål, 1775).

TYPE MATERIAL. *Neotype*: RMNH S874, female (TL 63 mm), Djeddah, Red Sea.

OTHER MATERIAL EXAMINED. *Northland*: NIWA 23968, 1 male (TL 16 mm), 6 females (TL 9–30 mm), south of Three Kings Islands, 34°57.79'S, 172°18.10'E, 400 m, NZOI stn P597, 2 Jul 1978.

Lord Howe Island, Tasman Sea: AM P1173–1181, 1 male (TL 46 mm), 8 females (TL 52–68 mm), 31°33'S, 159°05'E, coll. Mrs Nicholls, Jan 1907; AM P53615, 4 males (TL 26–67 mm), 9 females (TL 27–65 mm), 31°33'S, 159°05'E, coll. J. Booth, 18 Sep 1962; AM P73336–73337, 1 female (TL 45 mm), 1 male (TL 39 mm), Potholes, 31°33.84'S, 159°04.32'E, intertidal, under rocks, coll. G. Kelly, 19 Sep 2004; AM P73335, 1 female (TL 54 mm), Neds Beach, 31°31.02'S, 159°04.08'E, reef flat, low tide, under rocks, coll. G. Kelly, 7 Apr 2004; AM P73339, 1 female (TL 54 mm), North Bay, 31°31.38'S, 159°02.7'E, reef flat, coll. G. Kelly, 26 Oct 2003; AM P64231, 2 females (TL 52–58 mm), North Bay, 31°31.2'S, 159°03.5'E, coll. G. Kelly, 22 Jun 2002.

Middleton Reef, Tasman Sea: NIWA 23971, 1 female (TL 47 mm), 29°26.59'S, 159°04.69'E, shore, NZOI stn Q63, 31 May 1978; NIWA 23970, 1 male (TL 19 mm), 29°27.00'S, 159°05.50'E, 3 m, NZOI stn Q61, 30 May 1978. RED SEA: MNHN, 4 males (TL 34–63 mm), 4 females (TL 38–54 mm), Masfaur, Red Sea, coll. E. Ninni, 25 Nov 1929.

DIAGNOSIS. Rostral plate with blunt, rounded anterolateral angles. AS1–5 without fine transverse grooves. AS6 with or without short median carina. Telson knob usually medially emarginated, bilobed; usually with fewer than 13 submedian denticles. Terminal spines of uropodal protopod with 1 or 2 lobes between spines; endopod outer margin with single row of marginal setae, directed dorsally.

DESCRIPTION. Eyes elongate; cornea subconical. Ocular scales separate, apices rounded. Antennular peduncle length 0.51–0.65CL. Antennal scale length 0.49–0.58CL.

Rostral plate about as long as wide; basal portion with transverse or posteriorly sloping anterior margins; anterolateral angles rounded; lateral margins divergent anteriorly; median spine longer than base, without ventral keel.

Raptorial claw dactylus without proximal notch in adults. Carpus dorsal margin unarmed. Propodus opposable margin sparsely pectinate proximally.

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

TS6–7 lateral process width subequal; lower margins rounded, slightly flattened. TS8 anterolateral margin rounded; sternal keel obsolete.

Pereopodal endopods slender, linear, 2-segmented; basal segment unarmed.

Pleopod 1 endopod with distinct lateral lobe on posterior 'endite'.

Abdominal somite 1–5 dorsal surface without transverse grooves; posterolateral angles unarmed. AWCLI 757–838. Abdominal somite 6 with posteriorly armed submedian, intermediate and lateral carinae; usually with short median carina.

Telson wider than long, surface without dorsal spinules; with 8–14 spiniform submedian denticles. Submedian teeth unarmed dorsally, dorsal carina relatively slender. Intermediate teeth distinct, apices sharp, extending posteriorly well beyond apices of intermediate denticles; intermediate carina slender, extending anteriorly as far as accessory median and anterior submedian carinae; emargination between submedian and intermediate teeth acute. Lateral teeth demarcated by short notch, apex angular, not projecting well off margin of telson. Median carina more strongly inflated in males than in females; with posterior spine. Accessory median carinae with posterior spine, extending anteriorly beyond dorsal pit but not as far as anterior end of median carina. Anterior submedian carina smooth, unarmed, arcuate, as long as accessory median carina. Knob usually medially emarginate. Ventral surface with low carina on submedian teeth and short post-anal carina.

Uropodal protopod terminal spines with outer spine longer, with small lobe on inner proximal margin of outer spine, occasionally with small lobe on outer proximal margin of inner spine. Uropodal exopod proximal segment outer margin with 11–16 (usually 11 or 12) movable spines, distalmost extending to or exceeding apex of distal segment; margin fully setose; distal margin with ventral spine; exopod distal segment rounded, entire margin setose. Uropodal endopod narrow, length about 4 times width; with low dorsolateral carina; margins with single setal row.

COLOUR IN LIFE. Highly variable. The body colouration varies from uniform or mottled yellow to orange red

to black green. 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.

MEASUREMENTS. Male ($n = 12$) TL 16–67 mm, female ($n = 33$) TL 9–65 mm. Ah Yong (2001) recorded specimens to TL 80 mm.

HABITAT. Crevices in or under rocks, rubble, boulders, corals, mussels, sponges and fouling on rocky and coral reefs and associated seagrass beds. Usually from intertidal or shallow subtidal habitats but possibly to 400 m depth (this study).

REMARKS. *Gonodactylaceus falcatus* is one of the most widespread gonodactylids, ranging from the western Indian Ocean to French Polynesia and, more recently, Hawaii, where it was accidentally introduced after the Second World War (Kinzie 1968). It is common in most tropical reef habitats in the western Pacific including the Great Barrier Reef, New Caledonia, Lord Howe Island and Norfolk Island. In eastern Australia, *G. falcatus* is known as far south as the Sydney region (Ah Yong 2001), so the discovery of *G. falcatus* in northern New Zealand is not surprising.

The Three Kings specimens of *G. falcatus* agree well with published accounts (Manning 1978a; Manning & Lewinsohn 1981; Ah Yong 2001) and are the first New Zealand records of the species. The median carina on AS6, considered diagnostic for *G. falcatus* by Manning (1978a), has proved variable in *G. falcatus* throughout its geographical range (Ah Yong 2001), including the Red Sea (specimens examined herein). The median carina is present in the largest New Zealand specimen (female, TL 30 mm; Fig. 7H), but indistinct or absent in remaining New Zealand specimens (TL 9–26 mm), and variably developed in the Lord Howe Island and Norfolk Island specimens.

Gonodactylaceus falcatus is easily distinguished from other New Zealand gonodactylids by having five rather than three mid-dorsal carinae on the telson.

HABITAT. Crevices in sponge, coral and rock on coral and rocky reefs. *Gonodactylaceus falcatus* usually occurs in shallow water from the intertidal zone to less than 80 m, so the 400 m depth recorded for the present New Zealand specimens may not be accurate.

DISTRIBUTION. Eastern Africa and the Red Sea, to Indonesia, Australia, New Caledonia, Japan, Fiji, Hawaii (introduced), French Polynesia and now from New Zealand waters.

Gonodactylellus Manning, 1995

Gonodactylellus Manning, 1995: 56–57. [Type species: *Gonodactylus affinis* De Man, 1902, by original designation. Gender: masculine].

Gonodactylinus Manning, 1995: 66. [Type species: *Gonodactylus viridis* Serène, 1954, by original designation and monotypy. Gender: masculine].

DIAGNOSIS. Eye subcylindrical, cornea not broader than stalk in dorsal view. Ocular scales small, narrower than basal width of median spine of rostral plate, usually, rounded dorsally. Rostral plate with slender median spine and short, broad, trapezoid basal portion. Anterolateral margins of carapace convex, extending anteriorly beyond base of rostral plate. Mandibular palp present. Propodus of raptorial claw with proximal movable spine in adults. Telson with 3 or 5 mid-dorsal carinae; intermediate carina of telson without accessory longitudinal carina on mesial margin; anus located ventrally. Uropodal protopod without lobes between terminal spines; endopod without spines on inner margin.

COMPOSITION. *Gonodactylellus annularis* Erdmann & Manning, 1998; *G. affinis* (De Man, 1902); *G. barberi* Ahyong & Erdmann, 2007; *G. bicarinatus* (Manning, 1968b); *G. caldwelli* Erdmann & Manning, 1998; *G. chopraii* (Manning, 1967c); *G. crosnieri* (Manning, 1968b); *G. demanii* (Henderson, 1893); *G. dianae* Ahyong, 2008; *G. erdmanni* Ahyong, 2001; *G. espinosus* (Borradaile, 1898); *G. incipiens* (Lanchester, 1903); *G. kandi* Ahyong & Erdmann, 2007; *G. lanchesteri* (Manning, 1967c); *G. micronesicus* (Manning, 1971a); *G. molyneux* Ahyong, 2001; *G. osheai* sp. nov.; *G. rubriguttatus* Erdmann & Manning, 1998; *G. spinosus* (Bigelow, 1893); *G. snidvongsi* (Naiyanetr, 1987); *G. viridis* (Serène, 1954).

REMARKS. *Gonodactylellus* currently includes 21 species, all from the Indo-West Pacific (Ahyong 2001, 2008; Ahyong & Erdmann 2007). Species of *Gonodactylellus* are generally smaller than TL 30 mm and are abundant on subtropical and tropical coral and rocky substrates living in holes in coral rock, coralline algae, rubble and sponge. Telson morphology in *Gonodactylellus* is significantly heterogeneous suggesting that the genus is not monophyletic (Ahyong 2001). In particular, one group within *Gonodactylellus*, allied to *G. demanii* and *G. snidvongsi*, comprises species with a dorsally spinose telson, an upright spine at the base of the submedian teeth, and (usually) minimal or suppressed setation on the inner margin of the uropodal endopod and exopod (Ahyong & Erdmann 2007). Of the two species of *Gonodactylellus* known from New Zealand waters, *G. viridis* is allied to the type species of the genus, *G. affinis*, and the new species is allied to *G. demanii* and *G. snidvongsi*.

KEY TO SPECIES OF *GONODACTYLELLUS* FROM NEW ZEALAND

1. Telson with multiple dorsal spines. Uropodal endopod without setae along most of inner margin. *G. osheai*
- Telson without dorsal spines, at most with posterior spine on median carina. Uropodal endopod fully setose along inner margin *G. viridis*

Gonodactylellus osheai sp. nov. (Fig. 9)

TYPE MATERIAL. *Holotype*: USNM 1098983, male (TL 19 mm), New Zealand, USNS *Eltanin*, cruise 16, 1965. *Paratype*: USNM 1098984, 1 female (TL 24 mm), collected with holotype.

DIAGNOSIS. Ocular scales low, separate, bases slightly oblique. Rostral plate basal portion with straight anterior margins, sloping posteriorly; anterolateral margins rounded. Raptorial claw dactylus with shallow notch on outer proximal margin. Mandibular palp 3-segmented. Telson intermediate teeth distinct, apices sharp, extending posteriorly well beyond apices of intermediate denticles; lateral teeth projecting well off margin of telson. Telson median and accessory median carinae together with a group of 6 posterior spines; anterior submedian carina with 2 spines; submedian tooth with 2 spines proximally in transverse row; intermediate tooth with 1 dorsal spine preceded by 2 spines on anterior intermediate carina; submedian and intermediate teeth without ventral carinae. Uropodal protopod with low obtuse swelling behind dorsal carina. Uropodal exopod proximal segment inner margin smooth, glabrous; distal margin with ventral spine; exopod distal segment with outer margin setose, inner margin smooth, glabrous. Uropodal endopod about 3 times as long as wide; distal half of outer margin setose, inner margin smooth, glabrous except for 4 or 5 proximal setae.

DESCRIPTION. Eyes elongate; cornea subconical. Ocular scales low, separate, bases slightly oblique. Antennular peduncle length 0.58–0.61CL. Antennal scale length 0.48–0.47CL.

Rostral plate longer than wide; basal portion with straight anterior margins, sloping posteriorly; anterolateral margins rounded; lateral margins divergent anteriorly; median spine longer than base, laterally compressed, with obtusely angular ventral keel.

Raptorial claw dactylus with shallow notch on outer proximal margin. Carpus dorsal margin unarmed. Propodus proximal movable spine slender; opposable margin sparsely pectinate proximally.

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

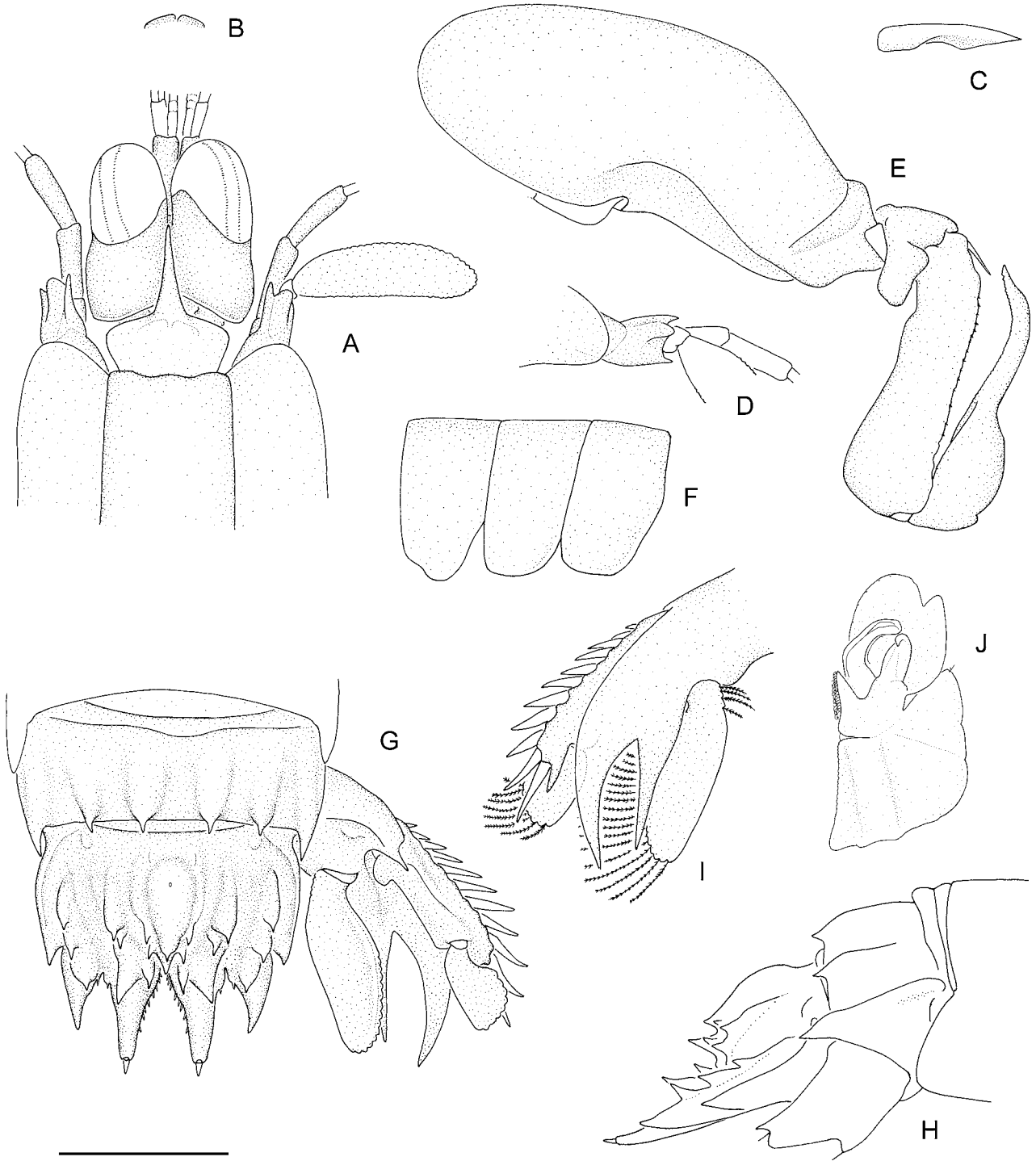


Figure 9. *Gonodactylellus osheai* sp. nov., male holotype, TL 19 mm, New Zealand region (USNM 1098983). A, anterior cephalothorax; B, ocular scales; C, rostral plate, right lateral view; D, right antennal protopod, lateral view; E, right raptorial claw; F, TS6-8, right lateral view; G, AS6, telson and right uropod; H, AS6 and telson, right lateral view; I, right uropod, ventral view; J, right pleopod 1 endopod, anterior view. Scale A-I = 2.0 mm, J = 1.0 mm.

TS6 lateral process subequal to that of TS7; lower margins subtruncate. TS8 anterolateral margin rounded; sternal keel obsolete.

Pereopodal endopods slender, linear, 2-segmented; basal segment unarmed.

Pleopod 1 endopod with well developed lateral lobe on posterior endite.

AS1–5 posterolateral angles unarmed. AWCLI 814–826. AS6 with submedian, intermediate and lateral spines.

Telson wider than long; with 9 or 10 spiniform submedian denticles; intermediate teeth distinct, apices sharp, extending posteriorly well beyond apices of intermediate denticles; lateral teeth demarcated by distinct notch, apex sharp, projecting well off margin of telson. Telson median carina ovate, not obscuring accessory median carina, together with a group of 6 posterior spines (2 spines on median, 2 spines on each accessory median); anterior submedian carina with 2 spines in longitudinal row; submedian tooth armed dorsally with 2 spines proximally in transverse row, mesial spine smaller; intermediate tooth with 1 dorsal spine preceded by 2 spines on anterior intermediate carina; knob absent; submedian and intermediate teeth without ventral carinae.

Uropodal protopod terminal spines with outer slightly longer than inner; upper proximal surface with low obtuse swelling behind dorsal carina. Uropodal exopod proximal segment outer margin with 10 or 11 movable spines, distalmost slightly exceeding apex of distal segment; inner margin smooth, glabrous; distal margin with ventral spine; exopod distal segment with outer margin setose, inner margin smooth, glabrous. Uropodal endopod length 2.91–2.95 times width; distal half of outer margin setose, inner margin smooth, glabrous except for 4 or 5 proximal setae.

COLOUR IN LIFE. Not known.

MEASUREMENTS. Male ($n = 1$) TL 19 mm, female ($n = 1$) TL 24 mm. Other measurements of holotype: CL 1.8 mm, antennular peduncle 1.1 mm, antennal scale 0.9 mm, abdominal somite 5 width 1.5 mm.

ETYMOLOGY. Named after Steve O'Shea (formerly NIWA) for his invaluable assistance during the initial stages of the project.

HABITAT. Not known.

REMARKS. *Gonodactylellus osheai* sp. nov. belongs to the group of species within the genus having reduced or suppressed setation on the inner margins of the uropodal exopod and endopod, and dorsally spinose telsons. Of these species, *G. osheai* most closely resembles *G. demanii* (Henderson, 1893) from the Indian Ocean in

having a small cluster of setae on the inner proximal margin of the uropodal endopod. Comparison of the New Zealand specimens with published accounts (Henderson 1893; Kemp 1913; Ingle 1963; Manning 1967c) and specimens collected from near the type locality in southern India (AM P3967, 2 females, TL 18–26 mm, Kilakarai, Ramnad District, Gulf of Mannar) shows that *G. osheai* differs in having the anterior margins of the rostral plate sloping posteriorly, the anterolateral corners of the rostral plate distinctly rounded, and the intermediate teeth of the telson distinctly longer than half the length of the submedian teeth. In *G. demanii*, the anterior margins of the rostral plate are concave and the anterolateral corners are angular to sharp. The slope of the anterior margins of the rostral plate can vary allometrically in many gonodactylids (Ahyong 2001), but the differences noted between *G. osheai* and *G. demanii* are present in size-matched adults. In *G. demanii*, the intermediate teeth of the telson are shorter than half the length of the submedian teeth. The known distributions of *G. osheai* and *G. demanii* are discrete, namely the south-western Pacific and Indian Ocean, respectively. Other congeners in the Australasian region having similar telson ornamentation and reduced or suppressed uropod setation are *G. snidvongsi* (Naiyanetr, 1987) [south-east Asia], *G. barberi* Ahyong & Erdmann, 2007 [Indonesia], *G. molyneux* Ahyong, 2001 [north-eastern Australia] and *G. dianae* Ahyong, 2008 [north-western Australia]. *Gonodactylellus osheai* differs from each of these species in rostral plate form, with rounded rather than angular anterolateral corners and posteriorly inclined rather than concave anterior margins of the basal portion.

Unfortunately, the precise collection locality of the type series of *Gonodactylellus osheai* is not known. *Eltanin* Cruise 16 (28 January to 25 February 1965) traversed the New Zealand region between Auckland and the Hjort Seamount (59°S), including the east side of the North Island, Cook Strait, both sides of the South Island, the Auckland Islands and Macquarie Island (Anonymous 1965). Given the warm-water preference of most gonodactylids, the type material of *G. osheai* probably originated from a northern locality visited by the *Eltanin*, possibly in the vicinity of Auckland.

DISTRIBUTION. Known only from New Zealand waters.

Gonodactylellus viridis (Serène, 1954)

(Figs 10, 11)

Gonodactylus chiragra var. *viridis* Serène, 1954: 6, 7, 10, 74, 75, 76, 87, fig. 13–3 [type locality: Cauda Bay, Vietnam].

Gonodactylellus viridis. — Manning, 1978a: 63–65, fig. 31. — Ahyong, 2001: 63–65, fig. 31.

Gonodactylellus aff. *viridis*. — Ahyong *et al.*, 2008: 13–14, fig. 8.

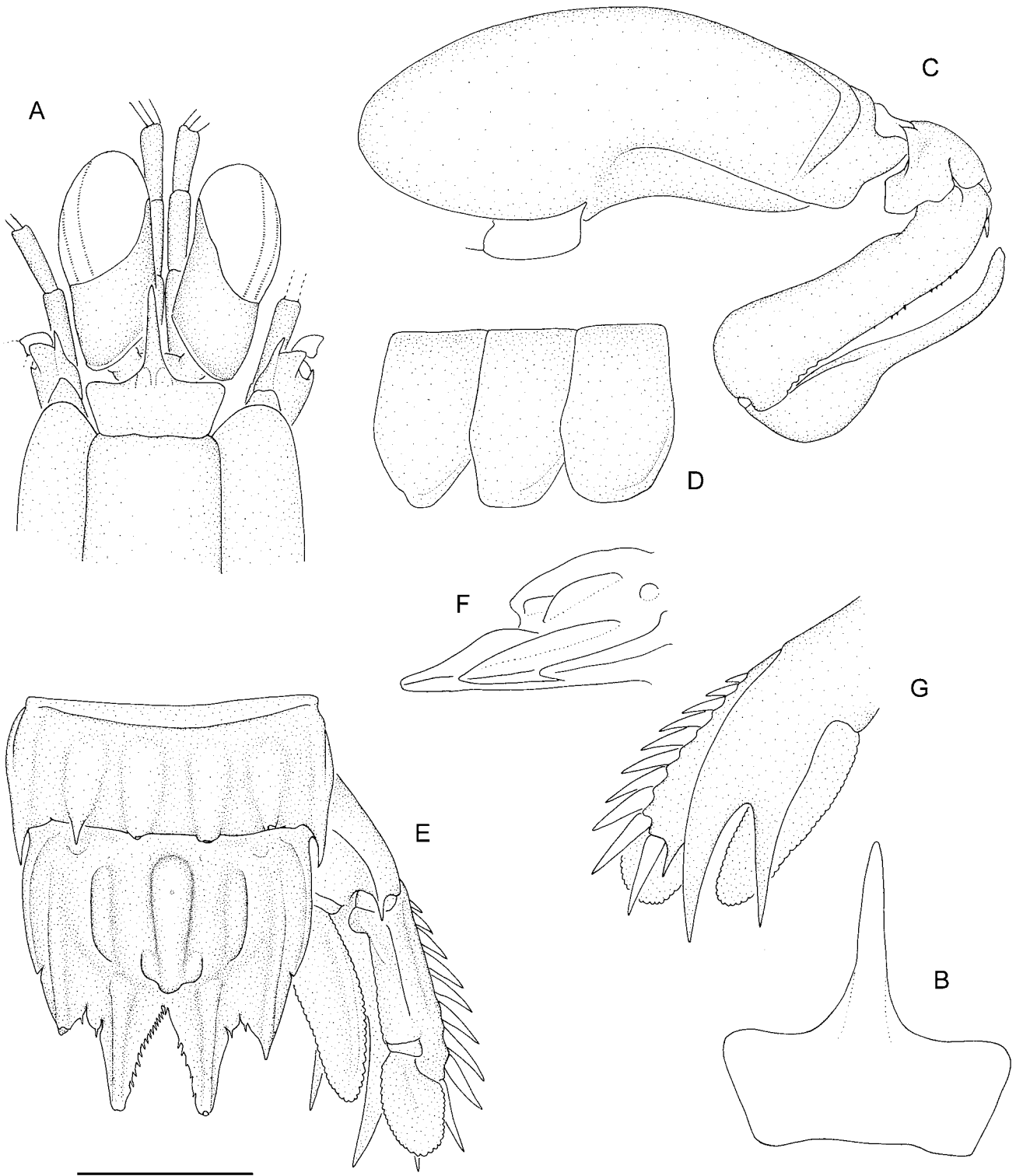


Figure 10. *Gonodactylellus viridis* (Serène, 1954), female, TL 29 mm, Chalky Sound (MNHW 6946). A, anterior cephalothorax; B, rostral plate; C, right raptorial claw; D, TS6–8, right lateral view; E, AS6, telson and right uropod; F, telson, right lateral view; G, right uropod, ventral view. Scale A, C–G = 2.5 mm, B = 1.2 mm.

TYPE MATERIAL. *Lectotype*: USNM 266628, male (TL 31 mm), Station Cauda, Cauda Bay, Vietnam, coll. R. Serène, 25 Jan 1947.

OTHER MATERIAL EXAMINED. *Southland*: MNHW 6946, 1 female (TL 29 mm), Chalky Sound (= Chalky Inlet), coll. Reischek, 11 May 1891.

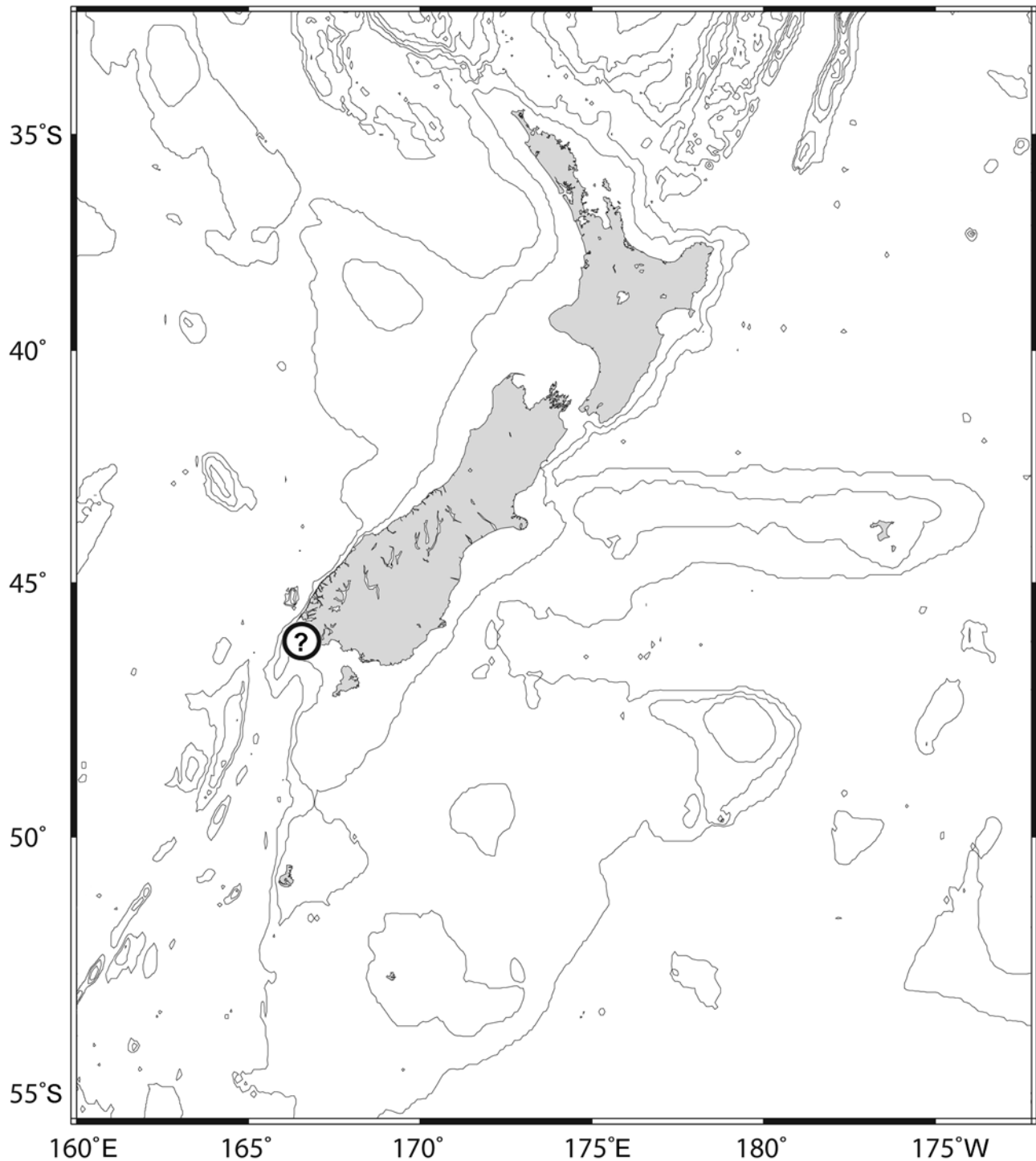


Figure 11. New Zealand distribution of *Gonodactylellus viridis* (Serène, 1954).

DIAGNOSIS. Ocular scales separate, rounded. Rostral plate with anterolateral angles rounded, anterior margins transverse. TS6-7 lateral process rounded, width subequal. AS1-5 without posterolateral spine. Telson intermediate teeth distinct, with apices extending posteriorly well beyond apices of intermediate denticles.

Telson without spinules over surface of mid-dorsal carinae; emargination between submedian and intermediate teeth acute; accessory median carinae short, not extending anteriorly to posterior one-third of median carina, unarmed posteriorly; anterior submedian carina unarmed posteriorly.

DESCRIPTION. Eyes elongate; cornea subconical. Ocular scales separate, apices rounded. Antennular peduncle length 0.67–0.68CL. Antennal scale length 0.48–0.50CL.

Rostral plate basal portion with transverse anterior margins; anterolateral angles rounded; lateral margins divergent anteriorly; median spine longer than basal portion, without ventral keel.

Raptorial claw dactylus without proximal notch in adults. Carpus dorsal margin unarmed. Propodus with proximal movable spine slender; opposable margin sparsely pectinate proximally.

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

TS6–7 lateral process width subequal; lower margins rounded. TS8 anterolateral margin rounded; sternal keel obsolete.

Pereopodal endopods slender, linear, 2-segmented; basal segment unarmed.

Pleopod 1 endopod with distinct lateral lobe on posterior 'endite'.

Abdominal somite 1–5 posterolateral angles unarmed. AWCLI 743–754. Abdominal somite 6 with posteriorly armed submedian, intermediate and lateral bosses.

Telson wider than long, surface without dorsal spinules; with 7–14 spiniform submedian denticles. Submedian teeth unarmed dorsally, dorsal carina relatively slender. Intermediate teeth distinct, apices sharp, extending posteriorly well beyond apices of intermediate denticles; intermediate carina slender, extending anteriorly beyond midlength of anterior submedian carina; emargination between submedian and intermediate teeth acute. Lateral teeth demarcated by short notch, apex blunt, not projecting well off margin of telson. Median carina more strongly inflated in males than in females; without posterior spine. Accessory median carinae blunt, unarmed, short not extending anteriorly to posterior one-third of median carina. Anterior submedian carinae smooth, unarmed, straight or slightly arcuate, extending anteriorly beyond dorsal pit of median carina. Knob absent. Telson ventral surface without carinae on submedian or intermediate teeth.

Uropodal protopod terminal spines with outer spine longer. Uropodal exopod proximal segment outer margin with 9–11 movable spines, distalmost exceeding apex of distal segment; inner margin setose; distal margin with ventral spine; exopod distal segment rounded, entire margin setose. Uropodal endopod narrow, length 3.20–3.23 times width; with low dorsolateral carina; entire margin setose.

COLOUR IN LIFE. Highly variable, from uniform light green to mottled dark green. Meral spot of raptorial claw white.

MEASUREMENTS. Male ($n = 1$) TL 31 mm, female ($n = 1$) TL 29 mm. Manning (1995) recorded *G. viridis* to TL 55 mm.

HABITAT. Intertidal and shallow subtidal coral and rocky reefs, in crevices and amongst fouling.

REMARKS. The specimen is referable to *Gonodactylellus viridis* as presently understood (Manning 1978a; Ah Yong 2001). *Gonodactylellus viridis*, however, may comprise several species (Ah Yong 2001; Ah Yong *et al.* 2008) and is currently under review. Of the New Zealand gonodactylids, *G. viridis* is clearly separable from *G. osheai* by lacking dorsal spines on the telson surface. From *Gonodactylus platysoma*, *G. viridis* is readily separated by having narrow, rounded ocular scales (versus broad and truncate) and the incision in the lateral margin of the telson indicating the lateral tooth (versus margin unbroken); and from *Gonodactylaceus falcatus*, *G. viridis* is readily separated by having three instead of five mid-dorsal carinae on the telson.

The given collecting locality for the present specimen, Chalky Inlet, at the south-western corner of the South Island of New Zealand, is probably erroneous. Andreas Reischek (1845–1902) made collections from the lower South Island, including Chalky Inlet, but the area is under subantarctic influence making it an unlikely habitat for warm-water stomatopods. Reischek, however, also collected extensively in northern New Zealand, including the Northland–Whangarei–Auckland region (Reischek 1952), a much more likely area for warm-water species to occur. Although *G. viridis* has not recently been found in the Northland region, its natural occurrence there is not unlikely, even if only occasional. Northern New Zealand is the southern 'limit' of numerous tropical marine species, some reproducing there, others as temporary residents that recruit as larvae but do not survive in the long term. Tropical crustaceans confirmed from northern New Zealand include the banded coral shrimp *Stenopus hispidus* (Olivier, 1811) (Yaldwyn 1968), the tropical shrimp *Lysmata vittata* (Stimpson, 1860) (Ah Yong 2010b) the portunid crab *Scylla serrata* (Forskål, 1775) (Heller 1865) and raninid crab *Lyreidus tridentatus* De Haan, 1841. Notably, Heller's (1865) New Zealand record of *Scylla serrata* was long questioned until corroborated almost a century later (Dell 1964b). Numerous habitats in northern New Zealand remain to be explored for stomatopods, and other tropical species almost certainly remain to be discovered from there.

DISTRIBUTION. Eastern Indian Ocean, the South China Sea, Japan, Indonesia to Australia, New Caledonia, Fiji and New Zealand.

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 in dorsal view. Ocular scales large, wider than basal width of median spine of rostral plate, distinctly wider than high, flattened dorsally. Rostral plate with slender median spine and short, broad, trapezoid basal portion. Mandibular palp present. Propodus of raptorial claw with or without proximal movable spine in adults. Anterolateral margins of carapace 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; anus located ventrally. Uropodal protopod without lobes between primary terminal spines; endopod without spines on inner margin.

COMPOSITION. *Gonodactylus acutirostris* De Man, 1898; *G. botti* Manning, 1975; *G. childi* Manning, 1971a; *G. chiragra* (Fabricius, 1781); *G. platysoma* Wood-Mason, 1895; *G. smithii* Pocock, 1893.

REMARKS. *Gonodactylus* includes the largest members of the Gonodactylidae, with some species exceeding TL 100 mm. The six species of *Gonodactylus* occur only in the Indo-West Pacific region, of which only *G. platysoma* is recorded from New Zealand waters. Other species of *Gonodactylus*, such as *G. chiragra* and *G. smithii* can be expected to occur, at least occasionally, in northern New Zealand waters; both are common in the tropical south-western Pacific and have been found off temperate eastern Australia (Ahyong 2001). All species of *Gonodactylus* occur on coral on rocky reefs living in cavities in coral rubble and rock.

KEY TO SPECIES OF *GONODACTYLUS*

1. Telson without lateral tooth, with margin of telson between anterolateral angle and apex of intermediate tooth unbroken. Ocular scales extending laterally almost to anterolateral angle of rostral plate ..
.....*G. platysoma*
- Telson with lateral tooth indicated by shallow notch in margin of telson between anterolateral angle and apex of intermediate tooth. Ocular scales not extending laterally to anterolateral angle of rostral plate2
2. Lateral margins of rostral plate strongly divergent3

- Lateral margins of rostral plate subparallel or slightly divergent4
3. Anterolateral angles of rostral plate spinular
..... *G. acutirostris*
- Anterolateral angles of rostral plate blunt or angular, but not spinular.....*G. smithii*
4. Rostral plate with anterior margins deeply concave..... *G. chiragra*
- Rostral plate with anterior margins transverse or slightly concave5
5. Telson with blunt intermediate teeth. Anterior margin of ocular scales transverse..... *G. botti*
- Telson with sharp intermediate teeth. Anterior margin of ocular scales inclined posteriorly
G. childi

Gonodactylus platysoma Wood-Mason, 1895

(Figs 12, 13)

Gonodactylus platysoma Wood-Mason, 1895: 11, pl. 3, figs. 3–9 [type locality: restricted to Society Islands, 17°00'S, 150°00'W, by lectotype selection (Ghosh & Manning 1988)]. – Ahyong & Norrington 1997: 101. – Ahyong, 2001: 71–72, fig. 35. – Ahyong *et al.*, 2008: 19–20, fig. 14.

Gonodactylus chiragra var. *platysoma*. – Kemp, 1913: 4, 11, 147, 162, fig. 1.

Gonodactylus chiragra var. *tumidus* Lanchester, 1903: 447, 456, pl. 23: fig. 1 [type locality: Minikoi, Laccadive Islands (= Lakshadweep), 8°17'S, 73°02'E].

Gonodactylus chiragra var. *acutus* Lanchester, 1903: 447, 456, pl. 23: fig. 3 [type locality: Minikoi, Laccadive Islands (= Lakshadweep), 8°17'S, 73°02'E].

MATERIAL EXAMINED. *Southland*: NHMW 4671, 1 female (TL 87 mm), Chalky Sound (= Chalky Inlet), coll. A. Reischek.

India: MZC, 2 males (TL 54–68 mm) (syntypes of *Gonodactylus chiragra* var. *tumidus* Lanchester, 1903), Minikoi Laccadive Islands, 8°17'S, 73°02'E, coll. J.S. Gardiner.

French Polynesia: WAM, 1 female (TL 68 mm), Taka Kota Atoll, Marquesas, reef flat, 8 Oct 1967; AM P60120, 1 male (TL 49 mm), Tikehau Island, Tuamotus, 15°00'S, 148°10'W.

DIAGNOSIS. Ocular scales broad, flattened, separate, together almost as broad as rostral plate. Rostral plate basal portion with anterior margins strongly concave; anterolateral angles rounded; lateral margins subparallel or slightly divergent anteriorly; apical spine longer than base. Lateral margin of TS6 and TS7 subequal. Telson without lateral tooth, margin of telson unbroken

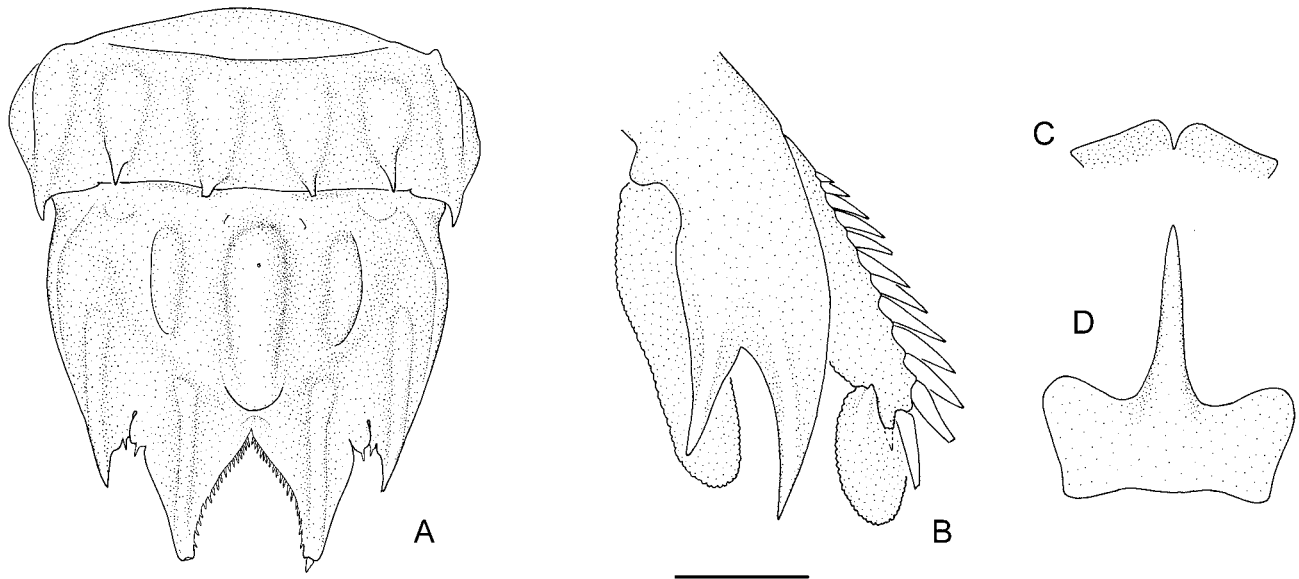


Figure 12. *Gonodactylus platysoma* Wood-Mason, 1895, female, TL 87 mm, Chalky Sound (NHMW 4671). A, AS6 and telson; B, left uropod, ventral view; C, ocular scales; D, rostral plate. Scale A-B = 5.0 mm, C-D = 2.5 mm.

between anterolateral angle and apex of intermediate tooth; dorsal carinae blunt, neither sharp nor cristate dorsally; median carina unarmed posteriorly; accessory median carinae indistinct or obsolete.

DESCRIPTION. Eyes elongate; cornea subconical. Ocular scales broad, flattened, separate, together almost as broad as rostral plate. Antennular peduncle length 0.60–0.73CL. Antennal scale length 0.63–0.67CL.

Rostral plate about as long as wide; basal portion with strongly concave anterior margins; anterolateral angles rounded; lateral margins subparallel anteriorly; median spine longer than base, without ventral keel.

Raptorial claw dactylus without proximal notch in adults. Carpus dorsal margin unarmed. Propodus without proximal movable spine, opposable margin sparsely pectinate proximally.

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

TS6–7 lateral process width subequal; lower margins rounded. TS8 anterolateral margin rounded; sternal keel obsolete.

Pereopodal endopods slender, linear, 2-segmented; basal segment unarmed.

Pleopod 1 endopod with distinct lateral lobe on posterior ‘endite’.

Abdominal somite 1–5 posterolateral angles unarmed. AWCLI 917–991. Abdominal somite 6 with posteriorly armed submedian, intermediate and lateral bosses.

Telson wider than long, surface without dorsal spinules; with 16–18 spiniform submedian denticles. Submedian teeth unarmed dorsally, dorsal carina relatively slender. Intermediate teeth distinct, apices

sharp, extending posteriorly well beyond apices of intermediate denticles; intermediate carina slender, not extending anteriorly beyond midlength of anterior submedian carina; emargination between submedian and intermediate teeth acute. Lateral teeth absent, margin of intermediate tooth entire, unbroken. Median carina more strongly inflated in males than in females; without posterior spine. Accessory median carinae unarmed, short, indistinct, not extending anteriorly to posterior quarter of median carina. Anterior submedian carinae smooth, unarmed, straight, extending anteriorly as far as base of median carina. Knob absent. Telson ventral surface without carinae on submedian or intermediate teeth.

Uropodal protopod terminal spines with outer spine longer. Uropodal exopod proximal segment outer margin with 10–17 movable spines (usually 11), distalmost not exceeding apex of distal segment; inner margin setose; distal margin with ventral spine; exopod distal segment rounded, entire margin setose. Uropodal endopod narrow, length about 4 times width; inner margin slightly sinuous; with low dorsolateral carina; entire margin setose.

COLOUR IN LIFE. Mottled with white, brown and green overall. AS1 and AS5 with posterolateral ‘eye-spots’. AS6 and telson with dorsal carinae marbled with blue. Antennular flagella red. Antennal scale clear yellow-green flecked with white. Raptorial claw with white meral spot; carpus red; propodus reddish proximally, bluish distally; dactylus dull blue.

MEASUREMENTS. Male ($n = 3$) TL 54–68 mm, female ($n = 2$) TL 68–87 mm. Kemp (1915) recorded specimens to TL 110 mm.

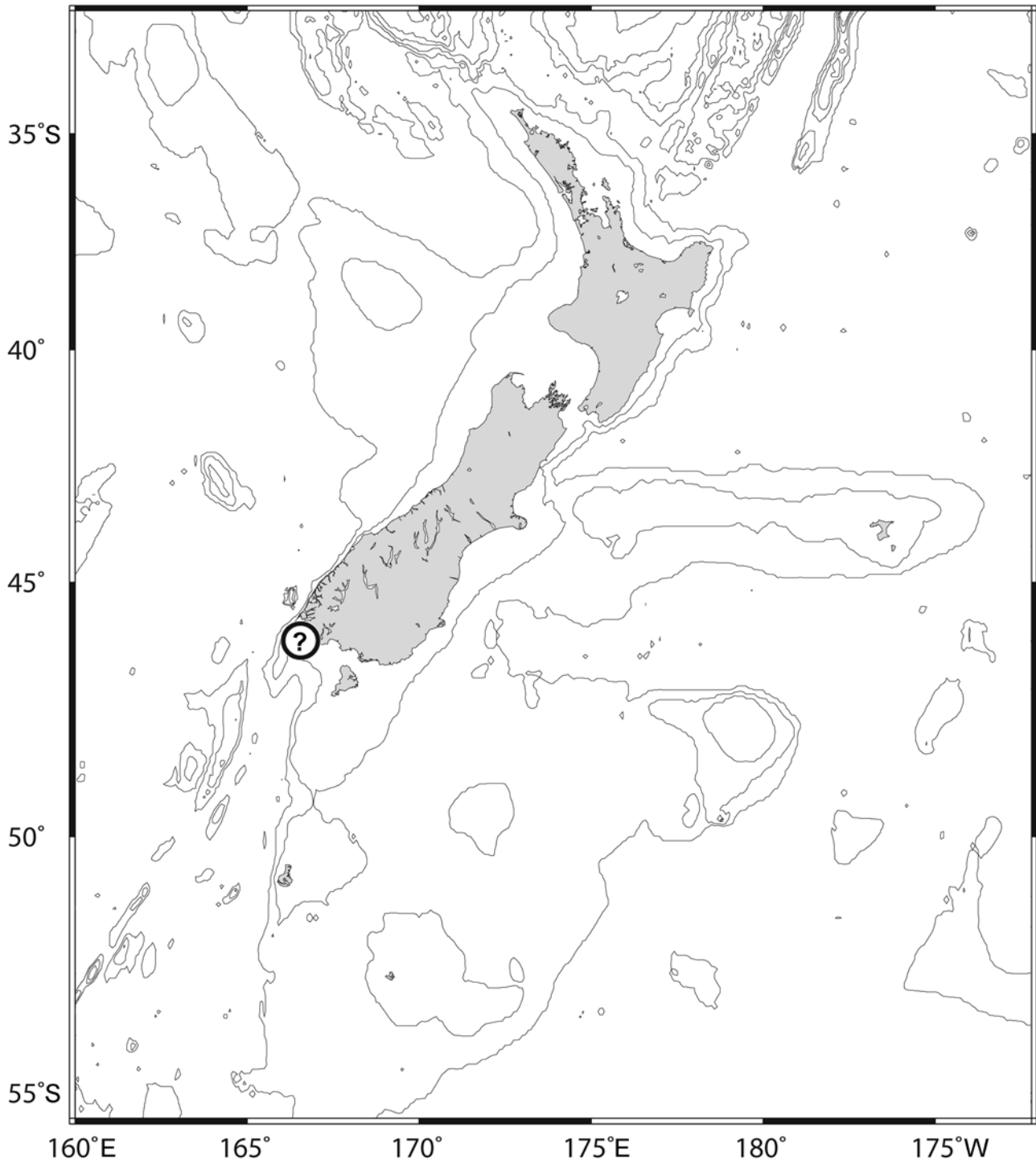


Figure 13. New Zealand distribution of *Gonodactylus platysoma* Wood-Mason, 1895.

HABITAT. Intertidal and shallow subtidal coral and rocky reefs.

REMARKS. The New Zealand specimen, an adult female, is damaged and in poor condition, but readily identified as *G. platysoma*; it agrees well with specimens examined from French Polynesia and syntypes of *G. chiragra* var. *tumidus* from Lakshadweep. The broad ocular scales

and abdomen, and absence of the lateral tooth of the telson are characteristic of the species, separating it from all other New Zealand gonodactylids.

As with *Gonodactylellus viridis*, *Gonodactylus platysoma* is a warm-water species so the locality indication of the specimen, Chalky Sound, at the south-western corner of the South Island, is probably incorrect. The specimen most likely originated from a northern New

Zealand locality when Andreas Reischek collected in the Northland region during the late 1800s. Prior to the present record from New Zealand, the southernmost Tasman Sea record of *G. platysoma* was from Lord Howe Island (Ahyong & Norrington 1997).

DISTRIBUTION. Western Indian Ocean to the South China Sea, Australia and French Polynesia; a new record for New Zealand.

HEMISQUILLIDAE Manning, 1980

Hemisquillidae Manning, 1980: 366, 369.

DIAGNOSIS. Eye with cornea subglobular to subcuboid, set obliquely on stalk. Rostral plate triangular. Antennal protopod dorsally with flattened, articulated plate. Raptorial claw dactylus unarmed; ischiomeral articulation terminal. Telson submedian teeth with movable apices; submedian denticles absent in adults; dorsal surface with distinct median carina and anterior submedian carina in addition to carinae of primary teeth. Uropodal protopod terminating in a single primary spine; outer margin with strongly convex lobe with at most a minute outer spine; exopod segments with terminal articulation; exopod proximal segment outer margin with straight, movable spines.

COMPOSITION. *Hemisquilla* Hansen, 1895.

REMARKS. Hemisquillids differ from all other gonodactylids in having a terminal ischiomeral articulation of the raptorial claw in combination with an unarmed inner margin of the dactylus.

Recent molecular phylogenetic analyses (Ahyong & Jarman 2009; Porter *et al.* 2010) identified Hemisquillidae as the potential sister group to the remaining crown-group stomatopods, corroborating observations that, of all extant taxa, hemisquillids are phenotypically closest to the Cretaceous stem-lineage pseudosculdid stomatopods (Ahyong *et al.* 2007).

Hemisquillids are a temperate water group occurring in disjunct, widely separated populations off south-eastern Australia and New Zealand, California, Chile and Brazil.

Hemisquilla Hansen, 1895

Hemisquilla Hansen, 1895: 72. [Type species: *Gonodactylus styliferus* H. Milne Edwards, 1837, by original designation (a junior subjective synonym of *G. ensiger* Owen, 1832). Gender: feminine].

DIAGNOSIS. As for family.

COMPOSITION. *Hemisquilla braziliensis* (Moreira, 1903); *H. ensigera* (Owen, 1832); *H. californiensis* Stephenson, 1967; *H. australiensis* Stephenson, 1967.

REMARKS. Hemisquillids occur in temperate waters at scattered localities in the western Atlantic and Pacific Ocean. Although seemingly phylogenetically ancient (Ahyong & Jarman 2009; Porter *et al.* 2010), species of *Hemisquilla* are morphologically conservative with only minor morphological distinctions between the species. *Hemisquilla australiensis* and *H. californiensis* were previously regarded as subspecies of *H. ensigera* but Ahyong (2001) showed that they should be treated as separate species given that each has distinct morphology, colour pattern and geographical distribution. *Hemisquilla australiensis* is the only Indo-West Pacific hemisquillid. *Hemisquilla ensigera* and *H. californiensis* both occur in the eastern Pacific, and *H. braziliensis* occurs in the western Atlantic.

Of the New Zealand stomatopods, *Hemisquilla* is morphologically most similar to *Odontodactylus* in the subcylindrical body form, similar maximum body size, subglobular eyes, and articulated plate on the inner margin of the antennal protopod. *Hemisquilla*, however, is easily separated from *Odontodactylus* by the terminal rather than subterminal ischiomeral articulation of the raptorial claw and in unarmed occlusal margin of the raptorial dactyli.

KEY TO SPECIES OF *HEMISQUILLA*

1. Lobes between submedian and intermediate teeth of the telson each usually with spiniform apex in adults; lobe between intermediate and lateral teeth spiniform *H. braziliensis*
 - Lobes between submedian and intermediate teeth of the telson rounded, at most with minute point in adults; lobe between intermediate and lateral teeth round or obsolete in adults 2
2. Uropodal exopod with 4 (rarely with 3 on one side) movable spines on outer margin of proximal segment *H. australiensis*
 - Uropodal exopod with 5 (rarely with 4 on one side) movable spines on outer margin of proximal segment 3
3. Propodus of raptorial claw yellow in life
 - *H. californiensis*
 - Propodus of raptorial claw blue in life
 - *H. ensigera*

***Hemisquilla australiensis* Stephenson, 1967**
(Figs 14, 15, Frontispiece 1B)

Hemisquilla ensigera. — Manning, 1966: 102 [not *H. ensigera* (Owen, 1832)].

Hemisquilla ensigera australiensis Stephenson, 1967: 15, 16 [type locality: 19 km east of Broken Bay, New South Wales, Australia].

Hemisquilla australiensis. — Ahyong, 2001: 76–78, fig. 37. — Webber *et al.*, 2010: 136, 218.

TYPE MATERIAL. *Holotype*: AM P11695, male (TL 140 mm), 19 km east of Broken Bay, New South Wales, Australia, 33°40'S, 151°30'E, seine trawl, coll. H. Arnold, Nov 1946.

OTHER MATERIAL EXAMINED. *Norfolk Ridge*: AM P66302, 1 male (TL 136 mm), 32°36.34'S, 167°35.73'E, 127 m, TAN0308/117, 30 May 2003.

Northland: NMNZ Cr9335, 1 male (TL 108 mm), ca. 2 miles off Whangaroa Heads, Northland, 34°58.7'S, 173°46.5'E, 160 ft [53 m], sandy bottom, hook and line, coll. K. Johnston, 9 May 1972; NMNZ Cr9375, 1 male (TL 97 mm), off Cavalli Islands, 35°01.4'S, 173°57.6'E, 110 m, craypot, coll. G. Clifford.

Auckland & Coromandel: NIWA 76527, 1 male (TL 121 mm), off Leigh, 36°06.88'S, 174°52.25'E, 55–60 m, on long-line bait over mixed bottom, coll. M. Goldsworthy, 17 Sep 2004; NMNZ Cr16723, 1 male (TL 114 mm), 48 km north-west of Mayor Island, north-east of Coromandel Peninsula, 36°52.3'S, 175°54.5'E, 90 m, on snapper longline hook, coll. J. Sutton, 3 Oct 1997.

Bay of Plenty: NMNZ Cr9333, 1 male (TL 110 mm), off Motiti Island, 37°37'S, 176°26'E, coll. A.G. Burton, 3 May 1976.

Taranaki: NMNZ Cr19740, 1 female (TL 147 mm), north-north-east of New Plymouth, 38°53.083'S, 174°12.933'E, 57 m, shelf, COR9001/181, FV *Cordella*, 12 Mar 1990.

No specific locality: NMNZ Cr1493, 1 male (TL 120 mm), northern New Zealand, trawled, 1964 or earlier; NMNZ Cr9334, 1 damaged female, North Island, trawl, 1971.

DIAGNOSIS. Rostral plate as long as or longer than wide. Raptorial claw propodus blue in life. Telson with 2 or 3 rounded lobes (usually unarmed) between submedian and intermediate teeth; at most with small rounded tubercle between intermediate and lateral teeth. Outer margin of proximal segment of uropodal exopod with 4 (rarely 3 on one side) movable spines, distalmost extending to or beyond midlength of distal segment.

DESCRIPTION. Eyes not extending anteriorly beyond antennular peduncle segment 2. Anterior margin of ophthalmic somite triangular. Ocular scales separate,

antero-posteriorly compressed, triangular, directed laterally. Antennular peduncle length 0.85–0.95CL. Antennal protopod inner movable plate rounded distally. Antennal scale length 0.72–0.85CL.

Rostral plate triangular, as long as or longer than wide; apex blunt; lateral margins slightly convex proximally, otherwise straight; dorsally and ventrally smooth.

Carapace anterior margins straight or faintly concave; anterior and lateral margins approximately forming right-angle, bluntly rounded; surface without carinae; cervical groove shallow, not indicated medially; posterior margin slightly concave; posterolateral margins rounded, slightly produced ventrally.

Raptorial claw dactylus outer proximal margin inflated but not forming distinct heel without proximal notch in adults. Carpus dorsal margin with small distal tooth. Propodus with 2 proximal movable spines; occlusal margin pectinate becoming sparse distally.

Mandibular palp usually 2-segmented (rarely 1- or 3-segmented). Maxillipeds 1–5 with epipod.

TS6–8 lateral processes rounded. TS8 sternal keel blunted pointed.

Pereopodal endopods slender, linear, 2-segmented; basal segment unarmed.

Pleopod 1 endopod with distinct lateral lobe on posterior 'endite'.

AS1–5 each with marginal carina only; posterolaterally unarmed. AS6 with low, blunt, unarmed submedian, intermediate and lateral carinae; with low unarmed swelling between submedian and intermediate carinae; small ventrolateral spine anterior to uropod articulation.

Telson flattened, wider than long; median and anterior submedian carinae straight, low, blunt, unarmed; with few shallow pits on surface between median and anterior submedian carinae; inner margin of submedian teeth smooth. Submedian teeth triangular with low dorsal carina; movable apices slender, short; inner margins separated by narrow fissure in anterior half, divergent in posterior half, smooth. Intermediate teeth distinct, triangular, with low dorsal carina; apices sharp, extending posteriorly well beyond apices of intermediate denticles. Intermediate denticles represented by 2 or 3 rounded lobes (usually unarmed posteriorly). Lateral teeth demarcated by short notch, apex sharp; with low, dorsal carina; intermediate denticle absent or at most a small rounded tubercle. Ventral surface without carinae or spines.

Uropodal protopod flattened, distally with large, prominent, ventrally carinate inner spine and minute outer spine, intervened by rounded lobe. Uropodal exopod proximal segment short, less than one-third length of distal segment; outer margin with 4 (rarely 3) straight, graded, movable spines, distalmost extending

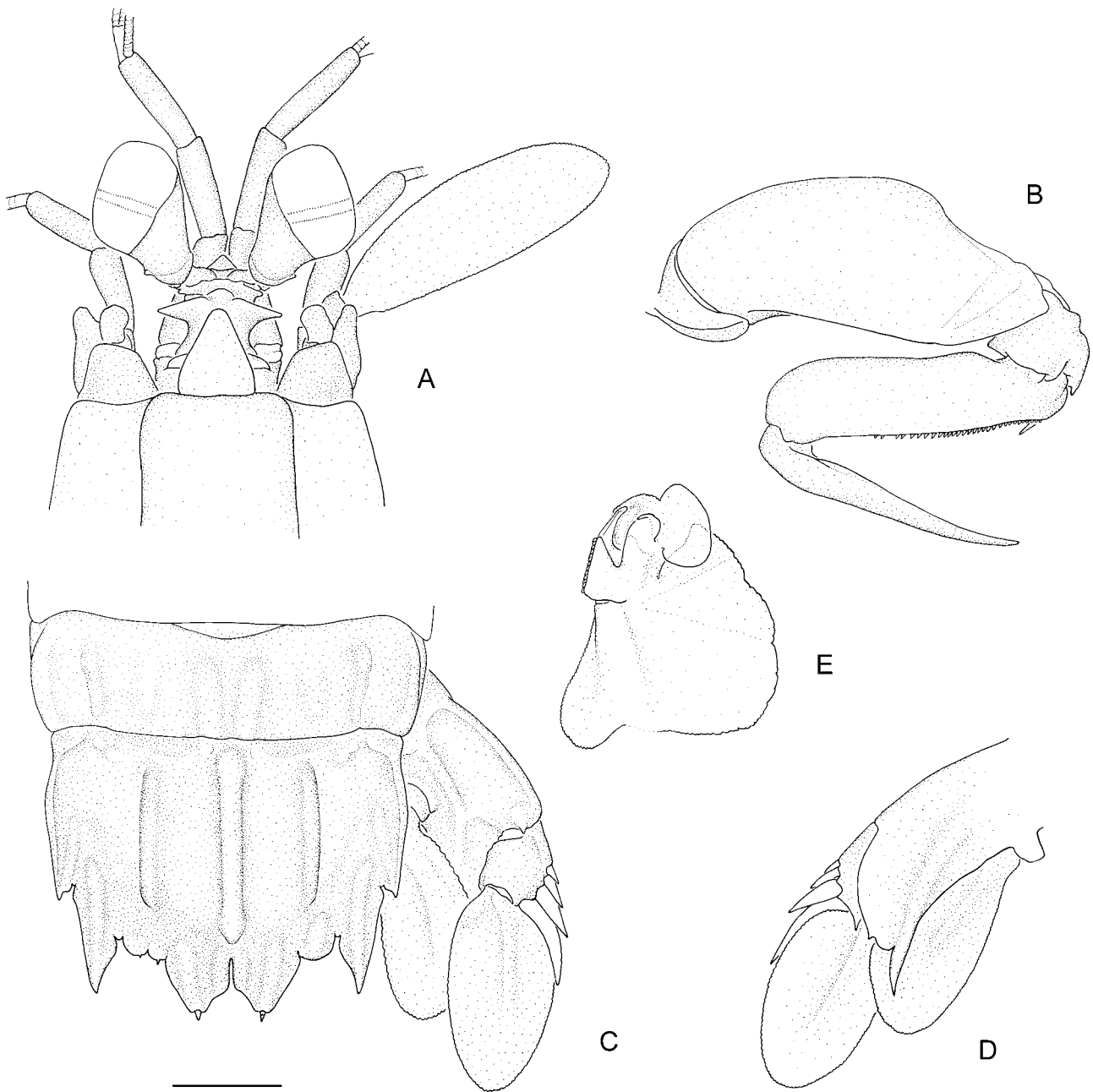


Figure 14. *Hemisquilla australiensis* Stephenson, 1967. A–D, male, TL 97 mm, off Cavalli Islands (NMNZ Cr9375). E, male, TL 136 mm, Norfolk Ridge (AM P66302). A, anterior cephalothorax; B, right raptorial claw; C, AS6, telson and right uropod; D, right uropod, ventral view; E, right pleopod 1 endopod, anterior view. Scale A–D = 5.0 mm, E = 2.5 mm.

to about midlength of distal segment; distal margin with small ventral spine; exopod distal segment ovate, entire margin setose. Uropodal endopod broad, ovate, length 2.33–2.81 width; low dorsal median carina.

COLOUR IN LIFE. Overall pale blue-grey, dorsally, white ventrally. Antennular peduncle bright blue, flagella red. Antennal scale clear, marginal setae red. Raptorial claw propodus and dactylus pale blue. Pereopods blue proximally, white distally. Uropodal exopod proximal

segment with dark blue extending onto proximal one-quarter of distal segment; remainder of distal segment iridescent blue; marginal setae red.

MEASUREMENTS. Male ($n = 8$) TL 97–140 mm, female ($n = 2$) TL 147 mm. Ah Yong (2001) recorded specimens to TL 174 mm.

HABITAT. Soft sandy-mud substrates in depths between 18 m and 439–476 m (Ah Yong 2001). In New Zealand,

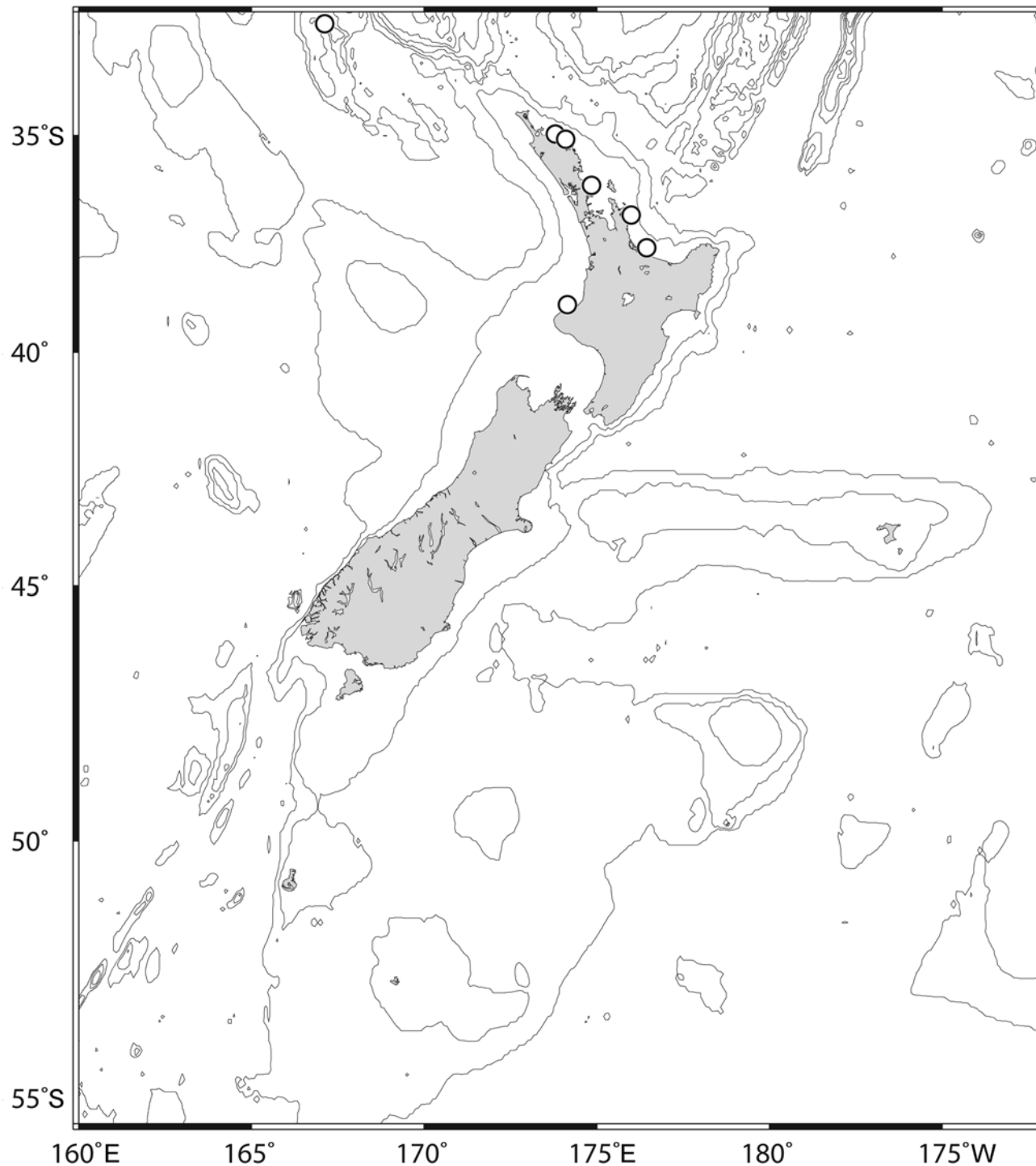


Figure 15. New Zealand distribution of *Hemisquilla australiensis* Stephenson, 1967.

Hemisquilla australiensis has been recorded at depths of 55–127 m.

REMARKS. The New Zealand specimens of *H. australiensis* agree well with the most recent account of the species (Ahyong 2001). The rostral plate is longer than wide and four movable spines are present on the outer margin of the proximal segment of the uropodal exopod.

DISTRIBUTION. Australia, from northern New South Wales, south to Victoria and Tasmania, and from New Zealand. In New Zealand, known from the North Island from Cavalli Islands south to the vicinity of New Plymouth on the west coast (~39°S) and the Bay of Plenty in the east (~37°S).

ODONTODACTYLIDAE Manning, 1980

Odontodactylidae Manning, 1980: 366, 369.

DIAGNOSIS. Eyes subglobular. Rostral plate rounded to trapezoid. Raptorial claw with subterminal ischiomerall articulation; propodus occlusal margin non-pectinate, without proximal movable spines; dactylus with short teeth on occlusal margin and strongly inflated heel on outer proximal margin. Telson and AS6 fully articulating, not fused. Distal segment of uropodal exopod articulating at distal end of proximal segment; distal movable spines on outer margin of proximal segment not recurved anteriorly.

COMPOSITION. *Odontodactylus* Bigelow, 1893.

REMARKS. Odontodactylids are all 'smashers' and as suggested by their name, differ from gonodactylids and protosquillids by having teeth on the occlusal margin of the dactylus of the raptorial claw.

Odontodactylus Bigelow, 1893

Odontodactylus Bigelow, 1893: 100. [Type species: *Cancer scyllarus* Linnaeus, 1758, by subsequent designation by Bigelow (1931: 144). Name on *Official list of International Commission on Zoological Nomenclature*. Gender: masculine].

Raoulius Manning, 1995: 86. [Type species: *Gonodactylus cultrifer* White, 1851, by original designation. Gender: masculine].

DIAGNOSIS. As for family.

COMPOSITION. *Odontodactylus brevis* (Miers, 1884); *O. hansenii* (Pocock, 1893); *O. havanensis* (Bigelow, 1893); *O. hawaiiensis* Manning, 1967; *O. japonicus* (De Haan, 1844); *O. latirostris* Borradaile, 1907; *O. scyllarus* (Linnaeus, 1758).

REMARKS. *Odontodactylus* includes the largest of the 'smashing' stomatopods with *O. japonicus* reaching at least TL 192 mm (Ahyong *et al.* 2008). Species of *Odontodactylus* occur only in the Indo-West Pacific and Western Atlantic regions; two species are known from New Zealand.

KEY TO NEW ZEALAND SPECIES OF *ODONTODACTYLUS*

1. Dactylus of raptorial claw with 5 or more small teeth on inner margin *O. hawaiiensis*
– Dactylus of raptorial claw with 2 or 3 small teeth on inner margin *O. scyllarus*

Odontodactylus hawaiiensis Manning, 1967

(Figs 16, 17, Frontispiece 1C)

Odontodactylus japonicus. – Bigelow, 1893: 145, pl. 1, fig. 1. [Not *O. japonicus* (De Haan, 1844)].

Odontodactylus hawaiiensis Manning, 1967a: 16–18, fig. 4, pl. 1 [type locality: off Maui Island, Hawaiian Islands]. – Moosa, 1991: 161–162. – Ahyong, 2001: 79. – Retamal, 2002: 73–75, fig. 1. – Ahyong 2002c: 829–830.

Odontodactylus brevis. – Manning, 1991: 4. – Webber *et al.*, 2010: 136, 218. [Not *O. brevis* (Miers, 1884)].

TYPE MATERIAL. *Holotype*: USNM 64861, male (TL 107 mm), off coast of Maui, Hawaiian Islands, 173–276 m, Albatross stn 4098, 23 Jul 1902.

OTHER MATERIAL EXAMINED. *Kermadec Islands*: ZMUC CRU 3670, 1 female (TL 29 mm), Raoul Island, 29°13'S, 177°57'W, 60 m, stones, 3 Mar 1952; NMNZ, 1 female (TL 35 mm), off Hutchinson Bluff, Raoul Island, 29°14.7'S, 177°49.4'W, 84–113 m, beam trawl, RV *Acheron*, BS296, 24 Aug 1972; NMNZ Cr12536, 1 juvenile female (TL 26 mm), south-east of Esperance Rock, 31°07.00'S, 178°27.00'W, 50–54 m, from fish stomach, FV *Kaiyu Maru*, stn 52, 9 Mar 1982; NMNZ Cr16301, 1 juvenile female (TL 24 mm), south-east of Esperance Rock, 31°07.00'S, 178°27.00'W, 50–54 m, from fish stomach, FV *Kaiyu Maru*, stn 52, 9 Mar 1982.

Norfolk Ridge: NIWA 23961, 1 female (TL 24 mm), off Norfolk Island, 29°33.59'S, 168°01.60'E, 80–81 m, NZOI stn P19(DR), 25 Jan 1977; AM P65970, 1 female (TL 98 mm), northern Norfolk Ridge, 29°54.38'S, 167°41.05'E, 111–113 m, TAN0308/024.

Philippines: AM P84137, 1 male (TL 105 mm), Balut Island, Philippines, 5°24'N, 125°22.98'E, coll. A. Miskelly 2010.

Tonga: MNHN, 1 female (TL 69 mm), 23°20'S, 176°16'W, 220–249 m, from seamount, BORDAU 2 stn CP1626, Bouchet *et al.*, 19 Jun 2000; MNHN, 1 male (TL 51 mm), from seamount, 216–237 m, 22°59'S, 175°47'W, BORDAU 2 stn DW1610, coll. P. Bouchet *et al.*, 17 Jun 2000.

DIAGNOSIS. Ocular scales oblique to midline, appressed medially. Antennal scale with anterior margin setose in adults. Rostral plate triangular, apex deflexed. Raptorial claw dactylus with 6–8 teeth on occlusal margin. AS5 with posterolateral spine in adults. Telson mid-dorsal surface with distinct median carina and 3 longitudinal carinae either side of midline (double accessory median; anterior submedian) in addition to carinae of primary teeth; carina of intermediate denticle short, not extending onto mid-dorsal surface. Uropodal exopod proximal segment distinctly longer than distal segment; distalmost movable exopod spines evenly tapering to sharp point; distal segment shorter than proximal segment length.

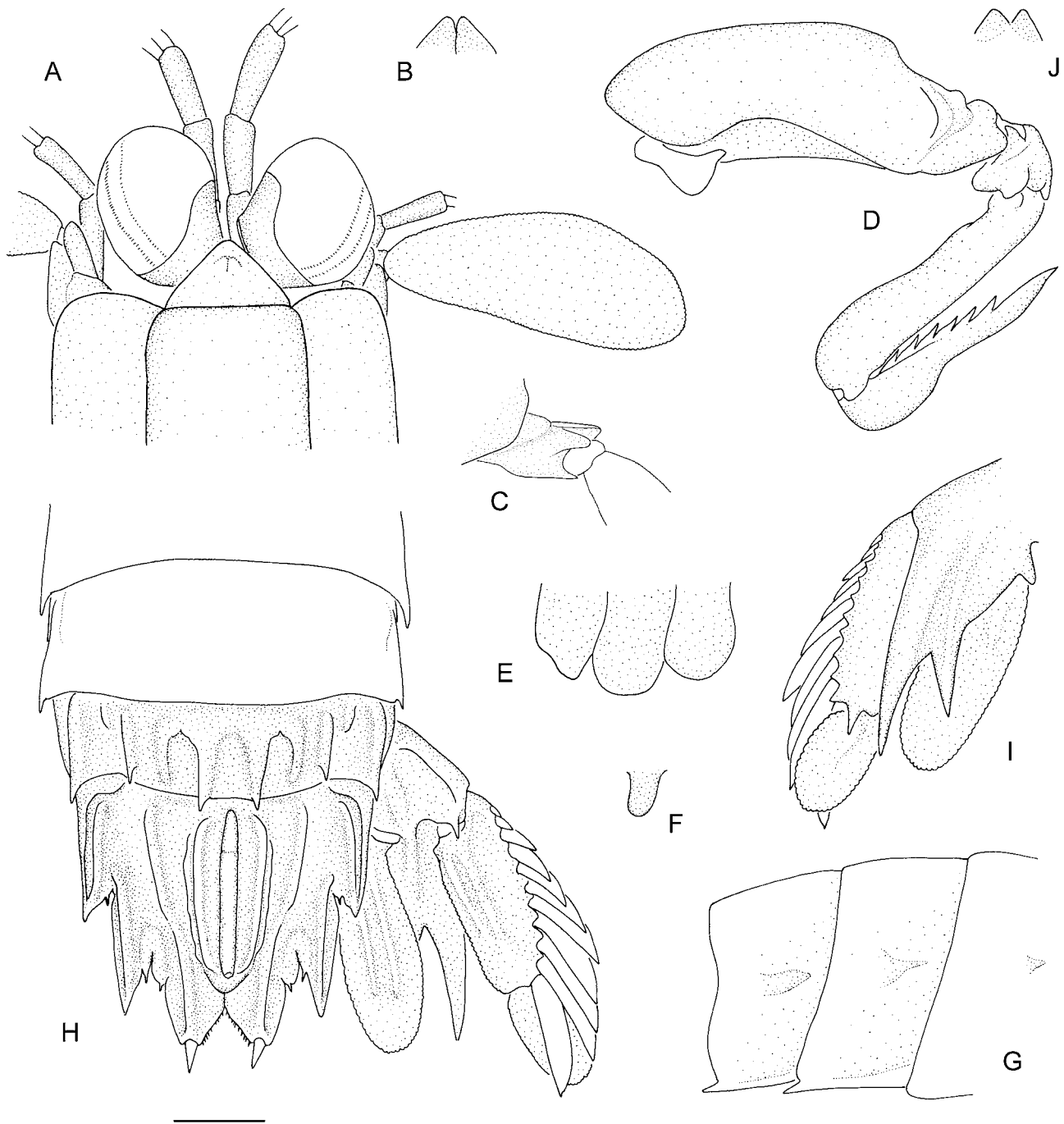


Figure 16. *Odontodactylus hawaiiensis* Manning, 1967. A–I, female, TL 35 mm, Raoul Island (NMNZ). J, female, TL 29 mm, Raoul Island (ZMUC CRU 3670). A, anterior cephalothorax; B, ocular scales; C, right antennal protopod, lateral view; D, right raptorial claw; E, TS6–8, lower right lateral view; F, TS8 sternal keel, right lateral view; G, AS3–5, right lateral view; H, AS4–6, telson and right uropod; I, right uropod, ventral view; J, ocular scales. Scale A, C–E, G–I = 2 mm; B, F, J = 1.0 mm.

DESCRIPTION. Eyes with cornea subglobular. Anterior margin of ophthalmic somite faintly convex. Ocular scales triangular, lateral margins oblique to midline, medially appressed.

Antennular peduncle length 0.65–0.76CL. Antennal protopod inner movable plate with rounded apex.

Antennal scale length 2.14–2.76CL, entire margin setose.

Rostral plate triangular, wider than long, apex deflexed, lateral margins straight or slightly convex proximally, otherwise straight; dorsally and ventrally smooth.

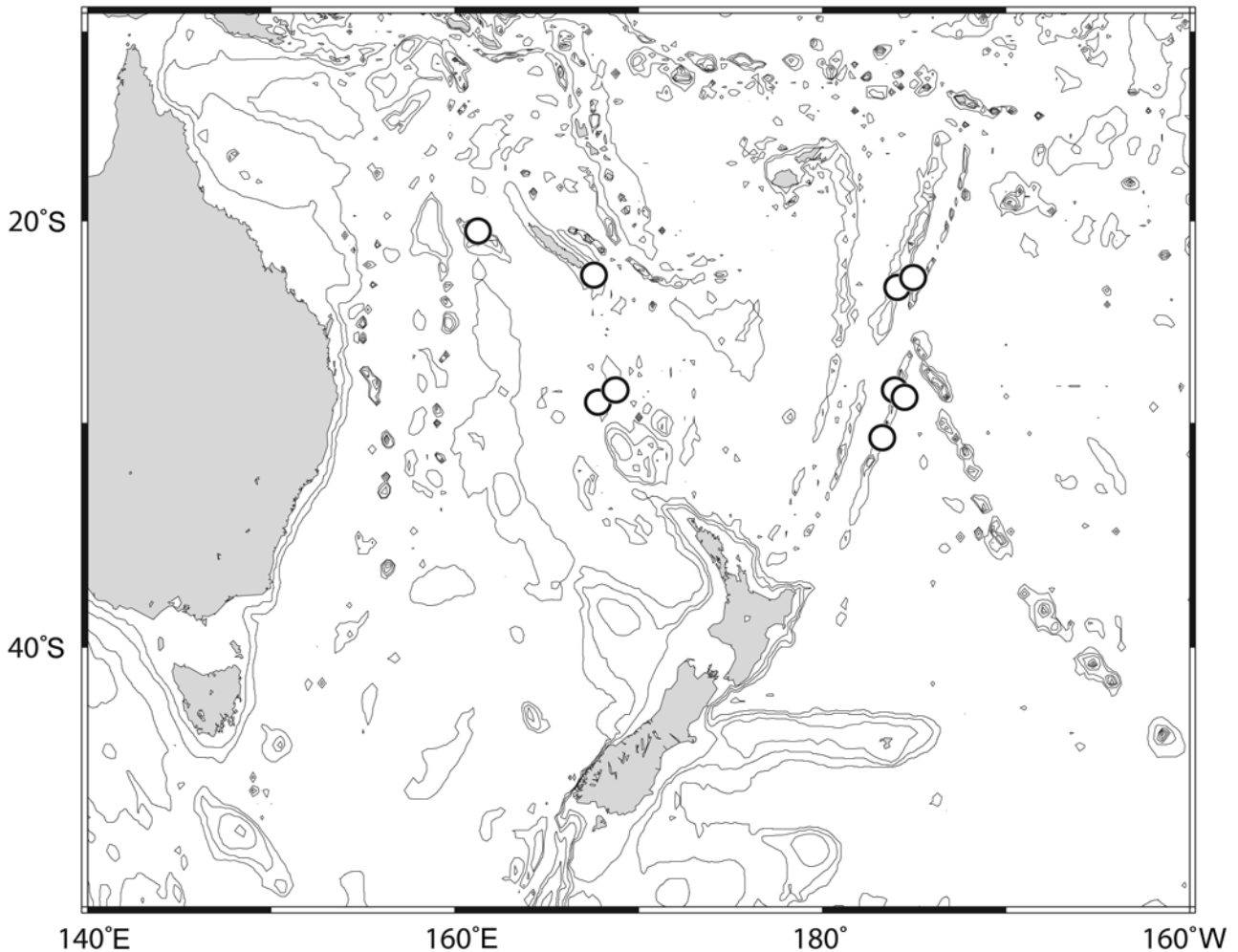


Figure 17. South-western Pacific distribution of *Odontodactylus hawaiiensis* Manning, 1967.

Carapace anterolateral margins rounded; surface without carinae; cervical groove shallow, not indicated medially; posterior margin slightly concave; posterolateral margins rounded.

Raptorial claw dactylus occlusal margin with 6–8 small teeth; outer proximal margin strongly inflated forming distinct heel, without proximal notch in adults. Carpus dorsal margin unarmed. Propodus without proximal movable spines; occlusal margin irregular, without spines or pectinations.

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

TS6–8 lateral processes rounded. TS8 sternal keel rounded.

Pereopodal endopods slender, linear, 2-segmented.

Pleopod 1 endopod with distinct lateral lobe on posterior ‘endite’.

AS1–5 each with marginal carina only. AS(4)5 with posterolateral spine. AS6 with posteriorly armed submedian, intermediate and lateral carinae; unarmed reflected submedian carina; short, unarmed anterior ca-

rina between intermediate and lateral carinae; without ventrolateral spine anterior to uropod articulation.

Telson slightly wider than long; median carina with posterior spine; double accessory median carinae straight to slightly irregular; submedian carina continuous with anterior submedian carina; intermediate carina extending anteriorly slightly beyond base of lateral denticle; intermediate denticle with short carina, not extending onto mid-dorsal surface; lateral and marginal carinae subparallel. Submedian teeth separated by V-shaped emargination, appressed basally; with 11–18 submedian denticles either side of midline. Ventral surface without carinae or spines.

Uropodal protopod primary spines flattened, outer longer than inner, margins smooth, ventrally carinate. Uropodal exopod proximal segment distinctly longer than distal segment; outer margin with 10–12 flattened, movable spines, distalmost tapering to sharp point; distal margin with slender ventral spine. Exopod distal segment ovate, entire margin setose. Uropodal endopod ovate, length about 3 times width; with 2 low dorsal carinae.

COLOUR IN LIFE. Dull pinkish-tan dorsally, white to colourless ventrally. AS2 with lateral spot and broken, dark brown transverse line medially. AS3–5 with transverse row of five evenly spaced dark brown spots. Telson with black patch lateral to accessory median carinae at junction of submedian and anterior submedian carinae. Antennal protopod, raptorial claw and pereopods white. Antennal scale dull orange-red distally, marginal setae red. Uropodal exopod and endopod pale blue, marginal setae red. Outer movable spine of uropodal exopod dull orange.

MEASUREMENTS. Male ($n = 2$) TL 105–107 mm, female ($n = 6$) TL 24–100 mm. Ah Yong (2002c) recorded specimens to TL 145 mm.

HABITAT. Sandy, shelly and coarse substrates; 50–276 m.

REMARKS. *Odontodactylus hawaiiensis* is similar to *O. japonicus* and originally went unrecognised as a distinct species by Bigelow (1893), who first recorded the species from Hawaii under the name *O. japonicus*. *Odontodactylus japonicus* ranges from the Indian Ocean to the western margin of the western Pacific (Japan to eastern Australia) and *O. hawaiiensis* ranges from Easter Island and Hawaii to New Caledonia, the Chesterfield Islands, New Zealand and the Philippines. Thus, the two species have largely discrete distributions but overlap in the South China Sea.

Odontodactylus hawaiiensis differs from *O. japonicus* in having setose anterior margins on the antennal scale in adults (glabrous in adult *O. japonicus*), a postero-lateral spine on AS5 in adults (unarmed in *O. japonicus*), and in the short carina of the intermediate denticle of the telson. In *O. hawaiiensis*, the carina of the intermediate denticle does not extend beyond the base of the denticle, whereas in *O. japonicus*, the carina extends anteriorly onto the mid-dorsal surface of the telson. The only other odontodactylid recorded from New Zealand, *O. scyllarus*, is readily recognised by its bright, red, blue and green colouration and the presence of only two or three rather than six or more teeth on the inner margin of the dactylus of the raptorial claw.

All New Zealand specimens of *O. hawaiiensis* were collected from northern waters, along the Norfolk or Kermadec ridges; several juvenile specimens were taken from fish stomachs. In juvenile specimens smaller than TL 35 mm, the mandibular palp is 2- rather than 3-segmented. The ocular scales of juveniles smaller than about TL 30 mm are slightly separated, rather than appressed as in larger specimens, approaching the condition in species of the *O. brevirostris* group (Ah Yong 2001). All specimens have a posterolateral spine on AS4–5, except the Philippine specimen, in which AS4 is unarmed on the left side.

Manning's (1991) record of *Odontodactylus brevirostris* (Miers, 1884) from Raoul Island, Kermadec Islands, is a juvenile female *O. hawaiiensis* with separate ocular scales (Fig. 16J); *O. brevirostris* is not yet known from New Zealand waters. A specimen of *O. hawaiiensis* from the Philippines and specimens collected by the French expedition, BORDAU2, from Tonga are reported to document its presence at those localities.

DISTRIBUTION. Pacific Ocean from Easter Island, Hawaii, Tonga, the Philippines, New Caledonia, the Chesterfield Islands and northern New Zealand waters.

Odontodactylus scyllarus (Linnaeus, 1758) (Figs 18, 19)

Cancer Scyllarus Linnaeus, 1758: 633 [type locality: Rinca, Greater Sunda Island, Sulawesi, Indonesia, by neotype selection (Ah Yong 2001)].

Gonodactylus Bleekeri A. Milne-Edwards, 1868: 65, footnote [type locality: Batavia, Indonesia (= Jakarta, 6°10'S, 106°48'E)].

Gonodactylus elegans Miers, 1884: 566, 575, pl. 52: fig. b [type localities: Providence Island (9°14'S, 51°02'E) and Providence Reef (9°23'S, 51°03'E), Seychelles].

Odontodactylus scyllarus. — Manning 1967a: 10–15, fig. 3. — Ah Yong, 2001: 85, fig. 41. — Ah Yong *et al.*, 2008: 29–30, fig. 22.

TYPE MATERIAL. *Neotype*: USNM 274325, male (TL 96 mm), Rinca, Greater Sunda Island, Sulawesi, Indonesia, coll. M. Erdmann, 1993.

OTHER MATERIAL EXAMINED. *Auckland*: MNHW 4682, 2 females (TL 120–130 mm), Auckland, Saida Expedition, Dr Brilliant, Jan 1892.

DIAGNOSIS. Ocular scales oblique to midline, appressed medially, margin truncate. Antennal scale with entire margin setose, anterior setae shorter. Rostral plate triangular; lateral margins convex; apex deflexed. Raptorial claw dactylus with 2 or 3 small teeth on occlusal margin. AS(3)4–5 with posterolateral spine. Telson mid-dorsal surface with distinct median carina and 3 longitudinal carinae either side of midline (double accessory median, anterior submedian) in addition to carinae of primary teeth; carina of intermediate denticle short, not extending onto mid-dorsal surface. Uropodal exopod proximal distinctly longer than distal segment; outer margin with flattened movable spines, apices sharp, evenly tapering.

DESCRIPTION. Eyes with cornea subglobular. Anterior margin of ophthalmic somite faintly convex. Ocular scales triangular, lateral margins oblique to midline, medially appressed. Antennular peduncle length 0.76–0.87CL. Antennal protopod inner movable plate

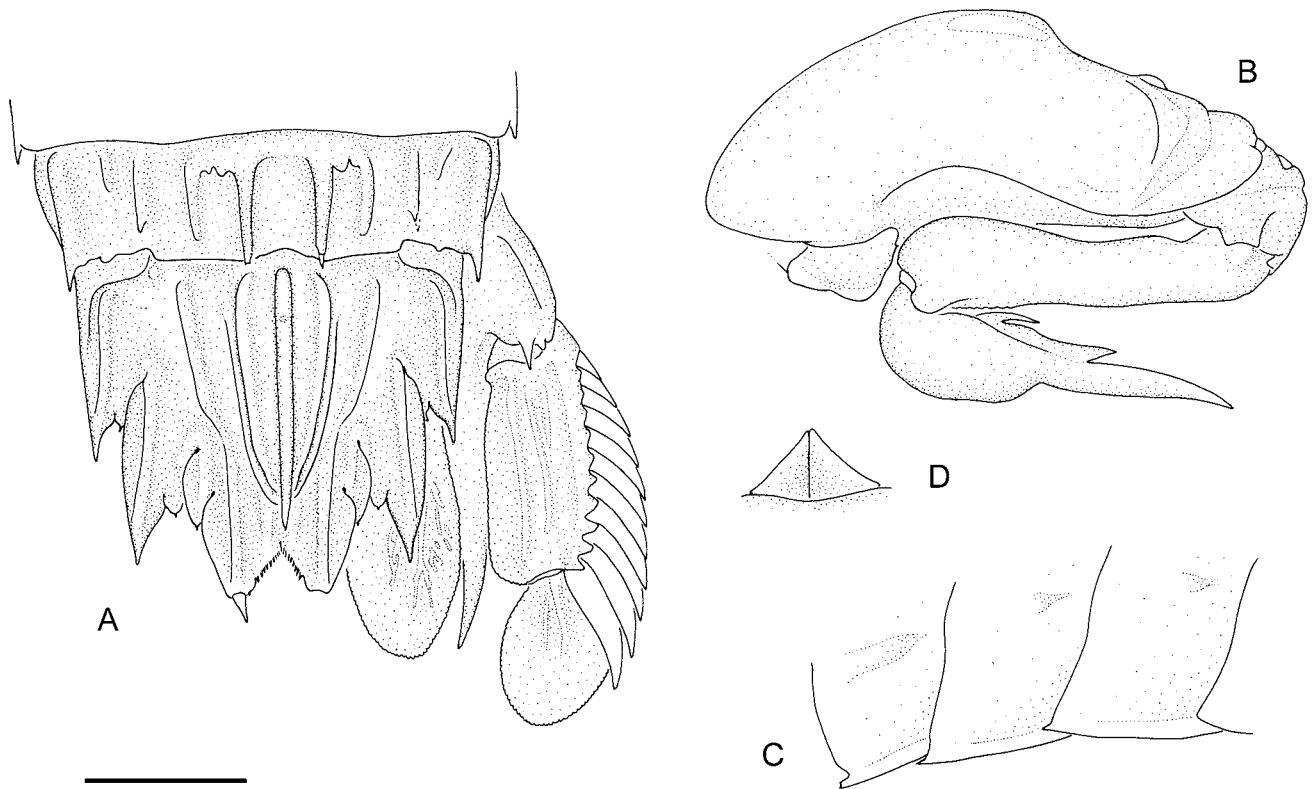


Figure 18. *Odontodactylus scyllarus* (Linnaeus, 1758), female, TL 120 mm, Auckland (MNHW 4682). A, AS6, telson and right uropod; B, right raptorial claw; C, AS2-5, lower right lateral view; D, ocular scales. Scale A-C = 10.0 mm, D = 5.0 mm

with rounded apex. Antennal scale length 2.50–2.70CL, entire margin setose.

Rostral plate triangular, wider than long, apex deflexed, lateral margins slightly convex proximally, otherwise straight; dorsally and ventrally smooth.

Carapace anterolateral margins rounded; surface without carinae; cervical groove shallow, not indicated medially; posterior margin slightly concave; posterolateral margins rounded.

Raptorial claw dactylus occlusal margin with 2 or 3 small teeth; outer proximal margin strongly inflated forming distinct heel, without proximal notch in adults. Carpus dorsal margin unarmed. Propodus without proximal movable spines; occlusal margin irregular, without spines or pectinations.

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

TS6–8 lateral processes rounded. TS8 sternal keel rounded.

Pereopodal endopod slender, linear, 2-segmented; basal segment unarmed.

Pleopod 1 endopod with distinct lateral lobe on posterior ‘endite’.

AS1–5 each with marginal carina only. AS(3)4–5 with posterolateral spine. AS6 with posteriorly armed

submedian, intermediate and lateral carinae; unarmed reflected submedian carinae, anteriorly bituberculate; short, unarmed anterior carina between intermediate and lateral carinae; without ventrolateral spine anterior to uropod articulation.

Telson slightly wider than long; median carina with posterior spine; double accessory median carinae straight to slightly irregular; submedian carina continuous with anterior submedian carina; intermediate carina extending anteriorly slightly beyond base of lateral denticle; intermediate denticle with short carina or swelling, not extending onto mid-dorsal surface; lateral and marginal carinae subparallel. Submedian teeth separated by V-shaped emargination, appressed basally; with 11–14 submedian denticles either side of midline. Ventral surface without carinae or spines.

Uropodal protopod primary spines flattened, outer longer than inner, margins smooth, ventrally carinate. Uropodal exopod proximal segment distinctly longer than distal segment; outer margin with 11 or 12 flattened, movable spines, distalmost tapering to sharp point; distal margin with slender ventral spine. Exopod distal segment ovate, entire margin setose. Uropodal endopod ovate, length about 3 times width; 2 low dorsal carinae and several short, irregular carinae.

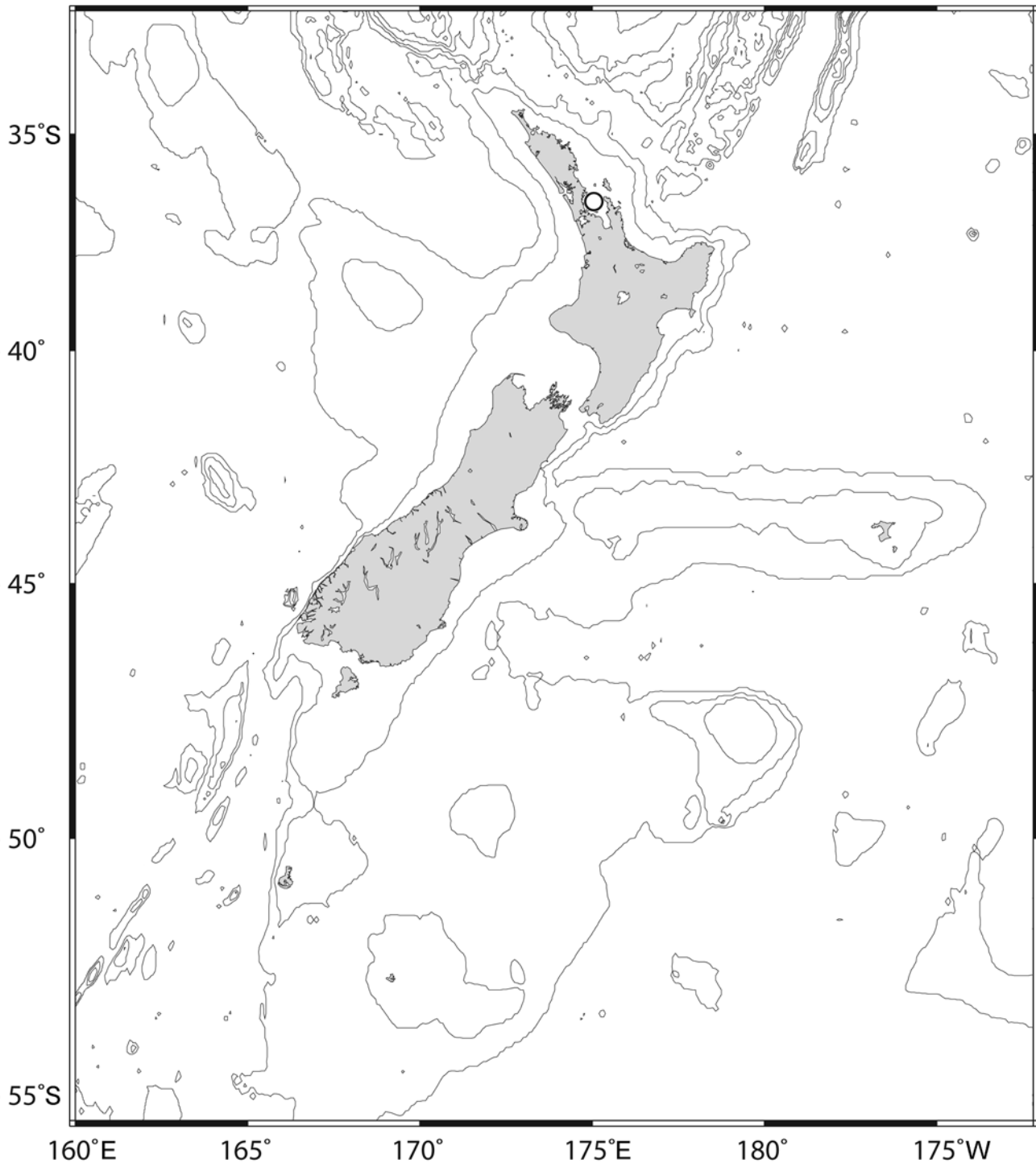


Figure 19. New Zealand distribution of *Odontodactylus scyllarus* (Linnaeus, 1758).

COLOUR IN LIFE. Overall dorsal colour reddish brown to green, often with diffuse banding and dark lateral spot on each somite. Large males deep-green. Posterior margin of thoracic and abdominal somites orange-red. Carapace with anterolateral and usually posterolateral areas with large dark brown spots outlined in white. Antennal scale orange yellow with dark apex; setae red. Ventral surface, dactylus of raptorial claw and pereopods

red. Uropodal protopod pale basally; exopod blue with iridescent blue outline and red marginal setae; endopod dark blue with iridescent blue outline and red marginal setae.

MEASUREMENTS. Male ($n = 1$) TL 96 mm, female ($n = 2$) TL 120–130 mm. Manning (1967a) reported specimens to TL 171 mm.

HABITAT. Coral and rocky reefs from the reef flat to about 30 m depth, from burrows under coral and boulders.

REMARKS. *Odontodactylus scyllarus* is a warm-water species known from New Zealand only by the present Auckland specimens. Although the Auckland locality could be suspected as erroneous, the natural occurrence of *O. scyllarus* in northern New Zealand waters is not unlikely given that it is common in the tropical waters to the north of New Zealand and ostensibly suitable habitats are present around much of Northland including the Hauraki Gulf. Additionally, *O. scyllarus* occurs in eastern Australia, south to at least about 33°S, and other tropical gonodactyloids have occasionally been found as far south as Sydney (~34°S) and even Bass Strait (~38°S) (Ahyong 2001). Thus, the present records are considered reliable. It remains to be confirmed, however, whether *O. scyllarus* is an occasional resident on the basis of sporadic larval recruitment from the north or a 'permanent' element of the northern New Zealand fauna along with other tropical stomatopods such as *Gonodactylaceus falcatus*. *Odontodactylus scyllarus* can be expected to occur at the Kermadec Islands, from which *O. japonicus* is already known.

The New Zealand specimens are in poor condition but agree well with the most recent revision of the species (Ahyong 2001). Both specimens have posterolateral spines on AS3–5 and two small teeth on the occlusal margin of the dactyli of the raptorial claws.

Odontodactylus scyllarus is the most powerful 'smasher' whose visual system and raptorial claw biomechanics have been extensively studied (Patek *et al.* 2004). It is also popular in the aquarium trade and probably the most frequently photographed tropical stomatopod (Debelius 2001).

DISTRIBUTION. Western Indian Ocean to Australia, the South China Sea, Japan, New Caledonia, Fiji and now from northern New Zealand.

PROTOSQUILLIDAE Manning, 1980

Protosquillidae Manning, 1980: 366, 369.

DIAGNOSIS. Rostral plate trispinous. Antennal protopod dorsally with fixed, anteriorly directed spine or tooth. Raptorial claw with subterminal ischiomeral articulation; propodus occlusal margin sparsely pectinate; dactylus with smooth or microscopically serrated occlusal margin and strongly inflated heel on outer proximal margin. Telson and AS6 immovably fused forming pleotelson (though demarcation usually visible). Distal segment of uropodal exopod articulating at distal end

of proximal segment; distal movable spines on outer margin of proximal segment not recurved anteriorly.

COMPOSITION. *Chorisquilla* Manning, 1969c; *Echinosquilla* Manning, 1969c; *Haptosquilla* Manning, 1969c; *Protosquilla* Brooks, 1886; *Rayellus* Ahyong, 2010a; *Siamosquilla* Naiyanetr, 1989.

REMARKS. Protosquillids are unique in the Stomatopoda for having the telson and AS6 immovably fused in adults forming a pleotelson (though the demarcation is usually visible as a groove). This unusual feature was interpreted by Brooks (1886) as a 'primitive' or 'proto' lineage, prompting the generic name *Protosquilla* Brooks, 1886. Phylogenetic analyses of the stomatopods, however, show that protosquillids are highly derived within the Gonodactyloidea (Ahyong & Harling 2000). Six protosquillid genera are known worldwide, with one genus in the eastern Atlantic (*Protosquilla*) and the remainder in the Indo-West Pacific. One genus and species of protosquillid is known from New Zealand.

KEY TO GENERA OF PROTOSQUILLIDAE

1. Lateral and posterior margins of telson entirely and closely lined with soft, spine-like papillae.....
.....*Rayellus*
– Lateral and posterior margins of telson unarmed, spinose or setose, but not lined with soft, spine-like papillae.....2
2. Distinct dorsal groove between AS6 and telson absent. Telson posterior margin undivided; submedian teeth separated by shallow concave or biconvex margin, not by deep emargination or narrow fissure *Siamosquilla*
– Dorsal groove indicating demarcation of AS6 from telson. Telson posterior margin divided by narrow fissure or deep emargination3
3. AS1 without articulated pleural plate
.....*Protosquilla*
– AS1 with articulated pleural plate4
4. Telson with long dorsal spines, each with soft apex. Uropodal endopod with erect dorsal spines.....
.....*Echinosquilla*
– Telson dorsal surface with or without spines. Uropodal endopod without dorsal spines.....5
5. Posterior margin divided by wide, deep V- or U-shaped emargination*Chorisquilla*
– Posterior margin divided by narrow median fissure, with either side appressed*Haptosquilla*

Haptosquilla Manning, 1969

Haptosquilla Manning, 1969c: 159. [Type species: *Gonodactylus pulchellus* Miers, 1880, by original designation. Gender: feminine].

DIAGNOSIS. Eye cylindrical; cornea subglobular. Mandibular palp 2-segmented or absent. AS1 with articulated anterolateral pleural plate. Dorsal groove demarcating AS6 from telson. Telson margins smooth or at most minutely denticulate, not lined with flexible spiniform papillae. Posterior margin of telson divided posteriorly by narrow median fissure. Uropodal endopod without dorsal spines.

COMPOSITION. *Haptosquilla corrugata* Ahyong, 2001; *H. ectypa* (Müller, 1886); *H. glabra* (Lenz, 1905); *H. glyptocercus* (Wood-Mason, 1875); *H. hamifera* (Odhner, 1923); *H. helleri* sp. nov.; *H. moosai* Erdmann & Manning, 1998; *H. philippinensis* Garcia & Manning, 1982; *H. proxima* (Kemp, 1915); *H. pulchella* (Miers, 1880); *H. pulchra* (Hansen, 1926); *H. stoliura* (Müller, 1886); *H. tanensis* (Fukuda, 1911); *H. togianensis* Erdmann & Manning, 1998; *H. trispinosa* (Dana, 1852); *H. tuberosa* (Pocock, 1893).

REMARKS. Sixteen species of *Haptosquilla* are currently recognised of which one is newly described from New Zealand. Species of *Haptosquilla* are abundant on coral reefs and subtidal habitats, where they live in holes in coral, rock, sponge and encrusting algae. Adults rarely exceed TL 50 mm and most species do not exceed TL 30 mm.

Haptosquilla helleri sp. nov. (Figs 20, 21)

Gonodactylus trispinosus. — Heller, 1865: 126. — Miers, 1876: 90. — Filhol, 1885b: 436. [Not *G. trispinosus* Dana, 1852].

Protosquilla trispinosa. — Chilton, 1891: 61; 1911a: 134–135. [Not *P. trispinosa* (Dana, 1852)].

Gonodactylus glaber. — Kemp, 1913: 4, 11, 149, 182, pl. 10, fig. 121. — Serène, 1947: 381, 385, fig. 1, pl. 2; 1953: 506, 507. [Not *G. glaber* Lenz, 1905].

Gonodactylus Glaber. — Serène, 1939: 349. [Not *G. glaber* Lenz, 1905].

Gonodactylus lenzi Holthuis, 1941: 288 [unnecessary replacement name for *Gonodactylus glaber* (Lenz, 1905)]. — Serène, 1954: 5, 6, 7, 10, 11, 19, 28, 31, 34–41, 46, 47, 49–51, 52, 86, figs. 5–7, 11B–C, 13–12, pl. 1. [Not *G. glaber* Lenz, 1905].

Haptosquilla lenzi. — Moosa, 1986: 386. [Not *H. lenzi* (Holthuis, 1941)].

Haptosquilla glabra. — Manning, 1995: 100–102, figs 9l, 43c, 49–51, pl. 17. — Moosa, 2000: 424–425, tab. 1. [Not *H. glabra* (Lenz, 1905)].

TYPE MATERIAL. *Holotype*: MNHW 25398, female (TL 31 mm), Auckland, 'Novara'.

Paratypes: MNHW 4676, 1 male (TL 22 mm), 1 female (TL 21 mm), Auckland, 'Novara'.

OTHER MATERIAL EXAMINED. *Vietnam*: AMP12158–12159, 1 male (TL 20 mm), 1 female (TL 24 mm), Annam, Station Cauda, Vietnam, R 1005 & R 1052, coll. R. Serène, 25 Jan 1947; ZRC 1970.10.23.5–8, 2 males (TL 19–22 mm), 2 females (TL 20–24 mm), Nhatrang Bay, Station Cauda, Vietnam, coll. R. Serène, Jan 1947.

Tonga: USNM 307121, 3 males (TL 12–19 mm), 7 females (TL 17–22 mm), Pangai, Lifuka Island, Ha'apa Group, 19°49'05"S, 174°22'42"W, 7.5–12 m, JTW 93–29, coll. J. Williams, 11 Nov 1993.

DIAGNOSIS. Rostral plate sharply trispinous, each spine slender. Mandibular palp 2-segmented. AS5 smooth, without trace of pitting on dorsomedial surface. AS6 with submedian, intermediate and lateral bosses. Telson with 3 pairs of fixed primary teeth; lateral margins of telson, dorsal surface of bosses and surface between bosses smooth, margins of bosses smooth or weakly corrugated or eroded; submedian denticles present in adults; submedian bosses elongate, extending posteriorly beyond midlength, but not to posterior margin. Proximal segment of uropodal exopod with acute lobe lateral to articulation of distalmost movable spine.

DESCRIPTION. Eye with cornea not extending to end of antennular peduncle segment 2.

Antennular peduncle 0.63–0.75CL. Antennal protopod with blunt dorsal lobe. Antennal scale 0.50–0.53CL.

Rostral plate sharply trispinous, median spine extending anteriorly to base of cornea; lateral spines slender, directed anterolaterally; lateral margins faintly convex, divergent anteriorly.

Carapace with anterior margin of lateral plates slightly concave; anterolateral margin bluntly angular.

Raptorial claw dactylus with basal notch on outer margin. Carpus dorsal margin with blunt distal tooth. Propodus without movable spine proximally, occlusal margin sparsely pectinate.

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

Lateral margin of TS6–8 rounded. TS8 sternal keel obsolete. Pereopodal endopods slender, linear, 2-segmented; basal segment unarmed.

Pleopod 1 endopod in adult males with prominent lateral lobe on posterior endite.

AS1–4 smooth dorsally and laterally, with marginal carina indicated laterally; blunt posterolaterally. AS5 smooth dorsally; with marginal carina and shallow oblique grooves laterally; blunt posterolaterally. AS6 with distinct submedian, intermediate and lateral bosses, each irregularly eroded.

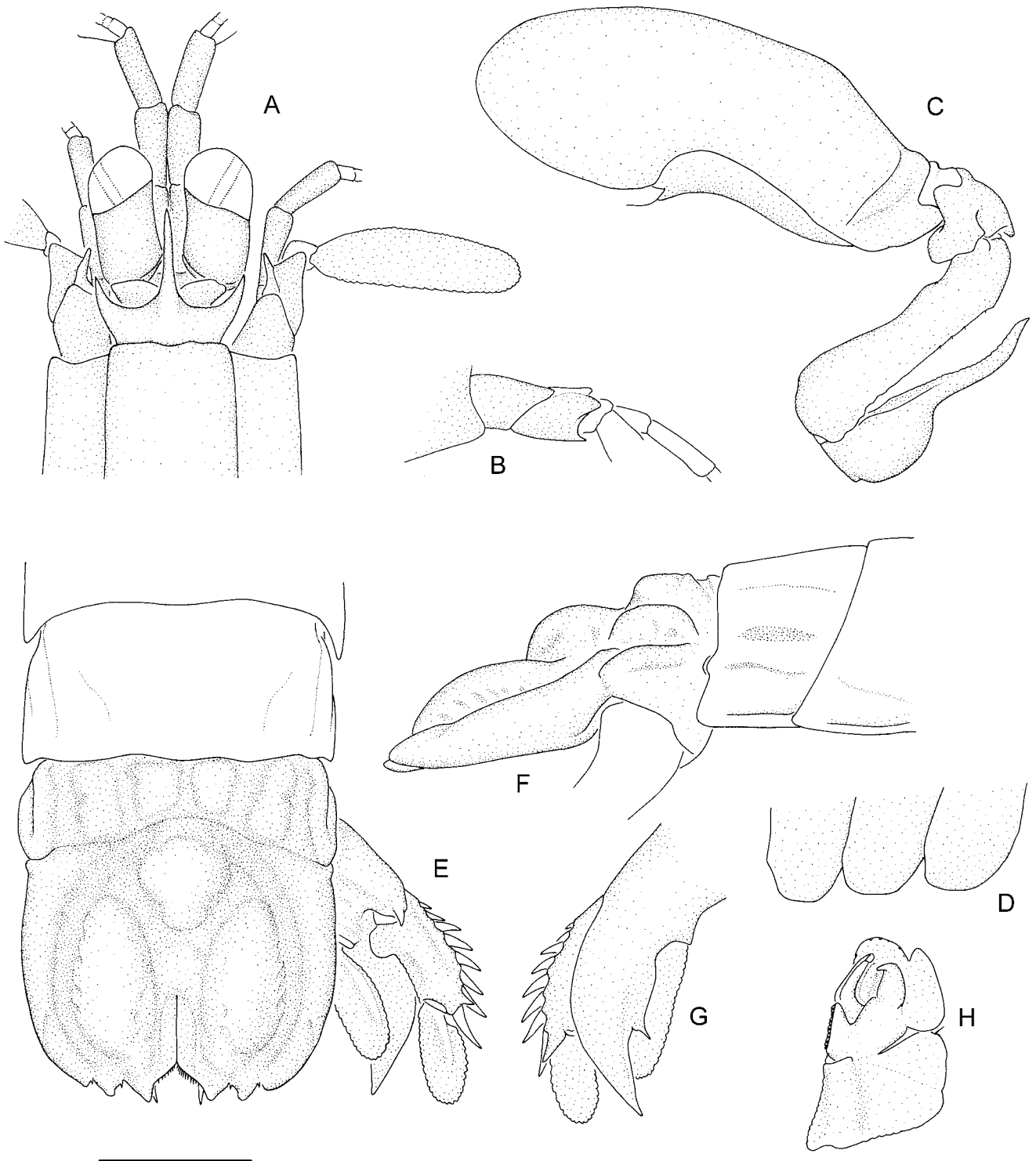


Figure 20. *Haptosquilla helleri* sp. nov. A–G, female holotype, TL 31 mm, Auckland (MNHW 25398). H, male paratype TL 22 mm, Auckland (MNHW 4676). A, anterior cephalothorax; B, right antennal protopod, lateral view; C, right raptorial claw; D, TS6–8, lower right lateral view; E, AS4–6, telson and right uropod; F, AS4–6 and telson, right lateral view; G, right uropod, ventral view; H, right pleopod 1 endopod, anterior view. Scale A–G = 2.5 mm, H = 1.25 mm.

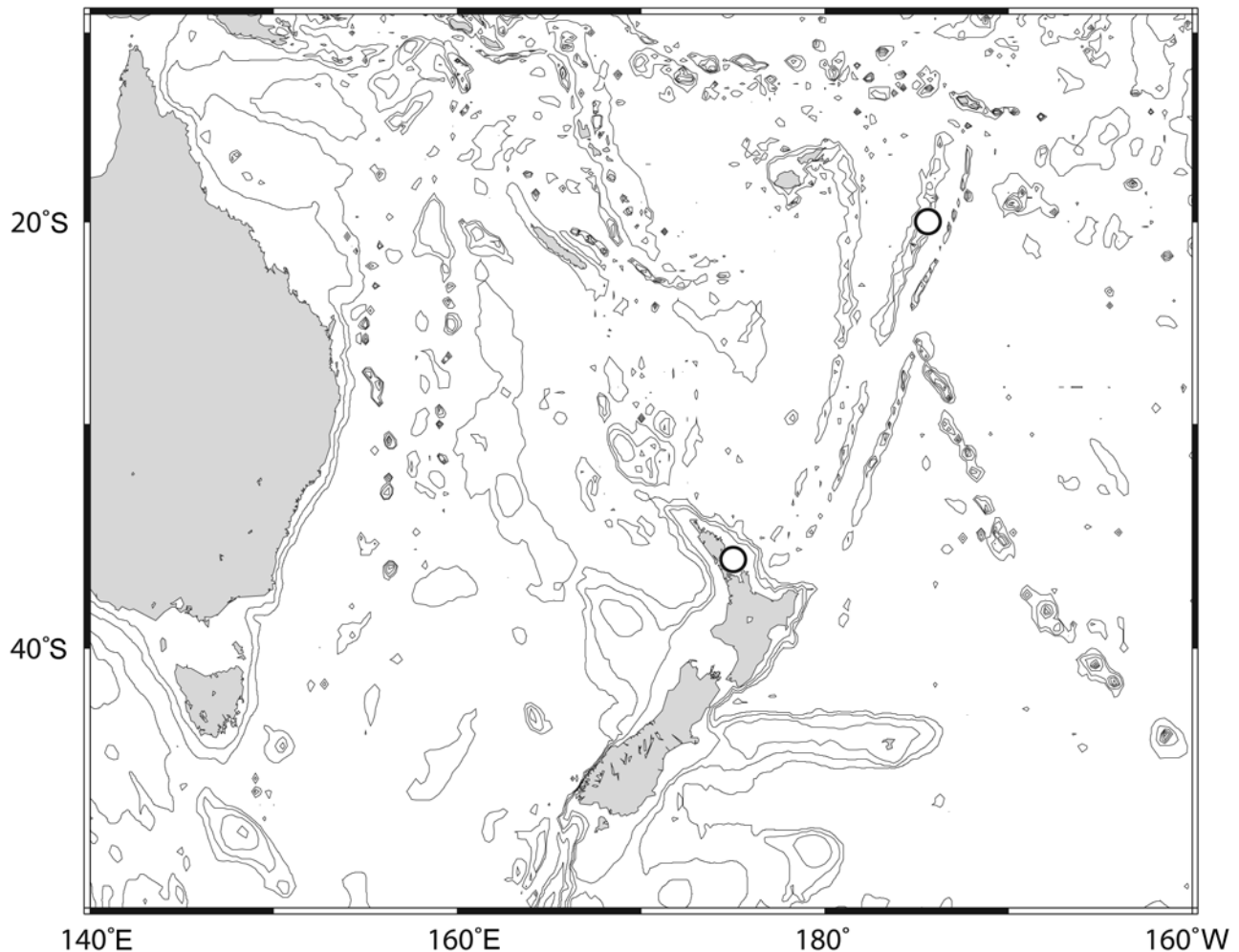


Figure 21. South-western Pacific distribution of *Haptosquilla helleri* sp. nov.

Telson broader than long; with 3 pairs of blunt primary teeth, separated by shallow V; median boss short irregularly slightly eroded laterally; submedian bosses elongate, smooth dorsally, smooth or weakly corrugated around margins, anteriorly continuous with median boss; submedian bosses demarcated from marginal carina by distinct groove; marginal carina smooth dorsally and laterally, lateral tooth indicated by short dorsal groove near posterior third of marginal carina.

Uropodal protopod smooth proximally; unarmed dorsally except for dorsal spine above proximal exopod articulation. Uropodal exopod proximal segment without pitting; outer margin with 8 or 9 movable spines, distalmost extending to midlength of distal segment; with acute lobe lateral to base of distal movable spine. Uropodal endopod with low dorsolateral carina; ventral surface smooth carinae; length 2.68–3.20 times width.

COLOUR IN LIFE. According to Manning (1995: pl. 17), *H. helleri* (as *H. glabra*) is drab gray-green overall with

a dark median stripe and diffuse white and gray mottling along the thorax and abdomen.

MEASUREMENTS. Male ($n = 6$) TL 12–22 mm, female ($n = 11$) TL 17–31 mm. Other measurements of holotype: CL 7.0 mm, antennal scale length 3.5 mm, antennular peduncle length 4.4 mm.

ETYMOLOGY. Named after Camil Heller, who first reported on the present New Zealand specimens under the name *Gonodactylus trispinosus*.

HABITAT. Shallow-water reefs. Serène (1939) reported *H. helleri* (as *Gonodactylus glaber*) to be common in oyster beds in southern Vietnam.

REMARKS. The Auckland specimens of *Haptosquilla helleri* sp. nov. are the basis of Heller's original record of *Gonodactylus trispinosus* from New Zealand waters, perpetuated by Miers (1876) and Chilton (1891). *Haptosquilla helleri* has not been recorded from New Zealand waters since first reported by Heller (1865).

As with several other warm-water species from New Zealand, however, *H. helleri* may be naturally rare or occur sporadically according to patterns of pelagic larval recruitment from source populations to the north of mainland New Zealand. Certainly, *H. helleri* could be easily overlooked in the field given its small size, cryptic habits and drab colouration. Although it may be tempting to question the veracity of locality data accompanying the Auckland specimens, numerous records of warm-water species from mainland New Zealand by Heller (1865) and Miers (1876), long considered erroneous, have since been validated by more detailed studies (e.g., Dell 1964a, b; McLaughlin & Dworschak 2001).

Haptosquilla helleri sp. nov. very closely resembles *H. glabra* (Lenz, 1905) [type locality: Zanzibar] and *H. ectypa* (Müller, 1886) [type locality: Trincomali, Sri Lanka] in telson ornamentation. Both *H. helleri* and *H. glabra* differ from *H. ectypa* in having submedian denticles on the telson, lacking in the latter. *Haptosquilla helleri* differs from *H. glabra* consistently, albeit subtly, in having a completely smooth mid-dorsal surface on AS5. In *H. glabra*, the mid-dorsal surface is marked by small pits. Previous records of *Haptosquilla glabra* from Vietnam (Serène 1954; Manning 1995) are referable to *H. helleri* as are probably records from the Andaman Sea (Kemp 1913) and Indonesia (Holthuis 1941) (if Kemp's (1913) figures are correct).

Kemp's (1915) record of *H. glabra* (as *Gonodactylus glaber*) from Port Galero, the Philippines, said to "differ considerably from the examples in the Indian Museum" as a possible preservation artefact (Kemp 1915: 186), are probably misidentified. These specimens, described as having a swollen hind body, lacking dorsal bosses on AS6, and lacking the groove demarcating the telson, correspond perfectly to *Siamosquilla laevicaudata* (Sun & Yang, 1998), to which Kemp's (1915) is herein attributed. Thus, rather than being widespread in the Indo-West Pacific, *H. glabra* is probably a western Indian Ocean species that is replaced by *H. helleri* in the western Pacific and probably also the Andaman Sea.

It is noteworthy that early authors such as Heller (1865) and Miers (1880, in part) misidentified *H. helleri* (or other very similar species) with *H. trispinosa*. Dana's (1852) identification of *H. trispinosa* from Fiji was apparently based, at least in part, on Adam White's figures of *H. trispinosa* intended for publication as plate V in the "The Zoology of the Voyage of the H.M.S. Erebus & Terror" authored decades later by Miers (1874). Although a number of authors apparently had pre-publication access to White's work, plate V was never published and has long been considered lost. Miers (1880) was the first to publish a figure of *H. trispinosa* sensu stricto (lectotype). White's original material that he called *H. trispinosa* (as *Gonodactylus trispinosus*), however, includes specimens from Australia and Mauritius.

The Australian specimen, probably White's intended type (Miers, 1880), is the lectotype and represents *H. trispinosa* sensu stricto (Ahyong 2001). The Mauritian paralectotype, however, represents *H. ectypa* (see Kemp 1913), which very closely resembles *H. glabra* and *H. helleri* in ornamentation and marginal armature of the telson. Given that authors prior to Borradaile (1907) had misidentified their material of '*H. trispinosus*' with *H. helleri* or a *helleri*-like species such as *H. ectypa*, it is likely that White depicted the Mauritian specimen in his now lost 'Erebus & Terror' plate. Curiously, apart from Dana's (1852) Fijian record, *H. trispinosa* sensu stricto has never been recorded east of the New Hebrides. Given Dana's (1852) familiarity with White's 'Erebus & Terror' plates and given that all confirmed reports of *H. trispinosa* lie west of the New Hebrides, Dana may have been dealing with *H. helleri* rather than *H. trispinosa*.

DISTRIBUTION. New Zealand to Tonga, Vietnam and possibly the Andaman Sea.

LYSIOSQUILLOIDEA Giesbrecht, 1910

DIAGNOSIS. Cornea with 6 (rarely 2) rows of hexagonal mid-band ommatidia. Maxillipeds 3–4 with propodi subquadrate, ribbed or beaded ventrally. Body flattened, loosely articulated or compact. Raptorial claw with terminal ischiomerall articulation; dactylus inflated or uninflated basally. Telson without distinct median carina; at most with movable submedian teeth. Uropodal protopod with at most two primary spines; articulation of exopod segments terminal.

COMPOSITION. Coronididae Manning, 1980; Lysiosquillidae Giesbrecht, 1910; Nannosquillidae Manning, 1980; Tetrasquillidae Manning & Camp, 1993.

REMARKS. One lysiosquilloid family is represented in New Zealand.

TETRASQUILLIDAE Manning & Camp, 1993

Tetrasquillidae Manning & Camp, 1993: 88–89.
Heterosquillidae Manning, 1995: 123.

DIAGNOSIS. Cornea bilobed. Raptorial claw dactylus uninflated basally; propodus with 3 or 4 proximal movable spines, occlusal margin pectinate; ischium shorter than half merus length. Pereopod 1–2 endopods subcircular or ovate. Pereopod 3 endopod slender or oval elongate. Abdominal articulation compact. Telson with primary teeth and denticles distinct, slender, not fused into margin. Proximal margin of uropodal endopod with weak dorsal fold.

COMPOSITION. *Acaenosquilla* Manning, 1991; *Allosquilla* Manning, 1977a; *Colubrisquilla* gen. nov.; *Heterosquilla* Manning, 1963b; *Heterosquilloides* Manning, 1966; *Heterosquillopsis* Moosa, 1991; *Kasim* Manning, 1995; *Pariliacantha* gen. nov.; *Tectasquilla* Adkison & Hopkins, 1984; *Tetrasquilla* Manning & Chace, 1990.

REMARKS. Three tetrasquillid genera are represented in New Zealand waters, of which two are newly proposed herein. They can be distinguished from the eight other tetrasquillid in the key below.

KEY TO GENERA OF THE TETRASQUILLIDAE

1. Telson ventral surface with post-anal spine. Ischium of raptorial claw with distoventral spine.....2
 - Telson ventral surface without post-anal spine. Ischium of raptorial claw without distoventral spine6
2. Eyes largely concealed by rostral plate. Rostral plate elongate, pentagonal. Dactylus of raptorial claw with 4 teeth. Uropodal protopod without ventral spine anterior to endopod articulation.....
..... *Tectasquilla*
 - Eyes not concealed by rostral plate. Rostral plate broad basally with slender anterior spine. Dactylus of raptorial claw with more than 4 teeth. Uropodal protopod with ventral spine anterior to endopod articulation3
3. Ischium of raptorial claw with distoventral spine; dactylus with 12 or more teeth.....*Pariliacantha*
 - Ischium of raptorial claw without distoventral spine; dactylus with 6-8 teeth4
4. Rostral plate distinctly longer than greatest width*Kasim*
 - Rostral plate distinctly shorter than greatest width5
5. Dactylus of raptorial claw with 6 or 7 teeth. Denticles on telson margin between movable submedian teeth and intermediate teeth of similar size, small.....
..... *Acaenosquilla*
 - Dactylus of raptorial claw with 8 teeth. Denticles on telson margin between movable submedian teeth and intermediate teeth markedly dissimilar in size, third from midline markedly larger than first, second and fourth denticles.....
..... *Heterosquillopsis*
6. Uropodal protopod with outer spine distinctly longer than inner. Cornea subglobular or broadened, not bilobed..... *Heterosquilla*
 - Uropodal protopod with inner spine as long as or longer than inner. Cornea distinctly bilobed7

7. Antennal protopod without mesial papilla. Uropodal protopod with ventral spine anterior to endopod articulation.....8
 - Antennal protopod with 1 or 2 mesial papillae. Uropodal protopod without ventral spine anterior to endopod articulation9
8. Ocular scales rounded or quadrate. Raptorial claw propodus with 4 movable spines along proximal occlusal margin. AS5 not distinctly narrowed posteriorly. Uropodal endopod spatulate, articulation on narrow anterior end.....*Heterosquilloides*
 - Ocular scales spiniform. Raptorial claw propodus with 3 movable spines along proximal occlusal margin. AS5 distinctly narrowed posteriorly. Uropodal endopod reniform, articulation on 'long edge'*Colubrisquilla*
9. Dactylus of raptorial claw with 4 teeth. Mandibular palp present. Upper posterior surface of telson with rows of posteriorly directed spines *Tetrasquilla*
 - Dactylus of raptorial claw with 6 or more teeth. Mandibular palp absent. Upper posterior surface of telson with rugosities out without rows of posteriorly directed spines..... *Allosquilla*

Colubrisquilla gen. nov.

DIAGNOSIS. Cornea bilobed, with 2 rows of ommatidia in the midband; eyes not concealed by rostral plate. Ocular scales separate, spiniform. Antennal protopod without mesial papillae. Pereopods 1-2 with oval, elongate endopods. Raptorial claw propodus with 3 movable spines proximally; dactylus outer margin uninflated. AS5 distinctly narrowed posteriorly, lateral surfaces with irregular sculpture and erosion. Telson swollen, with low, irregular dorsal carinae or spinules; posterior margin with movable submedian teeth and 2 pairs of fixed primary teeth; 4 'intermediate' denticles present; telson ventral surface without post-anal spine. Uropodal protopod produced anteriorly; primary spines slender, inner spine longer than outer spine; ventral spine anterior to endopod articulation; endopod reniform, articulation on 'long edge'.

TYPE SPECIES. *Colubrisquilla dempsey* gen. et sp. nov. by present designation.

EYTOLOGY. A combination of the Latin *colubris*, snake, serpent, and the generic name *Squilla*, alluding to the similarity between the forked reptilian tongue and the ocular scales of *C. dempsey*. Gender: feminine.

COMPOSITION. Monotypic.



REMARKS. Of the ten genera now recognised in the Tetrasquillidae, *Colubrisquilla* gen. nov. is phenotypically (and probably phylogenetically) closest to *Heterosquilloides*, sharing the strongly bilobed cornea with what appear to be two rows of midband ommatidia. *Colubrisquilla* differs from *Heterosquilloides* in having separate, spiniform ocular scales (rather than scales fused into a quadrate or rounded plate), 3 instead of 4 movable spines on the proximal occlusal margin of the raptorial claw propodus, in bearing numerous carinae on the telson and lateral portions of AS5–6, in the strong posterior narrowing of AS6, the anteriorly produced anterior margin of the uropodal protopod and a reniform rather than spatulate uropodal endopod in which the articulation is along the ‘long edge’ rather than anterior end (resembling that of *Heterosquilla*). The narrowing of AS6 in *Colubrisquilla* allows a more compact conformation of the uropods against the abdomen, reducing the overall lateral profile and width of the hind body, presumably improving mobility within the burrow. Similar adaptations are present in some species of *Eurysquilla* Manning, 1963 (*Eurysquilloidea*), also burrow dwellers.

Colubrisquilla dempsey gen. et sp. nov.

(Figs 22, 23)

TYPE MATERIAL. *Holotype*: NIWA 23974, male (TL 52 mm), Chatham Rise, 43°34.59'S, 175°58.09'E, 335 m, NZOI Stn S121, 20 Oct 1979.

Paratypes: NIWA 75299, 1 male (TL 50 mm), Tokomaru Bay, 38°14.71–14.45'S, 178°41.65–41.72'E, 137–136 m, beam trawl, TAN1108/206, 30 May 2011; NIWA 80770, 2 males (TL 39–45 mm), type locality; AM P87872, 2 males (TL 29–45 mm), 43°17.89'S, 177°34.05'E, 253–261 m, TAN1101/102, from stomachs of *Coelorinchus biclinozonalis*, coll. D. Stevens, 22 Jan 2011; NIWA 68008, 1 female (TL 63 mm), Chatham Rise, 43°37.09'S, 175°56.69'E, 322 m, NZOI Stn S123, 20 Oct 1979.

OTHER MATERIAL EXAMINED. NIWA 4123, 1 female (broken; CL 9.6 mm), south Mernoo Bank, 43°02.94'S, 175°17.29'E, 240–298 m, W449, 22 Feb 1995; NIWA 4104, 1 damaged male (CL 4.9 mm), 43°10.06'S, 177°26.33'W, 410–449 m, TAN0501/63, from stomach of *Coelorinchus* sp., #4444, coll. D. Stevens, 8 Jan 2005; NIWA 4119, 1 damaged male (TL 48 mm), 43°12.38'S, 176°52.67'W, 330–352 m, TAN0601/47, ZSQ 25943, from stomach of *Coelorinchus aspercephalus*, coll. D. Stevens, 5 Jan 2006; AM P87873, 1 male (TL 37 mm), 43°12.77'S, 177°29.89'W, 365–374 m, TAN1101/54/01, from *Coelorinchus biclinozonalis*, coll. D. Stevens, 13 Jan 2011; AM P87874, posterior abdomen, 43°19.47'S, 177°11.70'E, 215–230 m, TAN1101/103/14, from stomach of *Coelorinchus biclinozonalis*, coll. D. Stevens, 23 Jan 2011; AM P87875, 1 damaged specimen,

43°21.47'S, 176°48.76'E, 270–273 m, TAN1101/105/90, from *Coelorinchus biclinozonalis*, coll. D. Stevens, 23 Jan 2011; AM P87876, 1 juvenile male (CL 3.2 mm), 3 juvenile females (2 damaged; CL 3.3 mm), 43°27.18'S, 177°13.59'E, TAN1101/104, 245–259 m, from stomachs of *Coelorinchus biclinozonalis*, coll. D. Stevens, 23 Jan 2011; AM P87877, 2 damaged specimens, 43°29.77'S, 175°36.49'E, 234–250 m, TAN0901/99, from stomach of *Coelorinchus biclinozonalis*, coll. D. Stevens, 14 Jan 2009; NIWA 4186, 1 damaged male (ca TL 45 mm), 1 damaged female (TL 45 mm), 1 partial abdomen and telson, 43°29.91'S, 178°04.83'W, TAN0601/66, ZSQ 26823, from stomach of *Coelorinchus bollonsi*, coll. D. Stevens, 8 Jan 2006; NIWA 4199, 1 damaged male (TL 45 mm), 43°56.83'S, 179°05.41'W, 361–382 m, TAN0601/25, ZSQ 25147, from stomach of *Coelorinchus bollonsi*, coll. D. Stevens, 1 Jan 2006; NIWA 80769, 1 damaged male (CL 9.5 mm), Chatham Rise, from stomach of *Coelorinchus* sp. SPO ZSQ, coll. D. Stevens, 2006.

DIAGNOSIS. Rostral plate cordiform, widest near mid-length, apex a short spine. Ocular scales spiniform, directed anteriorly. Raptorial claw dactylus with 9–11 teeth; propodus with 3 movable spines proximally. Pereopods 1–2 basal segment with outer ventrolaterally directed spine and short inner tooth. Pereopod 3 with outer spine only. TS6–8 lateral process broadly rounded. AS4 smooth dorsally and posteriorly; with slender posterolateral spine. AS5 distinctly narrowed posteriorly, lateral surfaces with irregular sculpture and erosion. Telson thick, dorsal surface with small tubercles, longitudinal, irregular and vermiform accessory carinae on surface either side of median elevation. Uropodal protopod obtusely produced anteriorly; irregular sculpture dorsally; primary spines slender, inner longer than outer.

DESCRIPTION. Eye not extending beyond antennular peduncle segment 2; cornea strongly bilobed, set obliquely on stalk, inner margin longer than outer margin; CI 200–253. Ophthalmic somite anterior margin flattened. Ocular scales spiniform, directed anteriorly, fused in basal half.

Antennular peduncle 0.70–0.78CL. Antennular somite dorsal processes with acute apices, spiniform directed anterolaterally. Antennal protopod dorsally unarmed; with small ventrodiscal tooth and 2 ventral papillae. Antennal scale length 2.70–3.00 width, 0.33–0.39CL.

Rostral plate cordiform, slightly wider than long, widest near midlength, lateral margins evenly convex, apex a short spine. Carapace anterolateral angles rounded, anterior margins straight.

Raptorial claw dactylus with 9–11 (usually 10) teeth, outer margin straight, curving distally, proximal margin with distinct basal notch. Carpus dorsal margin

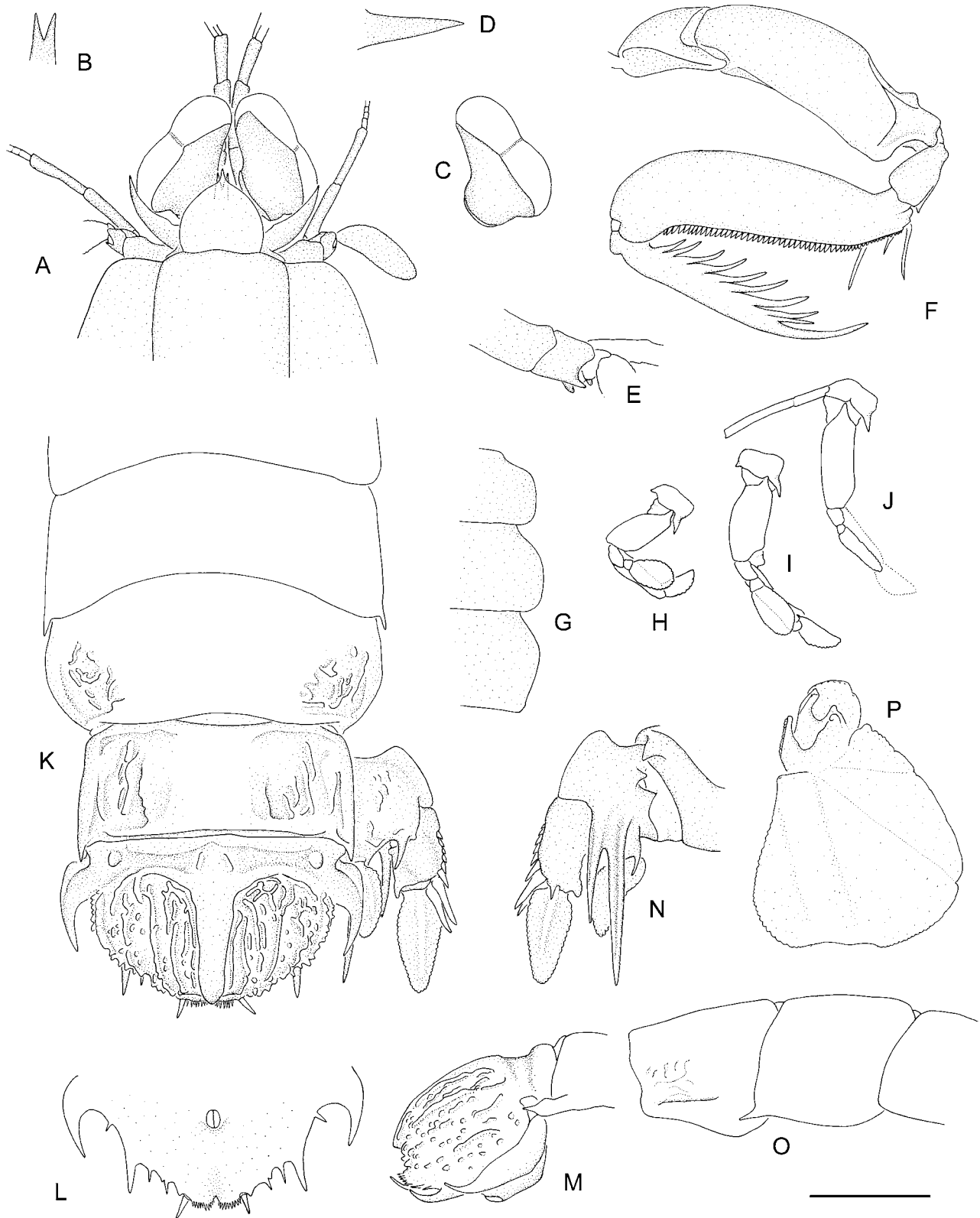


Figure 22. *Colubrisquilla dempsey* gen. et sp. nov., male holotype, TL 52 mm, Chatham Rise (NIWA 23974). A, anterior cephalothorax; B, ocular scales; C, right eye; D, right dorsal process of antennular somite, lateral view; E, right antennal protopod, lateral view; F, right raptorial claw; G, TS6-8, right dorsal view; H-J, right pereopods 1-3, posterior view; K, AS3-6, telson and right uropod, dorsal view; L, telson, ventral view; M, AS6 and telson, right lateral view; N, right uropod, ventral view; O, AS3-5, right lateral view; P, right pleopod 1 endopod, anterior view. Scale A, F-O = 4.0 mm; B-E, P = 2.0 mm.

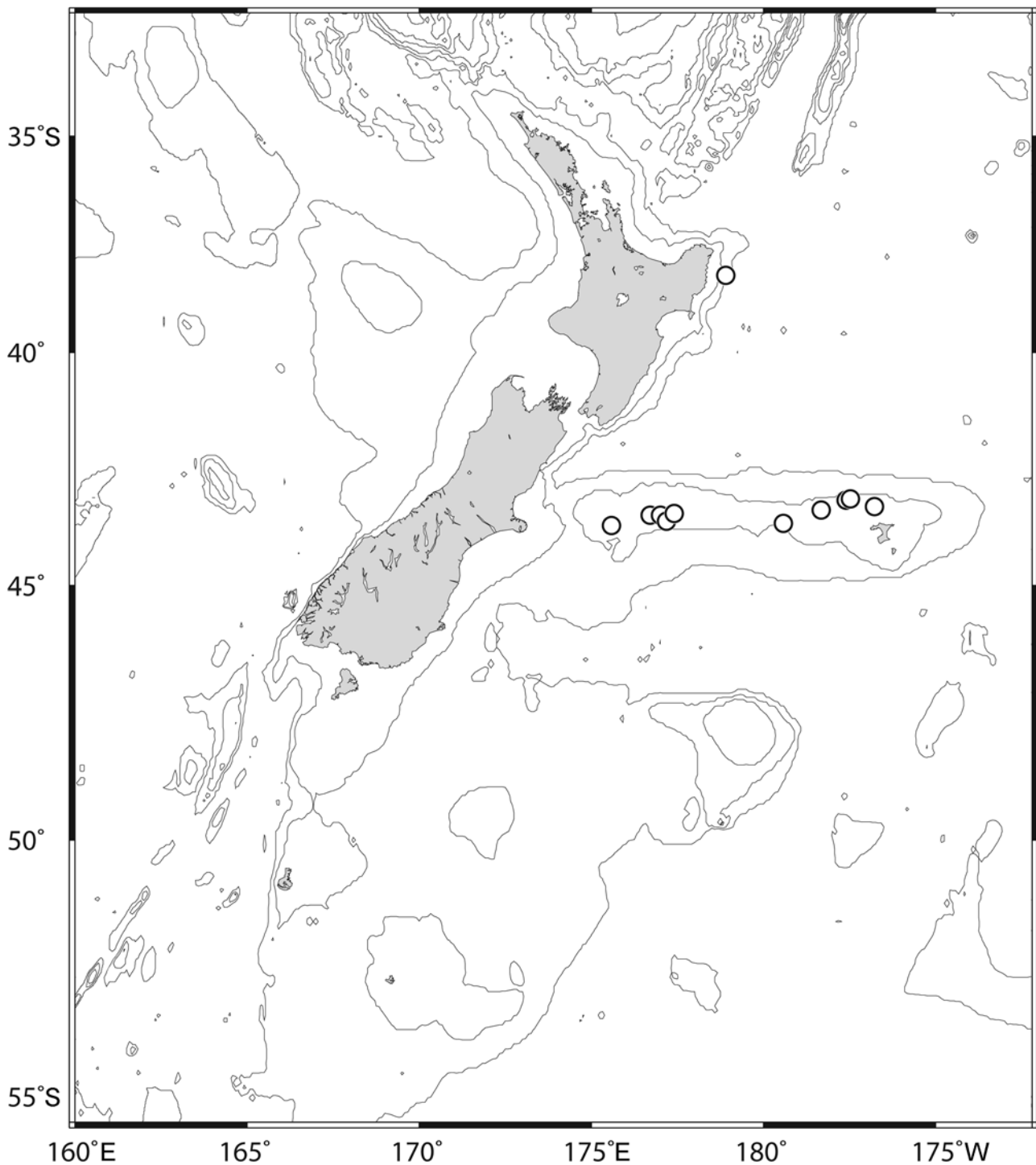


Figure 23. New Zealand distribution of *Colubrisquilla dempseyi* gen. et sp. nov.

terminating in short tooth, directed ventrally. Propodus with 3 movable spines proximally, distal margin unarmed; inferodistal margin broadly rounded; distal margin unarmed; propodus as long as or longer than carapace; PI 84–99 (male), 91–99 (female). Ischium shorter than one-third merus length.

Mandibular palp 2-segmented (except holotype, 3-segmented). Maxillipeds 1–5 with epipod. Maxilliped

5 basal segment without ventrally directed spine.

Pereopods 1–2 basal segment with outer ventrolaterally directed spine and short inner tooth. Pereopod 3 with outer spine only. Pereopodal endopod distal segments oval elongate, slenderest on pereopod 3.

TS5 lateral process obsolete, without ventrally directed spine. TS6–8 lateral process broadly rounded. TS8 sternal keel absent.

Male pleopod 1 endopod without lateral lobe on distal 'endite'.

AS1–3 smooth dorsally; posterior margin unarmed; unarmed posterolaterally. AS4 smooth dorsally and posteriorly; with slender posterolateral spine. AS5 distinctly narrowed posteriorly, lateral surfaces with irregular sculpture and erosion. AS6 about as wide as posterior width of AS5; surface smooth on medial one-third; surface of lateral one-third eroded, with irregular longitudinal carinae; posterolateral spine prominent, elongated; with pointed, triangular projection anterior to uropodal articulation; sternum posterior margin unarmed.

Telson thick, length slightly exceeding half width; submedian teeth slender, curved, separated by shallow fissure; with 7–10 minute submedian denticles in arcuate row either side of midline; with 4 'intermediate' denticles, second and fourth from midline spiniform, longer than triangular first and third denticles; lateral denticle spiniform. Intermediate teeth spiniform, straight, extending posteriorly to level of base of submedian teeth. Marginal teeth curved, margins unarmed, slightly incurved medially, apices reaching to level of base of intermediate teeth. Dorsal surface with broad, median flat elevation, anterior submedian carina, marginal carina and numerous, small tubercles, longitudinal, irregular and vermiform accessory carinae on surface either side of median elevation. Median elevation smooth, flat apex blunt, rounded. Anterior submedian carinae low, slender, often crenulated posteriorly. Marginal carina reaching posteriorly beyond midlength of margin of lateral tooth. Ventral surface without post-anal carina or spine.

Uropodal protopod obtusely produced anteriorly; irregular sculpture dorsally; inner and outer primary spines slender, ventrally carinate, outer spine reaching beyond midlength of inner margin of spine; with short slender ventral spine at endopod articulation. Uropodal exopod proximal segment with short, narrow, distal lobe on inner margin and short distal spine; outer margin with 8–10 graded movable spines, distalmost reaching midlength of distal segment. Exopod distal segment longer than proximal segment. Endopod reniform, length 2.58–3.60 times width; anterior margin produced anteriorly in advance of articulation with protopod.

COLOUR IN LIFE. Not known. Faded in preservative but with scattered chromatophores on outer distal margin of raptorial claw merus and transverse banding along posterior margin of thoracic and abdominal somites. Outer margin of dactylus of raptorial claw yellow-orange.

MEASUREMENTS. Male ($n = 13$) TL 29–52 mm, female ($n = 5$) TL 45–63 mm. Other measurements of holotype:

CL 9.4 mm, cornea width 4.4 mm, antennular peduncle length 6.9 mm, antennal scale length 3.1 mm, raptorial claw propodus length 10.1 mm.

ETYMOLOGY. Derived from the Irish Gaelic name, Dempsey, meaning estimable, as fitting for the type species of the new genus, *Colubrisquilla*, with its impressive telson ornamentation. It is also the family name of my good friends Gordon and Helen Dempsey; used as a noun in apposition.

HABITAT. Substrate not known; confirmed from depths between 136 and 449 m. Many specimens were taken from the stomachs of demersal fish (*Coelorinchus* spp.: Macrouridae).

REMARKS. Morphological variation in *Colubrisquilla dempsey* gen. et sp. nov. is slight in most respects. The mandibular palp is 3-segmented in the holotype but 2-segmented in remaining specimens. The distinctive telson carination of adults is less pronounced in juveniles, the surface sculpture and ornamentation superficially approaching that of adult *Heterosquilloides insignis* (Kemp, 1911) and *H. insolita* (Manning, 1963a). Nevertheless, all other diagnostic features of adult *C. dempsey* are also evident in juveniles, including the spiniform ocular scales. The male pleopod 1 endopod is fully developed in males of TL 39 mm and above.

Although few specimens of *C. dempsey* were collected via direct sampling such as trawling or dredging, the species may be common on the Chatham Rise. Most specimens were collected from stomachs of rat-tails (*Coelorinchus biclinozonalis* Arai & McMillan; *C. aspercephalus* Waite; and *C. bollonsi* McCann & McKnight). As with other lysiosquilloids, *C. dempsey* probably lives in deep burrows that they seldom leave.

DISTRIBUTION. Presently known only from eastern New Zealand between Tokomaru Bay (East Cape) and the Chatham Rise.

Heterosquilla Manning, 1963

Heterosquilla Manning, 1963b: 320. [Type species: *Lysiosquilla platensis* Berg, 1900, by original designation. Gender: feminine].

DIAGNOSIS. Cornea subglobular or broadened, not distinctly bilobed, eyes not concealed by rostral plate. Antennal protopod with 1 or 2 ventral papillae. Pereopods 1–2 with oval elongate endopods. Telson posterior margin with movable, submedian teeth and 2 pairs of fixed primary teeth; with 2–4 'intermediate' denticles; without post-anal spine. Uropodal protopod with outer spine distinctly longer than inner; with ventral spine anterior to endopod articulation; endopod reniform, anterior margin produced anteriorly in advance of articulation with protopod.

COMPOSITION. *Heterosquilla koning* sp. nov.; *H. laevis* (Hutton, 1879) stat. nov.; *H. pentadactyla* Ah Yong, 2001; *H. platensis* (Berg, 1900); *H. polydactyla* (von Martens, 1881); *H. tricarinata* (Claus, 1871); *H. tridentata* (Thomson, 1882); *H. trifida* sp. nov.

REMARKS. Eight species of *Heterosquilla* are now known, of which two are described as new and one is removed from synonymy. Ah Yong (2001) described *H. pentadactyla* from Australia and resurrected *H. tridentata*. Thus, since 2000, the number of recognised species of *Heterosquilla* has almost tripled, with five of the eight known species of the genus occurring in New Zealand. *Heterosquilla* is emerging as a Southern Hemisphere, cool-temperate group, each species having relatively restricted ranges at high southern latitudes. The five New Zealand species are endemic. *Heterosquilla pentadactyla* is currently known only from south-eastern Australia, *Heterosquilla platensis* is known only from Uruguay and central-southern Argentina, and *H. polydactyla* occurs around the southern tip of South America from Chiloé Island, Chile, to Golfo Nuevo, Argentina. *Heterosquilla* is not presently known from the Indian Ocean or eastern Atlantic.

The length of the outer primary spine of the uropodal protopod (distinctly longer than the inner spine, rather than shorter than the inner spine) will readily distinguish *Heterosquilla* from all other New Zealand tetrasquillids.

KEY TO SPECIES OF *HETEROSQUILLA*

1. Raptorial claw dactylus with 7 or 8 teeth. Ocular scales separate.....*H. koning* sp. nov.
 - Raptorial claw dactylus with 4-5 or 9 or more teeth. Ocular scales fused.....2
2. Rostral plate distinctly longer than wide. Dactylus of raptorial claw with 17-20 teeth.... *H. polydactyla*
 - Rostral plate as wide as or wider than long. Dactylus of raptorial claw with fewer than 17 teeth.....3
3. Dactylus of raptorial claw with 4 or 5 teeth4
 - Dactylus of raptorial claw with 9 or more teeth ..6
4. Dactylus of raptorial claw with 5 teeth. Rostral plate with concave lateral margins. Ocular scales fused into triangular plate *H. pentadactyla*
 - Dactylus of raptorial claw with 4 (rarely 5) teeth. Rostral plate with lateral margins convex. Ocular scales fused into rounded plate.....5
5. Apex of dorsal median prominence of telson produced to a slender projection..... *H. trifida*
 - Apex of dorsal median prominence of telson blunt *H. tridentata*

6. Antennal protopod with anteriorly directed dorsal spine. Rostral plate with sinuous lateral margins. AS6 with distinct intermediate carinae..... *H. platensis*
 - Antennal protopod without dorsal spine. Rostral plate with convex lateral margins. AS6 without intermediate carinae.....7
7. Raptorial claw with 12-16 teeth (usually 13 or 14) on dactylus. *H. laevis*
 - Raptorial claw with 9-11 teeth (usually 10, rarely 12 on one side) on dactylus. *H. tricarinata*

Heterosquilla koning sp. nov. (Figs 24, 25)

Lysiosquilla spinosa. – Chilton, 1911a: 139 [*Nora Niven* specimen only]; 1911b: 306. [Not *L. spinosa* (Wood-Mason, 1875)].

Lysiosquilla sp. – Calman, 1917: 144.

TYPE MATERIAL. *Holotype*: NMNZ Cr9379, female (TL 53 mm), off Spirits Bay, 34°25.00'S, 172°46.60'E, 29 m, NZOI Stn O662, sled, 3 Feb 1981.

Paratypes: NIWA 73081, 1 female (TL 44 mm), Rock Garden, North Cape, 34°16.33-16.14'S, 172°47.20-46.99'E, 66-67 m, epibenthic sled, TAN1105/27, 27 Mar 2011; NMNZ, 1 male (TL 32 mm), 4 females (TL 30-36 mm), Bay of Plenty, J12/28/75, 18 Aug 1975; NMNZ Cr9353, 2 males (TL 35 mm; 1 broken, CL 8.8 mm), 3 females (TL 44-53 mm), Cook Strait, from grouper stomach, Dec 1957.

OTHER MATERIAL EXAMINED. *Chatham Islands*: NMNZ, 1 female (TL 42 mm), Port Hutt, Chatham Island, 43°49'S, 176°42'W, taken on surface under flood-light, 14 Sep 1950, coll. F. Abernathy.

Otago: NMNZ Cr9351 (part), 2 females (TL 51-66 mm), off Oamaru, 45°05'S, 170°59'E, 37 m, trawled, from stomach of *Mustellus antarcticus*, coll. J. Graham, Apr 1962.

Southland: NMNZ, 1 male (TL 16 mm), Paterson inlet, Stewart Island, 46°56'S, 168°05'E, RV *Acheron*, coll. J. Richardson, 7-14 Feb 1977; NIWA-MITS 35098, 1 juvenile male (TL 19 mm), Big Glory Bay, Stewart Island, 46°58.934'S, 168°07.8438'E, marine farm 4, site 31, 1STW481DP; CM AQ3199, 1 female (broken, CL 8.0 mm), 50 miles east of Wreck Reef, Stewart Island, 47°10.3'S, 169°08.3'E, 119-335 m, soft sand, *Nora Niven* Stn 5, E.R. Waite, 13 Jun 1907.

DIAGNOSIS. Ocular scales rounded, separate. Antennal protopod with 1 ventral papilla. Rostral plate triangular, broader than long. Raptorial claw dactylus with 7 or 8 (usually 8) teeth. Pereopods 1-3 basal segment with triangular lappet on outer margin and small blunt tooth on inner margin. Telson dorsal surface with broad, flat, median elevation and anterior submedian



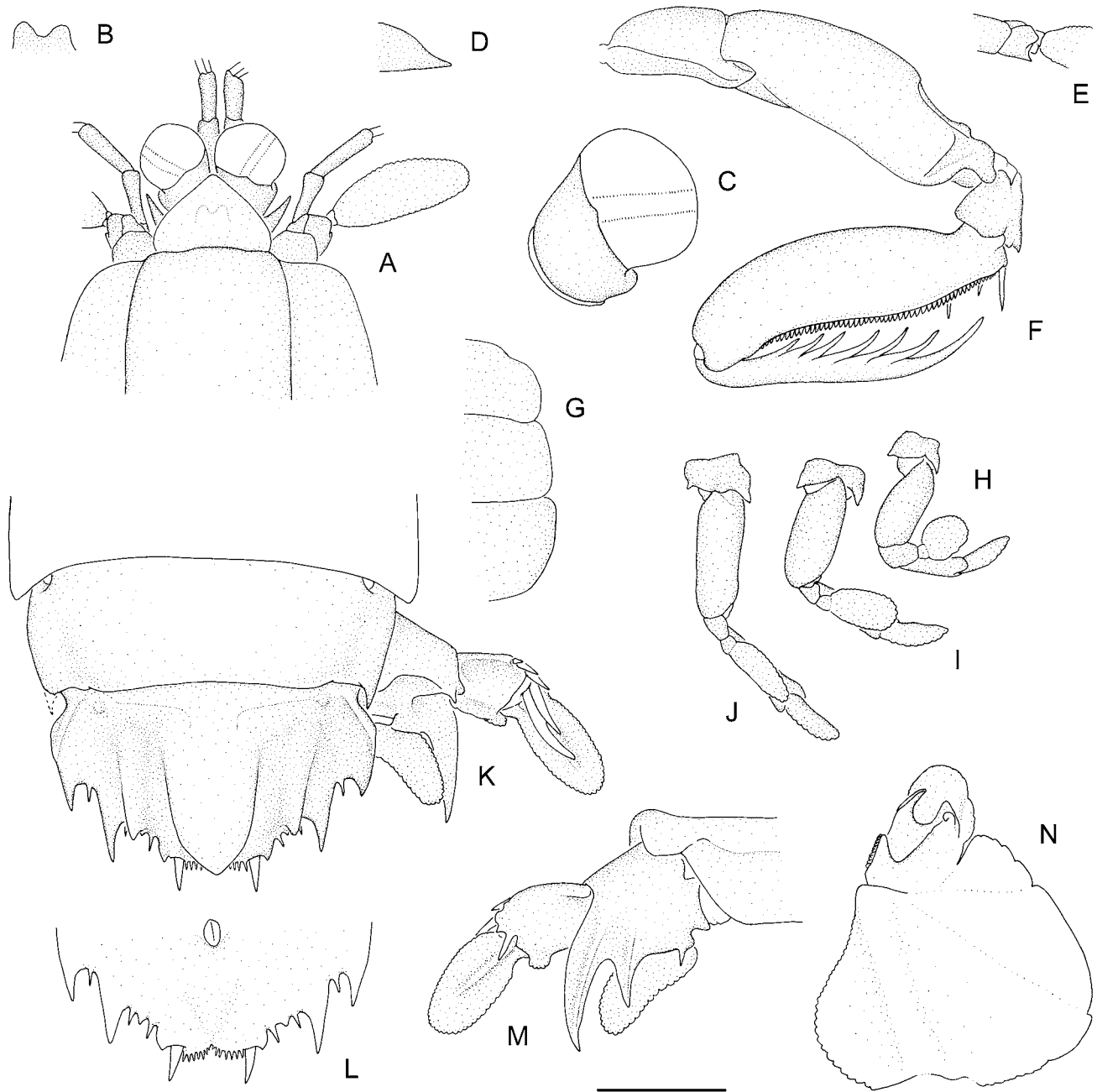


Figure 24. *Heterosquilla koning* sp. nov. A-M, female holotype, TL 53 mm, off Spirits Bay (MNZ Cr9379). N, male paratype, CL 8.8 mm, Cook Strait (MNZ Cr9353). A, anterior cephalothorax; B, ocular scales; C, right eye; D, right dorsal process of antennular somite, lateral view; E, right antennal protopod, lateral view; F, right raptorial claw; G, TS6-8, right dorsal view; H-J, right pereopods 1-3, posterior view; K, AS5-6, telson and right uropod, dorsal view; L, telson, ventral view; M, right uropod, ventral view; N, right pleopod 1 endopod, anterior view. Scale A, E-M = 4.0 mm; B-D, N = 2.0 mm.

carina terminating in a blunt lobe. Uropodal protopod inner spine slender, about half length of inner margin of outer spine; with slender ventral spine anterior to endopod articulation.

DESCRIPTION. Eye not extending beyond antennular peduncle segment 2; cornea subglobular, inclined laterally on stalk, partially concealed by rostral plate.

Ophthalmic somite anterior margin flattened. Ocular scales rounded, separate.

Antennular peduncle 0.42–0.60CL. Antennular somite dorsal processes with acute apices, spiniform, directed anterolaterally. Antennal protopod dorsally unarmed; with small ventrodorsal tooth and 2 ventral papillae. Antennal scale length 2.71–3.17 width, 0.38–0.44CL.

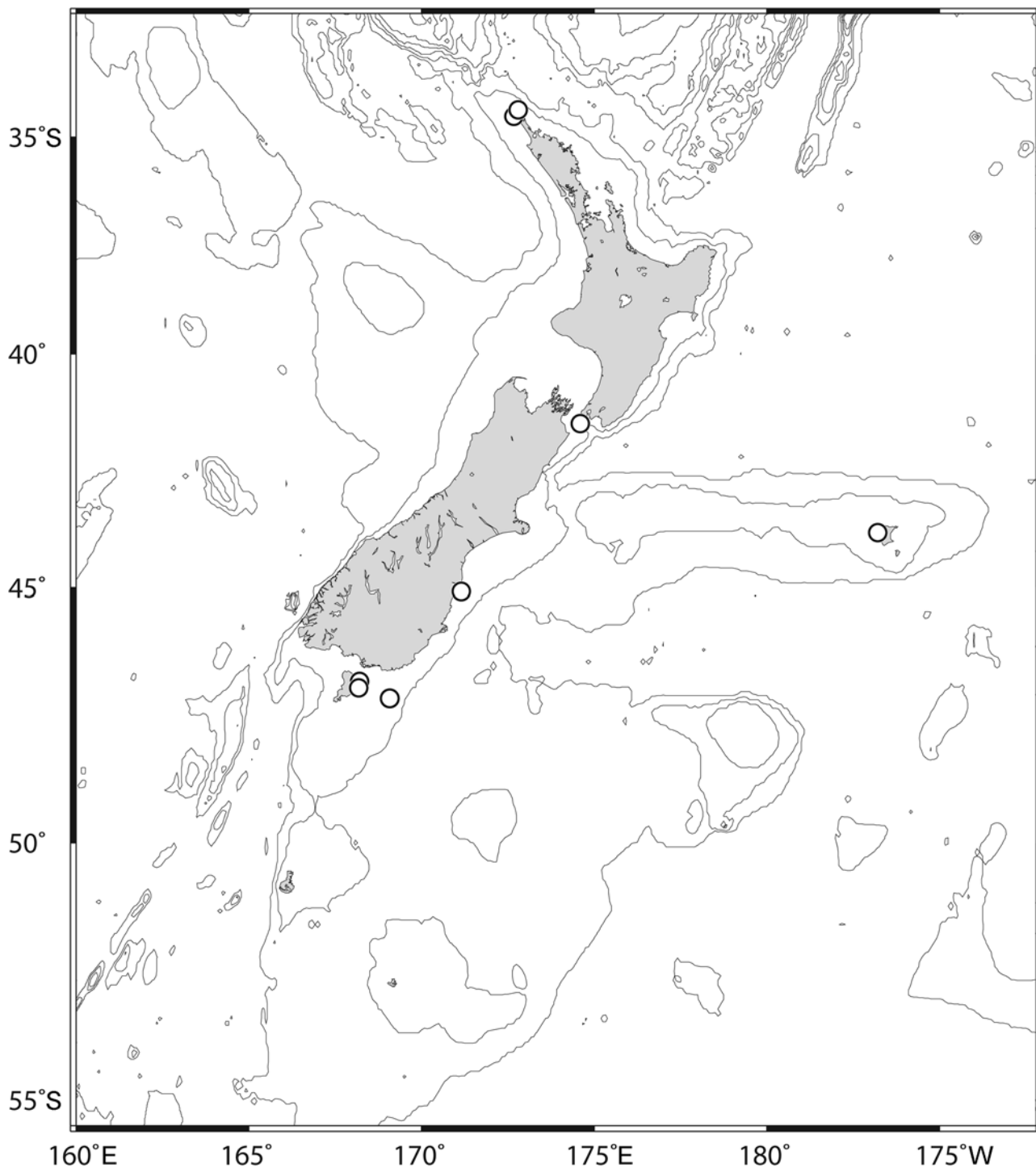


Figure 25. New Zealand distribution of *Heterosquilla koning* sp. nov.

Rostral plate triangular broader than long; anterior lateral margins faintly concave; apex angular; dorsum smooth. Carapace anterolateral angles broadly rounded.

Raptorial claw dactylus with 7 or 8 (usually 8) teeth, outer margin sinuous, without proximal notch. Carpus dorsal margin terminating in short blunt tooth, directed ventrally. Propodus with 3 proximal mov-

able spines, distal margin unarmed; outer inferodistal margin broadly rounded; length shorter than carapace; PI 107–117 (males), 108–114 (females). Ischium shorter than half merus length.

Mandibular palp 3-segmented in adults. Maxillipeds 1–5 with epipod. Maxilliped 5 basal segment without ventrally directed spine.

Pereopods 1–3 basal segment with triangular lappet on outer margin and small blunt tooth on inner margin. Pereopod 1 endopod distal segment subcircular. Pereopod 2 endopod distal segment ovate. Pereopod 3 endopod distal segment elongate.

Male pleopod 1 endopod without indication of lateral lobe of distal 'endite'.

TS5 lateral process obsolete, lacking ventrally directed spine. TS6–8 lateral process broadly rounded. TS8 sternal keel rounded.

AS1–5 smooth; posterior margin unarmed; posterolateral angles rounded, unarmed. AS6 smooth, lacking carinae; posterolateral spine prominent, elongated; with blunt, obtuse projection anterior to uropodal articulation; sternum posterior margin unarmed.

Telson thick; submedian teeth slender, curved; with 6–8 spiniform submedian denticles; with 4 acute 'intermediate' denticles, second and fourth from midline longer than first and third; lateral denticle spiniform. Dorsal surface with broad, median elevation, anterior submedian carina and marginal carina; surface between median elevation and anterior submedian carinae smooth, unarmed. Median elevation flat, smooth medially, margins evenly curved, converging posteriorly, apex blunt; not anteriorly continuous with anterior submedian carina. Anterior submedian carina low, terminating posteriorly in angular tooth. Marginal carina low, reaching posteriorly beyond midlength of margin of lateral tooth. Ventral surface without post-anal carina or spine.

Uropodal protopod inner spine slender, about half length of inner margin of outer spine; with slender ventral spine anterior to endopod articulation. Uropodal exopod proximal segment with low, round, distal lobe on inner margin and slender distal spine; outer margin with 5 or 6 movable spines, distalmost exceeding midlength but not apex of distal segment. Exopod distal segment longer than proximal segment. Endopod length 2.82–3.09 times width.

COLOUR IN LIFE. Not known. Largely faded in preservative; overall with light and dark transverse banding. Raptorial claw with dark brown patch on distal margin of merus and proximal margin of propodus. Telson with pair of dark, W-shaped patches. Uropodal exopod with dark patch on proximal segment extending onto proximal half of distal segment.

MEASUREMENTS. Male ($n = 4$) TL 16–35 mm, female ($n = 12$) TL 30–66 mm. Other measurements of holotype: CL 11.0 mm, antennular peduncle length 5.0 mm, antennal scale length 4.7 mm, raptorial claw propodus length 10.1 mm.

ETYMOLOGY. From the Dutch, *Koning*, meaning king or one who played the part of a king in theatre, as the

species of *Heterosquilla* occupying the largest known bathymetric 'realm'. It is also the family name of my good friends Frans and Jasmin Koning; used as a noun in apposition.

HABITAT. Sandy substrates; confirmed from depths between 29 and 335 m, but probably as shallow as 3 m depth.

REMARKS. *Heterosquilla koning* sp. nov. is distinguished from its congeners by the combination of separate instead of fused ocular scales, and seven or eight teeth on the dactylus of the raptorial claw. Other species of *Heterosquilla* have either more than eight teeth or fewer than six teeth on the dactylus of the raptorial claw. The new species most closely resembles *H. pentadactyla* from Australia, and two New Zealand species, *H. tridentata* and *H. trifida* sp. nov., sharing similar telson ornamentation and uropod structure. Aside from the greater number of dactylar teeth on the raptorial claw (seven or eight versus four or five), *H. koning* sp. nov. differs from each of these species by having separate instead of fused ocular scales.

The specimens of *H. koning* examined exhibit little morphological variation. Most specimens have eight teeth on the dactylus of the raptorial claw and five movable spines on the outer margin of the uropodal exopod. The pleopod 1 endopod of males TL 32 mm and above is fully developed. The mandibular palp is 3-segmented in all specimens except for the TL 16 mm juvenile in which the palp is 2-segmented, the third segment being undifferentiated.

Calman (1917) reported two postlarvae as '*Lysiosquilla* sp.' from Spirits Bay at 3 and 20 m depth. They were described as having seven teeth on the dactyli of the raptorial claws, and are probably referable to *Heterosquilla koning* sp. nov.

DISTRIBUTION. Known only from New Zealand, from localities between Spirits Bay, the Bay of Plenty, the Chatham Islands and Stewart Island.

Heterosquilla laevis (Hutton, 1879) (Figs 26, 27)

Squilla laevis Hutton, 1879: 340 [type locality: Auckland Islands]. — Filhol, 1886: 491. — Bigelow, 1894: 503. [Not *Squilla laevis* Hess, 1865].

Lysiosquilla spinosa. — Chilton, 1891: 61–67, pl. 10; 1909: 604, 615; 1911a: 139 [some Stewart Island records]. [Not *L. spinosa* (Wood-Mason, 1875) = *H. tricarinata* (Claus, 1871)].

Heterosquilla spinosa. — Manning, 1966: 118, 119.

Heterosquilla (*Heterosquilla*) *tricarinata*. — Manning, 1966: 120–124, fig. 8.

Heterosquilla tricarinata. — Fenwick, 1975: 132. — Yaldwyn, 1975: 362. — Manning, 1978b: 8, fig. 4. — Luckens, 1991: 255, 259. — Ahyong, 1997: fig. 2E.

TYPE MATERIAL. *Holotype*: OM IV1403, male (TL 38 mm), Auckland Islands, from stomach of *Notothenia microlepidota*.

OTHER MATERIAL EXAMINED. *Auckland & Coromandel*: AM P87878, 1 male (TL 28 mm), Ti Point, Omaha Bay, 36°19.52'S, 174°48.06'E, 15 m, muddy sand, coll. R. Taylor, 22 Jan 2004; AM P87879, 1 male (TL 53 mm), 2 females (TL 57–70 mm), Matatuahu Point, Kawau Bay, 36°22.80'S, 174°49.2'E, 4 m, muddy sand, coll. R. Taylor, 1 Jan 2004.

Wairarapa: NMNZ Cr9374, 1 female (TL 85 mm), Humenga, Palliser Bay, 41°31.1'S, 175°11.4'E, washed ashore, coll. R. Hoare, Feb 1965.

Wellington: NMNZ Cr9338, 1 male (TL 59 mm), York Bay, Wellington, 41°18'S, 174°54'E, from stomach of small dogfish, coll. J.C. Yaldwyn, 5 Mar 1953; NIWA 61494, 1 male (TL 56 mm), 1 female (TL 56 mm), Paekakariki, 40°59.0'S, 174°56.6'E, 14–15 m, from stomach of gurnard, coll. R. Stewart, 25 Jan 2010; NIWA 61492, 1 female (TL 70 mm), Paekakariki, 40°59.0'S, 174°56.6'E, 14–15 m, from stomach of gurnard, coll. R. Stewart, 25 Jan 2010.

Marlborough: OM IV1397, 1 female (TL 92 mm), Stephens Island.

Chatham Islands: NMNZ, 2 males (TL 35–46 mm), 3 females (TL 37–47 mm), Port Hutt, 43°49'S, 176°42'W, taken on surface under flood-light, 14 Sep 1950, coll. F. Abernathy; NIWA-MITS 22415, 1 female (TL 65 mm), Hanson Bay, Chatham Islands, 43°46.772'S, 176°18.140'W, box core, Site 34, 1CHT393DP, 12 Feb 2007.

Canterbury: NMNZ Cr3744, 1 male (TL 75 mm), 1 female (TL 76 mm), Kaikoura, 42°25'S, 173°41'E, RLCP collection.

Otago: AM P87880, 2 males (TL 75–77 mm), 1 female (TL 78 mm), "Anchors", 45°45.354'S, 170°47.454'E, about 26 m, fine sand burrows, air lift, coll. Murray, 9 Mar 2011; OM IV1405, 1 male (TL 90 mm), 1 female (TL 87 mm), Port Chalmers, 45°49'S, 170°37'E, coll. F. Sullivan; OM IV1953, 2 males (TL 30–41 mm), 1 female (TL 43 mm), Portobello, 18 Aug 1937; NMNZ Cr4375, 1 female (TL 25 mm), Otago Harbour, Mu66/53, 13.7 m, Portobello Marine Biological Station, 45°49.7'S, 170°38.4'E, 1 Nov 1966; AM P10955, 2 males (TL 40–53 mm), 1 female (TL 41 mm), Portobello Marine Fish Hatchery, Dunedin, 45°49.7'S, 170°38.4'E, coll. G. Howe.

Southland: NIWA 23920, 1 male (TL 43 mm), Ulva Island, 46°54.79'S, 168°09.49'E, 9 m, NZOI stn B232, 23 May 1960; OM IV1398(part), 2 males (TL 50–54 mm), 1 female (TL 60 mm), Ulva Island, 46°56'S, 168°08'E, coll. T.J. Parker; NMNZ, 1 female (TL 55 mm), Stewart Island, per Southland Museum, Nov 1953.

Auckland Islands: NIWA 76526, 1 male (TL 55 mm), Port Ross, Auckland Island, 50°33.10'S, 166°14.10'E,

23 m, NZOI Stn S114, 7 Dec 1978; NMNZ Cr19709, 1 female (TL 22 mm), 1 male (TL 29 mm), Port Ross, Auckland Island, 50°32.0'S, 166°14.1'E, 37 m, NZOI B178; AM P87952, 2 juvenile males (TL 16 mm; 1 damaged), Waterfall Inlet, Auckland Island, 50°49'S, 166°16'E, 13 m, medium to fine sand, K16 (1 mm, Y103gm), Smith-McIntyre grab, RV *Acheron*, coll. J.K. Lowry, 12 Feb 1973; AM P87951, 1 juvenile female (TL 17 mm), Sandy Bay, Port Ross, Enderby Island, 50°30'S, 166°17'E, 11–14.6 m, fine to very fine sand, K19 (1 mm, Y103gm), Smith-McIntyre grab, RV *Acheron*, coll. J.K. Lowry, 14 Feb 1973; AM P41832, 2 males (TL 27–55 mm), 1 female (TL 30 mm), 1 juvenile female (TL 15 mm), Waterfall Inlet, Auckland Island, 50°49'S, 166°13'E, 14.6 m, medium to fine sand, K18 (1 mm, Y103gm), Smith-McIntyre grab, RV *Acheron*, coll. J.K. Lowry, 12 Feb 1973.

DIAGNOSIS. Ocular scales fused into quadrate plate. Antennal protopod 2 ventral papillae. Rostral plate slightly wider than long, lateral margins convex proximally, almost straight distally; apex acute. Raptorial claw dactylus with 12–16 teeth, outer margin broadly curved; propodus, when folded reaching posteriorly as far as or slightly beyond proximal end of ischium; ischium about as long as merus. Pereopods 1–3 basal segment with inner and outer, ventrolaterally directed spine in both sexes. AS6 posterolateral spine prominent; sternum posterior margin unarmed. Telson thick, length about half width; with 4 acute 'intermediate' denticles, second and fourth shorter than first and third; lateral denticle spiniform. Dorsal surface with broad, flat, median elevation and anterior submedian carina each terminating in stout spine. Uropodal protopod outer spine broad, flat, tapering to sharp apex, ventrally carinate; inner spine slender, one-quarter length of inner margin of outer spine.

DESCRIPTION. Eye not extending beyond antennular peduncle segment 2; cornea subglobular, inclined laterally on stalk, not concealed by rostral plate. Ophthalmic somite anterior margin flattened. Ocular scales fused into quadrate plate.

Antennular peduncle length 0.44–0.55CL. Antennular somite dorsal processes with acute apices, spiniform directed anterolaterally. Antennal protopod dorsally unarmed; with small ventrodistal tooth and 2 ventral papillae. Antennal scale length 2.82–3.33 width, 0.37–0.46CL.

Rostral plate slightly wider than long, lateral margins convex proximally, almost straight in distally; apex acute. Carapace anterolateral angles rounded.

Raptorial claw dactylus with 12–16 teeth, outer margin broadly curved, proximal margin with indistinct basal notch. Carpus dorsal margin terminating in short tooth, directed ventrally. Propodus with 3

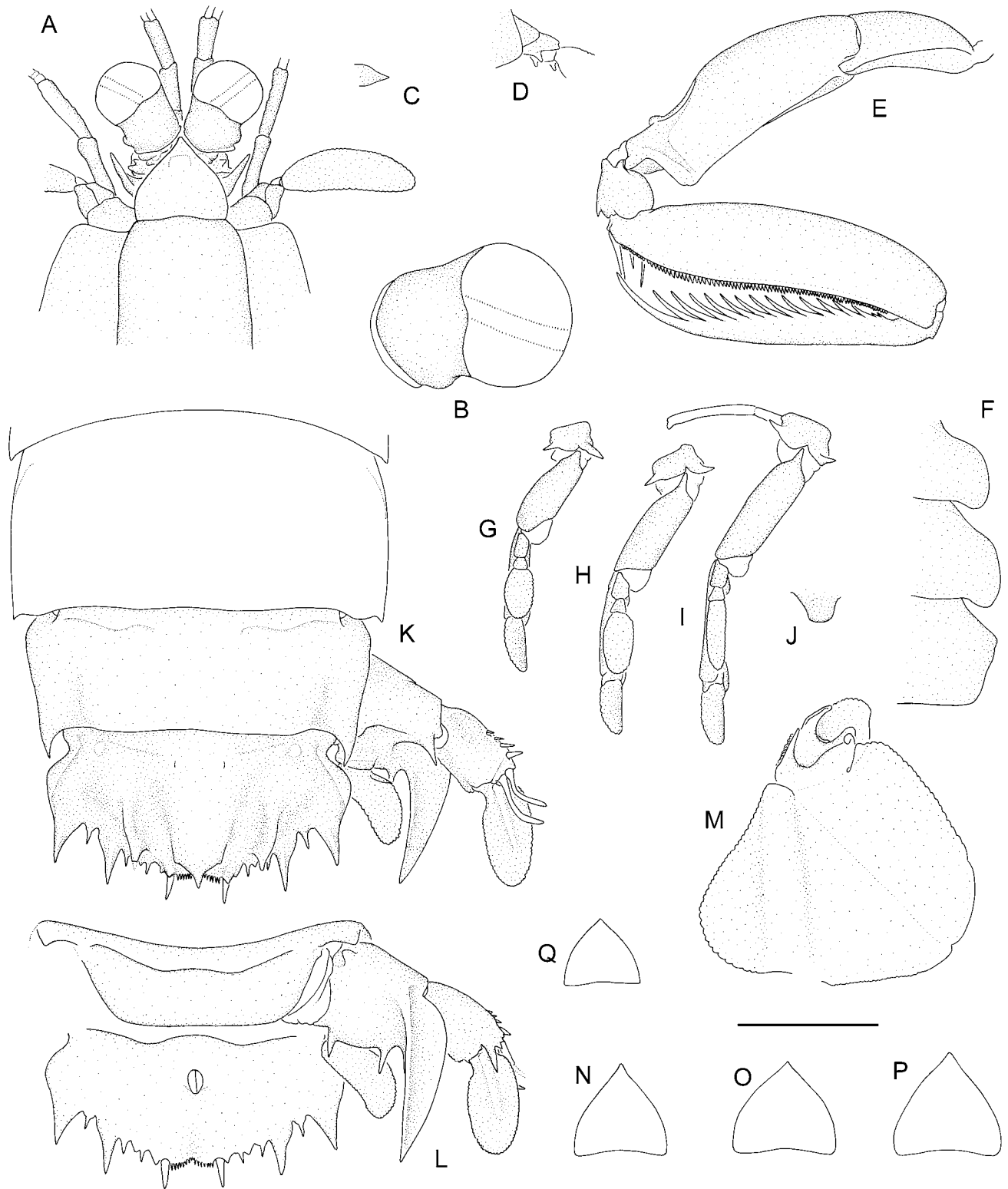


Figure 26. *Heterosquilla laevis* (Hutton, 1879). A-M, male, TL 53 mm, Kawau Bay (AM P87879). N-P, male (TL 50 mm), male (TL 54 mm), male (TL 60 mm), Ulva Island (OM IV1398). Q, holotype male, TL 38 mm (OM IV1403), Auckland Islands. A, anterior cephalothorax; B, right eye; C, right dorsal process of antennular somite, lateral view; D, right antennal protopod, lateral view; E, left raptorial claw; F, TS6-8, right dorsal view; G-I, right pereopods 1-3, posterior view; J, TS8 sternal keel, right lateral view; K, AS4-6, telson and right uropod, dorsal view; L, telson, AS6 sternum and left uropod, ventral view; M, right pleopod 1 endopod, anterior view; N-Q, rostral plate. Scale A, C-L, N-Q = 4.0 mm; B, M = 1.9 mm.

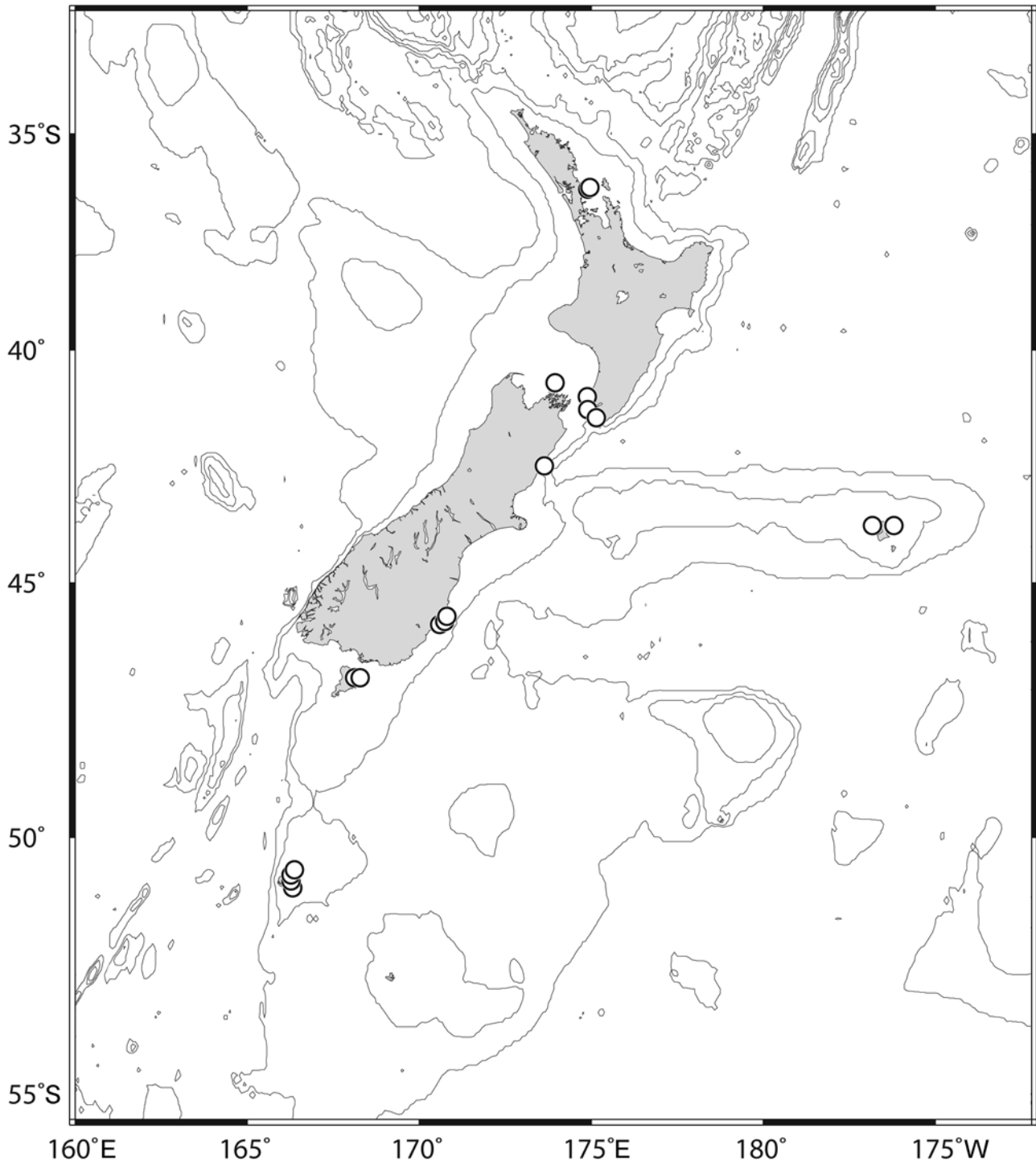


Figure 27. New Zealand distribution of *Heterosquilla laevis* (Hutton, 1879)

movable spines proximally, distal margin unarmed; outer inferodistal angle blunt, rounded, approximating a right angle; propodus, when folded reaching posteriorly as far as or slightly beyond proximal end of ischium; usually slightly longer than carapace; PI 90–108 (male), 91–102 (female). Ischium length about as long as merus.

Mandibular palp 3-segmented. Maxillipeds 1–5 with epipod. Maxilliped 5 basal segment without ventrally directed spine.

Pereopods 1–3 basal segment with inner and outer, ventrolaterally directed spine; endopod distal segments oval elongate, slenderest on pereopod 3.

Male pleopod 1 endopod without indication of lateral lobe of distal ‘endite’.

TS5 lateral process obsolete, lacking ventrally directed spine. TS6–7 lateral process broadly rounded. TS8 lateral process bluntly angular; sternal keel subquadrate.

AS1–5 smooth; posterior margin unarmed; AS4 posterolateral angle angular, pointed to blunt; AS5 with or without small posterolateral spine. AS6 smooth, lacking carinae; posterolateral spine prominent; with blunt, obtuse projection anterior to uropodal articulation; sternum posterior margin unarmed.

Telson thick, length about half width; submedian teeth slender, curved, separated by shallow fissure, with small tooth above articulation; with 7–11 minute submedian denticles in arcuate row either side of midline; with 4 acute ‘intermediate’ denticles, second and fourth from midline longer than first and third; lateral denticle spiniform. Dorsal median elevation broad, flat, posterolaterally angular (rarely rounded), terminating in sharp spine. Anterior submedian carinae cristate, terminating in stout spine. Ventral surface without post-anal carina or spine.

Uropodal protopod outer spine broad, flat, tapering to sharp apex, ventrally carinate; inner spine slender, one-quarter length of inner margin of outer spine; with short slender ventral spine anterior to endopod articulation. Uropodal exopod proximal segment with low, round, distal lobe on inner margin and slender distal spine flanked laterally by small, short spine; outer margin with 5–7 movable spines, proximal 3–5 straight, distal 2 longer, curved, distalmost reaching midlength of distal segment. Exopod distal segment longer than proximal segment. Endopod reniform, length 2.20–2.62 times width.

COLOUR IN LIFE. *Males:* Carapace translucent and speckled with white and brown chromatophores. Thorax and abdomen translucent with dark-brown transverse banding, darkest along posterior margins of somites; overall body also frequently with diffuse white and brown speckling. Raptorial claws with light brown speckling on merus, carpus and proximal portion of propodus; dactylus translucent white with orange-pink teeth. Telson surface with large, black patch on either side of midline; each patch interrupted by thin, longitudinal, white stripe covering anterior submedian carina, and by short narrow white stripe mesially. Uropodal protopod dark brown along anterior margin and proximally near articulation with AS6; exopod dark brown laterally and distally; exopod dark brown to black.

Females: Similar to males but with transverse abdominal and thoracic stripes more diffuse medially; gonads visible medially as broad orange longitudinal stripe in ‘ripe’ females.

MEASUREMENTS. Male ($n = 24$) TL 16–90 mm, female ($n = 21$) TL 15–87 mm.

HABITAT. *Heterosquilla laevis* lives subtidally in burrows in level in muddy sand at depths of 4–36 m. Several specimens were taken from the stomachs of dogfish, snapper and gurnard. Luckens (1991) reported *H. laevis* (as *H. tricarinata*) from sandy-mud sediments at the Auckland Islands together with the venerid bivalve, *Tawera bollonsi* Powell. Other macroinvertebrates collected together with *T. bollonsi* and *H. laevis* at NZOI station S114 (23 m depth) include the stomatopod *Heterosquilla tridentata* (as *H. tricarinata*), the decapod crustaceans *Callinassa filholi* (A. Milne-Edwards), *Munida* sp., the bivalve mollusc *Austrovenus stutchburyi* (Wood) (as *Chione aucklandia* Powell) and the polychaetes *Branchiomma serratibranchis* (Grube) and *Arabella iricolor* (Montagu) (Luckens 1991). At Kawau Bay, Auckland, *H. laevis* was sympatric with *Pariliacantha georgeorum*.

REMARKS. *Heterosquilla laevis* Hutton, 1879, has long been considered a junior synonym of *H. tricarinata*, but the two nominal species are herein regarded as valid. The two forms closely resemble each other and are potentially different ecomorphs of the same species. They differ consistently, however, and in the absence of intermediate forms, both nominal species are presently treated as separate. *Heterosquilla laevis* and *H. tricarinata* differ in the size and armature of the raptorial claw, the shape of the rostral plate, the armature of the sternite of AS6, in bathymetric preference, and colour-in-life of mature females. *Heterosquilla laevis* has a more elongate raptorial claw in which the propodus is as long as or slightly longer than the carapace (sometimes slightly shorter than the carapace in specimens smaller than about TL 45 mm), and in which the dactylus has 12–16 teeth on the occlusal margin and a straight to evenly curved outer margin (rarely faintly concave proximally). When the raptorial claw in *H. laevis* is folded, the distal margin of the propodus extends posteriorly to or slightly beyond the proximal margin of the ischium. *Heterosquilla tricarinata*, however, has a stouter raptorial claw, in which the propodus is occasionally as long as, but usually slightly shorter than the carapace; and the dactylus has 9–11 teeth (rarely 12 teeth on one side) and a distinctly sinuous outer margin. When folded, the distal margin of the propodus of the raptorial claw in *H. tricarinata* does not extend to the proximal margin of the ischium. The rostral plate of *H. laevis* is more triangular than in *H. tricarinata*, with the margins in the anterior half being almost straight rather than convex (cf. Figs 26A, N–Q; Figs 28A, 29A–C). The central posterior margin of the sternum of AS6 is always unarmed and straight both in juvenile and adult *H. laevis*. In *H. tricarinata*, however, a pair of angular projections develops on the posterior margin of the AS6 sternite, becoming more pronounced with increasing body size such that the posterior margin

appears to have two angular points separated by a distinct concavity (Figs 29D–N). *Heterosquilla laevis* also appears to differ ecologically from *H. tricarinata*, living subtidally (4–36 m) rather than intertidally, and mature females have a similar colouration to males, rather being dark green or black (see account of *H. tricarinata*; Frontispiece 2A–B).

The holotype of *H. laevis* is in poor condition (Fig. 26Q). Although currently preserved in ethanol, the specimen appears to have once been dried; glue on the ventral surface indicates that it was probably originally mounted on card or glass as was common practice amongst 19th century naturalists.

One lot from Ulva Island, Stewart Island, OM IV1398, includes three specimens of *H. laevis* and one of *H. tricarinata*. The natural colouration of all specimens is completely lost, but the three *H. laevis* specimens are faded to light brown, whereas the *H. tricarinata* specimen is faded to drab olive green, suggesting that the specimens were originally preserved under different conditions as separate lots and subsequently combined. Whilst it is not unlikely that *H. laevis* and *H. tricarinata* may occasionally be sympatric, the specimens from OM IV1398 were probably not collected together.

Heterosquilla laevis differs from most other congeners (*H. koning*, *H. pentadactyla*, *H. tridentata*, *H. trifida*) by the high number of dactylar teeth on the raptorial claw (12–16 versus 8 or fewer). It can be distinguished from *H. polydactyla* and *H. platensis* by the short rostral plate (versus longer than wide) and non-carinate AS6 (versus intermediate carinae present), respectively.

The pleopod 1 endopod of males is fully developed by about TL 41 mm in *H. laevis* versus about 29 mm in *H. tricarinata*, suggesting that the latter might mature at a smaller size than the former.

Heterosquilla laevis overlaps geographically with *H. tricarinata* throughout most of its range, but appears to extend further south than *H. tricarinata*, reaching the Auckland Islands. The southernmost confirmed record of *H. tricarinata* is from Stewart Island.

DISTRIBUTION. Omaha Bay, North Island, to the Chatham Islands and Auckland Islands.

Heterosquilla tricarinata (Claus, 1871) (Figs 28–30, Frontispiece 2A–B)

Coronis tricarinata White, 1847: 85 [nomen nudum].

Coronis tricarinata Claus, 1871: 21 [type locality: New Zealand].

Coronis spinosa Wood-Mason, 1875: 232 [type locality: Andaman Islands (in error)]; 1876: 263 [part].

Squilla indefensa Kirk, 1878: 466; 1879a: 394, unnumbered text fig (p. 394) [type locality: New Zealand, by present neotype designation]; 1879b: 401. — Miers, 1880: 12, 125. — Filhol, 1885a: 52; 1885b: 436, pl. 55: fig. 3. — Bigelow, 1894: 503.

Lysiosquilla spinosa. — Miers, 1880: 3, 12, 125, pl. 1, figs 10–12. — Chilton, 1891: 61–67, pl. 10; 1911a: 139 [part, Resolution Island specimen and a Stewart Island specimen]. — Bigelow, 1894: 503. — Wood-Mason, 1895: 1, pl. 1, figs. 1–3. — Hutton, 1904: 256. — Chilton, 1906: 270; 1911a: 139, fig. 4. — Thomson, 1913: 241. — Kemp, 1913: 120, pl. 8, fig. 94. — Thomson & Anderton, 1921: 10. — Young, 1929: 154. — Ralph & Yaldwyn, 1956: 58, 64, plate 1: fig. 5. — Morton & Miller, 1968: 524, fig. 193, 198. — Miller & Batt, 1973: 92, 94, 116, fig. 115. — Powell, 1998: 39, fig. 183. — Lindsey & Morris, 2011: 260, unnumbered colour photo of female.

Lysiosquilla tricarinata. — Miers, 1880: 12.

Heterosquilla spinosa. — Manning, 1966: 118, 119.

Heterosquilla (*Heterosquilla*) *tricarinata*. — Manning, 1966: 120–124, fig. 8.

Heterosquilla tricarinata. — Manning, 1978b: 8, fig. 4; 1995: 22. — Fussell, 1979: 1–57, figs. 1–24. — Innes, 1985: 827. — Ah Yong, 2010c: 12. — Webber *et al.*, 2010: 135, 136, 218.

TYPE MATERIAL. NHM, holotype male (CL 6.6 mm; dried specimen), New Zealand waters, no specific locality, Ross Antarctic Expedition.

OTHER MATERIAL EXAMINED. *Northland*: AM P87881, 2 males (TL 37–48 mm), 1 female (TL 40 mm), Calliope Bay, Whangarei Harbour, 35°49.67'S, 174°31.15'E, in channel between mainland and High Island, low intertidal sand and stones, coll. R. Taylor, 16 Apr 2004.

Auckland & Coromandel: AM P87882, 2 females (TL 44–47 mm), Ti Point wharf, Whangateau Harbour, 36°19.03'S, 174°47.07'E, light trap, coll. C. Radford, 8 Aug 2005; AM P87883, 1 male (TL 46 mm), Ti Point wharf, Whangateau Harbour, 36°19.03'S, 174°47.07'E, light trap, coll. C. Radford, 19 Sep 2004; AM P87884, 2 males (TL 34–42 mm), 3 females (TL 34–45 mm), Point Wells, Whangateau Harbour, 36°19.5'S, 174°45.8'E, intertidal sandflat, coll. R.B. Taylor & N. Usmar, 13 Aug 2002; AM P87885, 1 male (TL 43 mm), Point Wells, Whangateau Harbour, 36°19.5'S, 174°45.8'E, low intertidal muddy sand, coll. R.B. Taylor, 3 Jan 2004; AM P87886, 4 males (TL 34–68 mm), 4 females (TL 33–61 mm), Buffalo Beach, Mercury Bay, 36°48.4'S, 175°42.2'E, intertidal sandflat, yabby pump, coll. S. & B. Ah Yong, 23 Dec 2009; AM P87887, 2 males (TL 58–68 mm), Whitianga Harbour, 36°50.419'S, 175°42.212'E, opposite caravan park, intertidal flat, burrows in shelly-sand-mud, coll. S. & B. Ah Yong, 22 Dec 2009; AM P87888, 3 males (TL 45–60 mm), 7 females (TL 45–66 mm), Pepe Stream, Tairua, 37°00.207'S, 175°50.987'E, from burrows in muddy-sand flat, *Zostera*, yabby pump, coll. S. & B. Ah Yong, 21 Dec 2009; NIWA 50536, 1 male (TL 47 mm) 1 female (TL 42 mm), Mill Bay, north Manukau Harbour, 36°59.8'S, 174°00.3'E, low water sievings, 8 Jun 1992; NIWA 50537, 1 male (TL 30 mm), Awhitu, Manukau Harbour, 37°05.12'S, 174°37.80'E, muddy sandflat, mid-intertidal sievings, 10 Jun 1992.

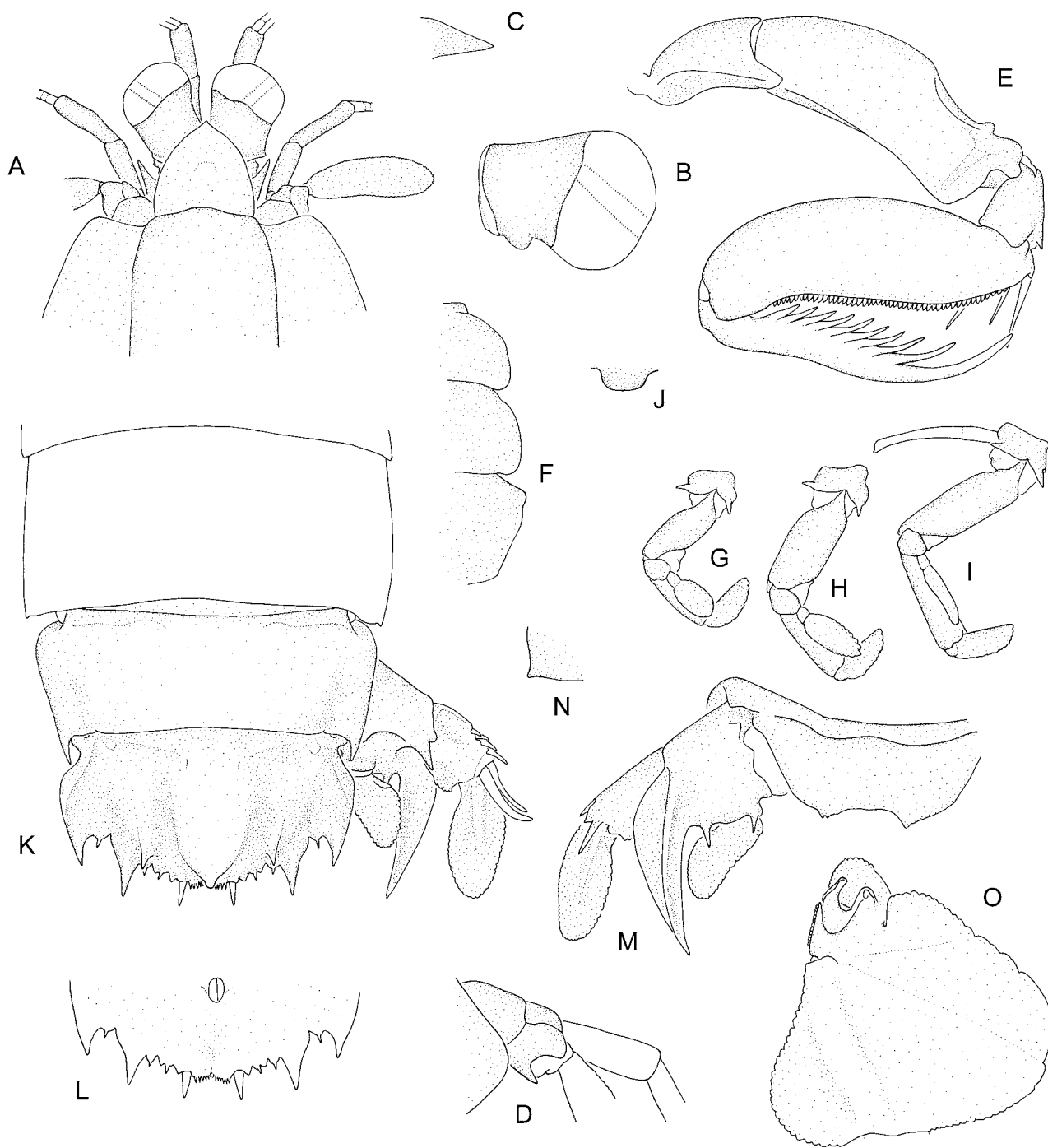


Figure 28. *Heterosquilla tricarinata* (Claus, 1871), male, TL 62 mm, Harwood, Otago (AM P87896). A, anterior cephalothorax; B, right eye; C, right dorsal process of antennular somite, lateral view; D, right antennal proto-pod, lateral view; E, right raptorial claw; F, TS6-8, right dorsal view; G-I, right pereopods 1-3, posterior view; J, TS8 sternal keel, right lateral view; K, AS4-6, telson and right uropod, dorsal view; L, telson, ventral view; M, AS6 sternum and right uropod, ventral view; N, AS5, right posterolateral corner; O, right pleopod 1 endopod, anterior view. Scale A, E-O = 5.0 mm; B-D = 2.5 mm.

Bay of Plenty: NMNZ Cr9339, 1 female (TL 60 mm), Tauranga, 37°41'S, 176°10'E, mud-flats, 1956.

Wairarapa: AM P87889, 1 male (TL 58 mm), Deliverance Cove, Castlepoint, 40°54.288'S, 176°13.601'E, 0.4 m, low tide, from burrow in sandy beach, yabby

pump, coll. S. & R. Ahyong, 26 Jan 2008; AM P87890, 1 male (TL 57 mm), Deliverance Cove, Castlepoint, 40°54.286'S, 176°13.627'E, 0.3 m, sand flat, low tide, yabby pump, coll. S. & R. Ahyong, A. George, 7 Feb 2010.

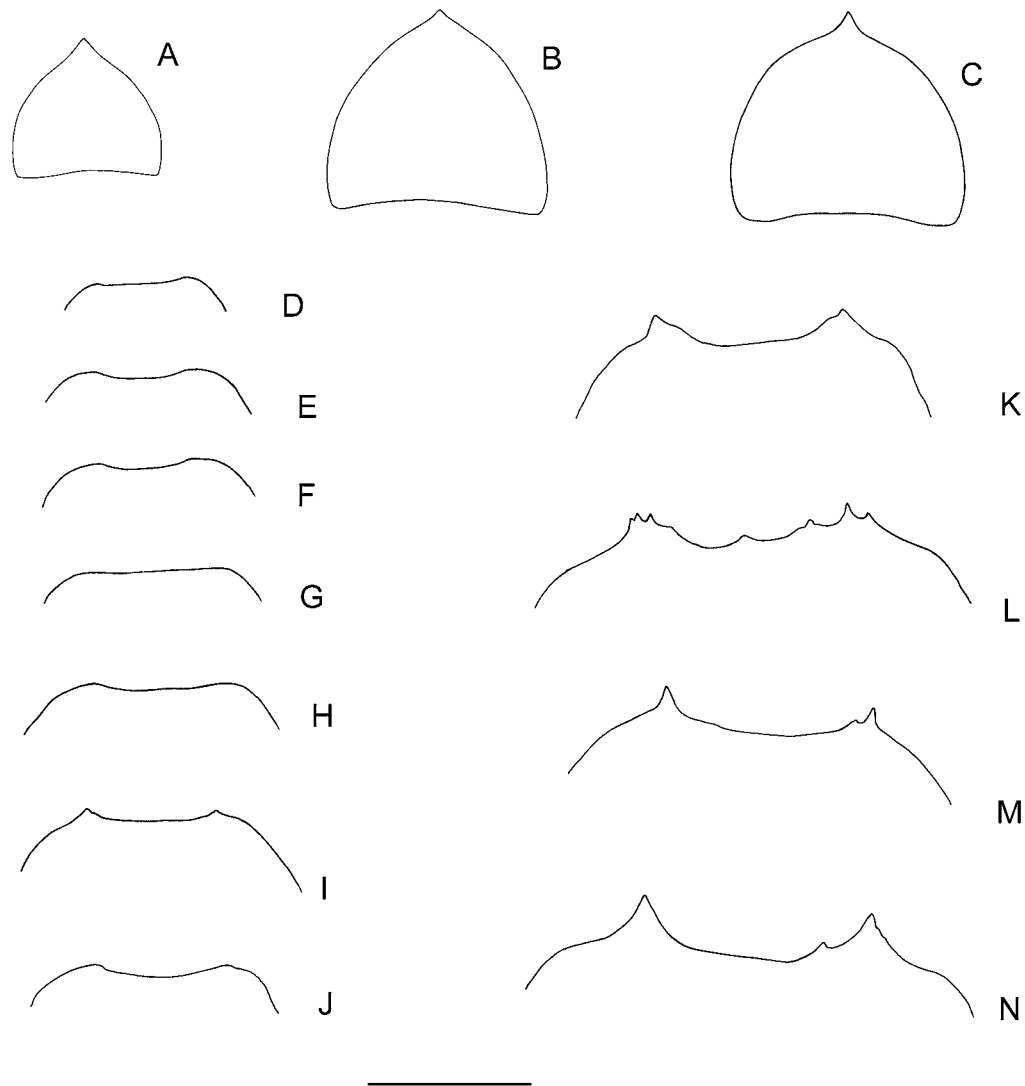


Figure 29. *Heterosquilla tricarinata* (Claus, 1871). Rostral plate (A–C): A, female, TL 45 mm, Stewart Island (OM IV1348); B, male, TL 55 mm, no specific locality (OM IV1399); C, male, TL 71 mm, Ivey Bay, Mana (AM P87895). AS6 sternum posterior margin (D–N): D–J, Harwood, Otago (AM P87896), D, male, TL 21 mm; E, male, TL 23 mm; F, male, TL 29 mm; G, male, TL 31 mm; H, male, TL 32 mm; I, male, TL 33 mm; J, female, TL 34 mm; K, male, Plimmerton, TL 48 mm (AM P87891); L, male, Deliverance Cove, Castlepoint, TL 57 mm (AM P87890); M, male, TL 58 mm, Deliverance Cove, Castlepoint, (AM P87889); N, male, TL 63 mm, Ivey Bay, Mana (AM P87892). Scale = 2.5 mm.

Wellington: AM P87891, 1 male (TL 48 mm), Plimmerton Beach, 41°04.99'S, 174°51.92'E, dug from burrow, low tide, fine sand, coll. S. Ahyong, 1 Feb 2010; AM P87894, 3 males (TL 56–91 mm), 4 females (TL 33–79 mm), Ivey Bay, Mana, 41°06.116'S, 174°52.250'E, intertidal sandflat burrow, yabby pump, coll. S. Ahyong, Jan 2007; AM P87892, 1 male (TL 63 mm), Ivey Bay, Mana, 41°06.148'S, 174°52.247'E, intertidal sandflat burrow, yabby pump, coll. S. & R. Ahyong, 31 Dec 2009; AM P87893, 5 males (TL 40–59 mm), 4 females (TL 48–72 mm), Ivey Bay, Mana, 41°06.149'S, 174°52.245'E, intertidal sandflat burrow, yabby pump, coll. S. Ahyong, Jan 2010; AM P87895, 2 males (TL 71–77 mm), 2 females (TL

29–34 mm), Ivey Bay, Mana, 41°06.139'S, 174°52.306'E, intertidal sandflat burrow, yabby pump, coll. S. Ahyong, 6 Feb 2007; NMNZ, 1 female (TL 74 mm), south-west side of Porirua Harbour, coll. R. Dalden, 19 Aug 1961; NMNZ, 1 female (TL 54 mm), Evans Bay Power House, Wellington, coll. C.D. Elvines, 20 Nov 1956; NIWA 70550, 1 male (TL 61 mm), Onehunga Bay, 41°05.62'S, 174°51.48'E, intertidal sand, yabby pump, coll. G. Read, 18 Feb 2011; NMNZ Cr9341, 2 males (TL 51–52 mm), 1 female (TL 56 mm), Hutt River mouth, Wellington Harbour, 41°14.4'S, 174°53.9'E, dug from burrows in mudflats, coll. J.C. Yaldwyn, Sep–Oct 1953; NMNZ, 1 female (TL 68 mm), Lyall Bay, Wellington,

41°20'S, 174°48'E, washed ashore after heavily southerly, coll. R.K. Dell, Feb 1947.

Tasman-Nelson: NMNZ Cr9378, 1 female (TL 48 mm), Puponga, Golden Bay, 40°31.4'S, 172°44.0'E, mudflats with *Zostera*, 9 Mar 1976; NMNZ Cr9380, 1 female (TL 49 mm), Tonga Beach, Tasman Bay, 40°53.2'S, 173°03'E, 11 Mar 1976; NMNZ, 4 males (TL 28–62 mm), 3 females (TL 23–63 mm), Puponga Inlet, Nelson, 40°31.5'S, 172°44.2'E, 0.15–0.45 m, mud, coll. F. M. Climo, 8 Oct 1969.

Marlborough: NMNZ, 2 males (TL 51–53 mm), Erie Bay, Tory Channel, 41°15'S, 174°13'E, coll. C. White, 29 Sep 1964.

Chatham Islands: NIWA 50654, 1 female (TL 78 mm), Te Whanga Lagoon, Chatham Island, near airport, 43°50'30"S, 176°30'40"W, coll. K. Gregory-Hunt, 1 Aug 2007.

Canterbury: CM AQ3194, 3 females (TL 90–92 mm), Akaroa Heads, 43°53'S, 172°59'E, gut of shark, coll. L. Vangioni, 1936.

Otago: AM P87896, 8 males (TL 21–62 mm), 3 females (TL 25–34 mm), Harwood, 45°49.4'S, 170°40.1'E, intertidal sand flat with patches of *Zostera*, dug from burrows, coll. S. & R. Ah Yong, 24 Oct 2001; NMV J39359, 1 male (TL 50 mm), 1 female (TL 36 mm), Harwood, Otago Peninsula, mudflat, coll. E. Wallis *et al.*, 18 Mar 1997; NMNZ Cr9352, 4 males (TL 40–75 mm), 1 female (TL 63 mm), Portobello, Otago Harbour, 45°50'S, 170°39'E, under light in mudflat, coll. J.M. Moreland, 15 Nov 1952; NMNZ Cr9340, 1 female (TL 53 mm), off Portobello, Otago Harbour, dug from burrows in sandflats, coll. J.C. Yaldwyn, 12 Nov 1961; OM IV1401, 1 female (TL 61 mm), spit of Otago Harbour, 45°49'S, 170°38'E, coll. H. Gilbert; OM IV1406, 1 female (TL 40 mm), Portobello; OM IV1400, 1 male (TL 65 mm), 1 female (TL 74 mm), Otago Harbour pre 1900; NIWA 8616, 1 female (CL mm), Otago Harbour, 45°50.53'S, 170°35.88'E, 1979; NMNZ Cr9277, 1 male (TL 48 mm), Aramoana Beach, 45°46.8'S, 170°42.6'E, coll. J. Graham, Mar 1977; NMNZ Cr3740, 2 males (TL 64–68 mm), 1 female (TL 62 mm), Otakou, 45°48'S, 170°42'E, Sep 1963.

Southland: OM IV1952, 2 males (TL 53–56 mm), 1 female (TL 57 mm), Resolution Island, Fiordland, 45°40'S, 166°40'E, dug in sand, coll. R. Henry, 1900; OM IV1398(part), 1 female (TL 45 mm), Ulva Island, 46°56'S, 168°08'S, coll. T.J. Parker; AM P87897, 1 male (TL 60 mm), Bluff Harbour, coll. M. Rodrigue, 2 Nov 2011.

No specific locality: OM IV1399, 1 male (TL 55 mm), coll. G.M. Thomson, 1910, no other data.

DIAGNOSIS. Ocular scales fused into quadrate plate. Antennal protopod 2 ventral papillae. Rostral plate slightly wider than long, lateral margins convex; apex acute. Raptorial claw dactylus with 9–11 teeth, outer

margin sinuous; propodus, when folded not reaching posteriorly as far as proximal end of ischium; ischium shorter than half merus length. Pereopods 1–3 basal segment with inner and outer, ventrolaterally directed spine in both sexes. AS6 posterolateral spine prominent; sternum posterior margin with pair of angular posterior projections, most prominent in adults. Telson thick, length about half width; with 4 acute 'intermediate' denticles, second and fourth shorter than first and third; lateral denticle spiniform. Dorsal surface with broad, flat, median elevation and anterior submedian carina each terminating in stout spine. Uropodal protopod outer spine broad, flat, tapering to sharp apex, ventrally carinate; inner spine slender, one-quarter length of inner margin of outer spine.

DESCRIPTION. Eye not extending beyond antennular peduncle segment 2; cornea subglobular, inclined laterally on stalk, not concealed by rostral plate. Ophthalmic somite anterior margin flattened. Ocular scales fused into quadrate plate.

Antennular peduncle 0.41–0.51CL. Antennular somite dorsal processes with acute apices, spiniform directed anterolaterally. Antennal protopod dorsally unarmed; with small ventrodorsal tooth and 2 ventral papillae. Antennal scale length 3.00–3.45 width, 0.33–0.43CL.

Rostral plate slightly wider than long, lateral margins evenly convex (most pronounced in adults), apex acute. Carapace anterolateral angles rounded.

Raptorial claw dactylus with 9–12 teeth (usually 10, rarely 12 on one side), outer margin broadly sinuous, proximal margin with indistinct basal notch. Carpus dorsal margin terminating in short tooth, directed ventrally. Propodus with 3 movable spines proximally, distal margin unarmed; outer inferodorsal angle blunt, rounded, approximating a right angle; propodus, when folded, not reaching posteriorly as far as proximal end of ischium; propodus as long as or shorter than carapace; PI 100–118 (male), 103–122 (female). Ischium almost one-third merus length.

Mandibular palp 3-segmented. Maxillipeds 1–5 with epipod. Maxilliped 5 basal segment without ventrally directed spine.

Pereopods 1–3 basal segment with inner and outer, ventrolaterally directed spine; endopod distal segments oval elongate, slenderest on pereopod 3.

Male pleopod 1 endopod without indication of lateral lobe of distal 'endite'.

TS5 lateral process obsolete, lacking ventrally directed spine. TS6–7 lateral process broadly rounded. TS8 lateral process bluntly angular; sternal keel subquadrate.

AS1–5 smooth; posterior margin unarmed; AS4 posterolateral angle blunt; AS5 with or without small posterolateral spine. AS6 smooth, lacking carinae;

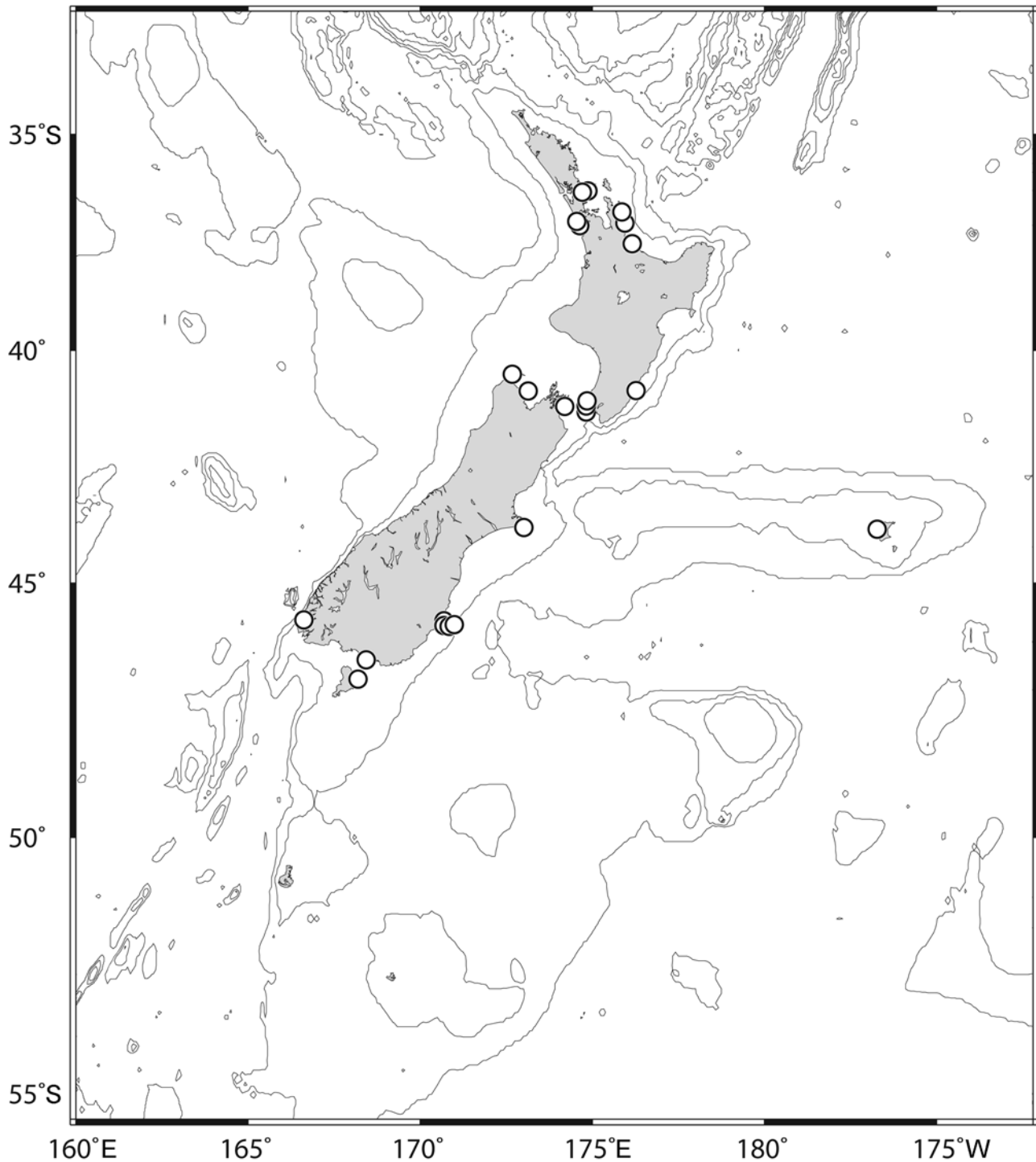


Figure 30. New Zealand distribution of *Heterosquilla tricarinata* (Claus, 1871).

posterolateral spine prominent; with blunt, obtuse projection anterior to uropodal articulation; sternum posterior margin with 2 angular to sharp, often irregular teeth, becoming more pronounced with increasing body size.

Telson thick, length slightly exceeding half width; submedian teeth slender, curved, separated by shallow fissure, with small tooth above articulation in specimens exceeding about TL 50 mm; with 6–10 minute

submedian denticles in arcuate row either side of midline; with 4 acute 'intermediate' denticles, second and fourth from midline longer than first and third; lateral denticle spiniform. Dorsal median elevation broad, flat, posterolaterally rounded, terminating in blunt to sharp point. Anterior submedian carinae low to slightly cristate, terminating in stout spine. Ventral surface without post-anal carina or spine.

Uropodal protopod outer spine broad, flat, tapering to sharp apex, ventrally carinate; inner spine slender, one-quarter length of inner margin of outer spine; with short slender ventral spine anterior to endopod articulation. Uropodal exopod proximal segment with low, round, distal lobe on inner margin and slender distal spine flanked laterally by small, short spine; outer margin with 5 or 6 movable spines, proximal 3 or 4 straight, distal 2 longer, curved, distalmost reaching midlength of distal segment. Exopod distal segment longer than proximal segment. Endopod reniform, length 2.08–2.39 width.

COLOUR IN LIFE. *Males* (Frontispiece 2A): Carapace translucent and speckled with white and brown chromatophores. Thorax and abdomen translucent with dark-brown transverse banding, darkest along posterior margins of somites; overall body also frequently with diffuse white and brown speckling. Raptorial claws with light brown speckling on merus, carpus and proximal portion of propodus; dactylus translucent white with orange-pink teeth. Telson surface with large, black patch on either side of midline; each patch interrupted by thin, longitudinal, white or yellowish stripe covering anterior submedian carina, and by irregular, broken longitudinal stripe mesially. Uropodal protopod dark brown along anterior margin and proximally near articulation with AS6; exopod dark brown laterally and distally; exopod dark brown to black.

Females (Frontispiece 2B): overall dark green to black; midline of thorax and abdomen transparent revealing orange-red gonadal stripe in 'ripe' females.

MEASUREMENTS. Male ($n = 61$) TL 21–91 mm; female ($n = 55$) TL 23–92 mm. The present series includes the largest known specimens of the species.

HABITAT. Intertidal sand and mudflats from the mid-intertidal zone to at least the lowest tide level. Sometimes found in clean sand habitats, but most common on sheltered silty-sand shorelines, sometimes in association with *Zostera*. Burrows have a single circular entrance with a vertical shaft of about three to four body lengths, after which the burrow may tend diagonally horizontally. Burrows may reach about 50 cm deep.

REMARKS. *Heterosquilla tricarinata* (Claus, 1871), sometimes known in Maori as "Mana", is the most common stomatopod in New Zealand (Powell 1998). White (1847) first used the name *Coronis tricarinata* as a nomen nudum but never subsequently described or figured the species. The name, *Coronis tricarinata*, was formally validated by Claus (1871) via documented examination of the type specimen and bibliographic reference to White's (1847) species name. Claus' (1871) validation of White's name, however, went unnoticed for almost

a century, until recognised by Lipke Holthuis (see Manning 1966). Owing to ambiguity over the identity and taxonomic status of the name *tricarinata*, however, Wood-Mason's (1875) name, *spinosa*, was used instead. Consequently, the common New Zealand species was referred to *Lysiosquilla spinosa* (Wood-Mason, 1875), which was described from specimens believed to originate from the Andaman Islands and New Zealand. Chilton (1891) (and most others for almost 80 years) retained Wood-Mason's species name, unaware that Claus (1871) validated the name *tricarinata*. Chilton (1891) also regarded *Squilla laevis* Hutton, 1879, *Squilla indefensa* Kirk, 1878, and *Squilla tridentata* Thomson, 1882, as junior synonyms of *H. tricarinata* (as *Lysiosquilla spinosa*). Hutton's species, however, is recognised as valid herein as *Heterosquilla laevis* and Thomson's species was recognised as valid by Ahyong (2001) as *Heterosquilla tridentata*. Kirk's (1878, 1879a) brief account and figures (albeit stylised) appear to fit *H. tricarinata*. Unfortunately, Kirk's syntypes from Kapiti Island and the Chatham Islands are now lost. Therefore, to formally fix the identity of the species, the holotype of *H. tricarinata* is herein designated as the neotype of *Squilla indefensa* Kirk. As such *Squilla indefensa* becomes an objective junior synonym of *H. tricarinata*.

Manning (1966) regarded *Heterosquilla spinosa* as a valid species occurring in the Andaman Islands, but redescribed *H. tricarinata* based on type and other material, and reinstated *tricarinata* as the appropriate specific epithet for what was previously called *spinosa* in New Zealand. Subsequently, Manning (1978b) showed that *H. spinosa* (Wood-Mason, 1875) is a junior synonym of *H. tricarinata*, and that the apparent differences between the two species were based on inaccuracies in the type description and figures of the former. Moreover, the alleged type locality of *H. spinosa* (Port Blair, Andaman Islands) is erroneous, almost certainly the result of mislabelling of a New Zealand specimen. Other material reported by Wood-Mason (1875, 1895) included specimens sent to the Indian Museum on exchange from the Otago Museum, New Zealand, such as the lectotype of *Gonodactylus platysoma*. Similarly, the Otago Museum specimen of *Oratosquilla oratoria* (a dried specimen currently in the Canterbury Museum), without locality data but assumed to be of New Zealand origin by Chilton (1911a), most likely originated from the collections of the Indian Museum. It is now clear that *Heterosquilla spinosa* is a junior synonym of *H. tricarinata* and does not occur in the Andaman Sea. Lanchester's (1901) Malaysian record of *Lysiosquilla spinosa* is referable to *Austrosquilla malayensis* (Manning, 1968a).

The number of teeth on the dactylus of the raptorial typically ranges from 9–11, usually 9 or 10. Two specimens (female TL 45 mm, OM IV1398; male TL 60 mm, AM P87897), however, are unusual in hav-

ing 10 or 11 dactylar teeth on one raptorial claw and 12 teeth on the other, partially overlapping with the number of dactylar teeth recorded for *H. laevis*, which always has 12 or more dactylar teeth on both claws. In all other respects the two specimens correspond well to *H. tricarinata* sensu stricto.

The margins of the rostral plate in adult *H. tricarinata* are convex, becoming more pronounced with increasing body size (Figs 28A, 29A–C). In juveniles and small specimens to about TL 30 mm, the rostral plate may be more triangular, with straighter margins approaching the rostral plate of adult *H. laevis*.

Mature male and female *H. tricarinata* differ considerably in colour pattern. The body of males is marked by light and dark transverse bands, whereas that of mature females is dark green to black overall, with a partially transparent midline through which the ripe gonads are evident as an orange median stripe.

Manning (1966) reported the presence of a pair of prominent angular projections on the posterior margin of sternum of AS6 in female *H. tricarinata*, apparently absent in males. Examination of the large series here indicates that the posterior projections are a feature of both sexes, generally becoming more pronounced with increasing body size (Fig. 29D–N). The projections may be absent or only slightly marked in juveniles, sometimes expressed as a mere irregularity on the sternal margin. By about TL 40–60 mm, the projections are usually distinct, forming two bluntly angular or sharp points separated by a distinct concavity. The margins of these projections are often uneven and irregular, sometimes forming additional smaller serrations.

Of the eight known species of *Heterosquilla*, *H. tricarinata* is most similar to *H. laevis*; distinctions between the two species are discussed under the account of the latter. *Heterosquilla tricarinata* is distinguished from *H. polydactyla* in the shorter rostral plate (slightly wider than long versus distinctly longer than wide) and fewer dactylar teeth on the raptorial claw (9–12 versus 17–20); from *H. platensis* by the absence of intermediate carinae on AS6; and from *H. koning*, *H. pentadactyla*, *H. trifida* and *H. tridentata* by the greater number of teeth on the dactylus of the raptorial claw (9–12 versus 8 or fewer).

Heterosquilla tricarinata is one of the few stomatopods for which complete larval development is known, and the only stomatopod known to have abbreviated development (Greenwood & Williams 1984). A single brood is produced per year and larvae appear in the plankton in spring or early summer when planktonic food is most abundant. In contrast to the usual two or three propelagic stages (which remain in the burrow of the female) and up to nine pelagic stages of other stomatopods, *H. tricarinata* has only one propelagic and two pelagic stages prior to postlarva. Larval duration is approximately 60–70 days (Williams *et al.* 1985).

Fussell (1979) studied the biology of *H. tricarinata* from tidal flats in the Otago region, noting a deviation from a 1:1 sex ratio in favour of females, and a preference for sandy rather than clay substrates. Permanent pairing does not appear to be the norm in *H. tricarinata* as in some other lysiosquilloids. Fussell (1979) reported an instance of a male–female pair from a single burrow in the field, and frequent possible pairing under laboratory conditions. However, during the course of the present study, no male–female pairs were observed in the field. *Heterosquilla tricarinata* is well adapted for aerobic respiration at low ambient oxygen tensions, as frequently experienced in mud or sand flat burrows during emersion at low tide (Innes 1985).

DISTRIBUTION. Known only from New Zealand waters from Northland south to Stewart Island, including the Chatham Islands.

Heterosquilla tridentata (Thomson, 1882)

(Figs 31, 32)

Squilla tridentata Thomson, 1882: 230 [type locality: Auckland Islands, by present neotype designation]. – Bigelow, 1894: 503. – Manning, 1966: 123.

Heterosquilla tridentata. – Ahyong, 2001: 173. – Webber *et al.*, 2010: 135, 218.

TYPE MATERIAL. *Neotype*: NIWA 23973, male (TL 58 mm), Port Ross, Auckland Island, Auckland Islands, 50°33.10'S, 166°14.10'E, 23 m, NZOI Stn S114, 7 Dec 1978.

OTHER MATERIAL EXAMINED. *Otago*: NMNZ Cr9351(part), 1 male (TL 64 mm), 1 female (TL 68 mm), off Oamaru, 45°05'S, 170°59'E, 37 m, trawled, from stomach of *Mustellus antarcticus*, coll. J. Graham, Apr 1962; NMNZ Cr19728, 1 male (TL 58 mm), off Oamaru, 45°05'S, 170°59'E, zone 2, coll. J. Graham, Apr 1962; NMNZ, 1 female (TL 81 mm), off Oamaru, 45°05'S, 170°59'E, zone 2, from stomach of 'smooth hound', coll. J. Graham, Apr 1962.

Southland: NIWA 23922, 1 male (broken, CL 14.2 mm), south-east of Papatowai, 46°40.00'S, 170°07.50'E, 165–181 m, NZOI Stn B569, 9 Oct 1962.

Auckland Islands: NIWA 4124, 1 female (TL 43 mm), 64 m, 50°48.1'S, 166°14.4'E, NZOI stn J523, 12 Dec 1973; NIWA 23939, 1 female (TL 36 mm), east of Cape Bennett, Auckland Island, 50°49.00'S, 166°20.80'E, 106 m, NZOI Stn D195, 22 Jan 1964; NIWA 80618, 2 males (TL 38 mm), 3 females (TL 42–47 mm), Auckland Islands, Port Ross, Auckland Island, 50°33.10'S, 166°14.10'E, 23 m, NZOI Stn S114, 7 Dec 1978.

DIAGNOSIS. Ocular scales fused into rounded plate. Antennal protopod with 2 ventral papillae. Rostral

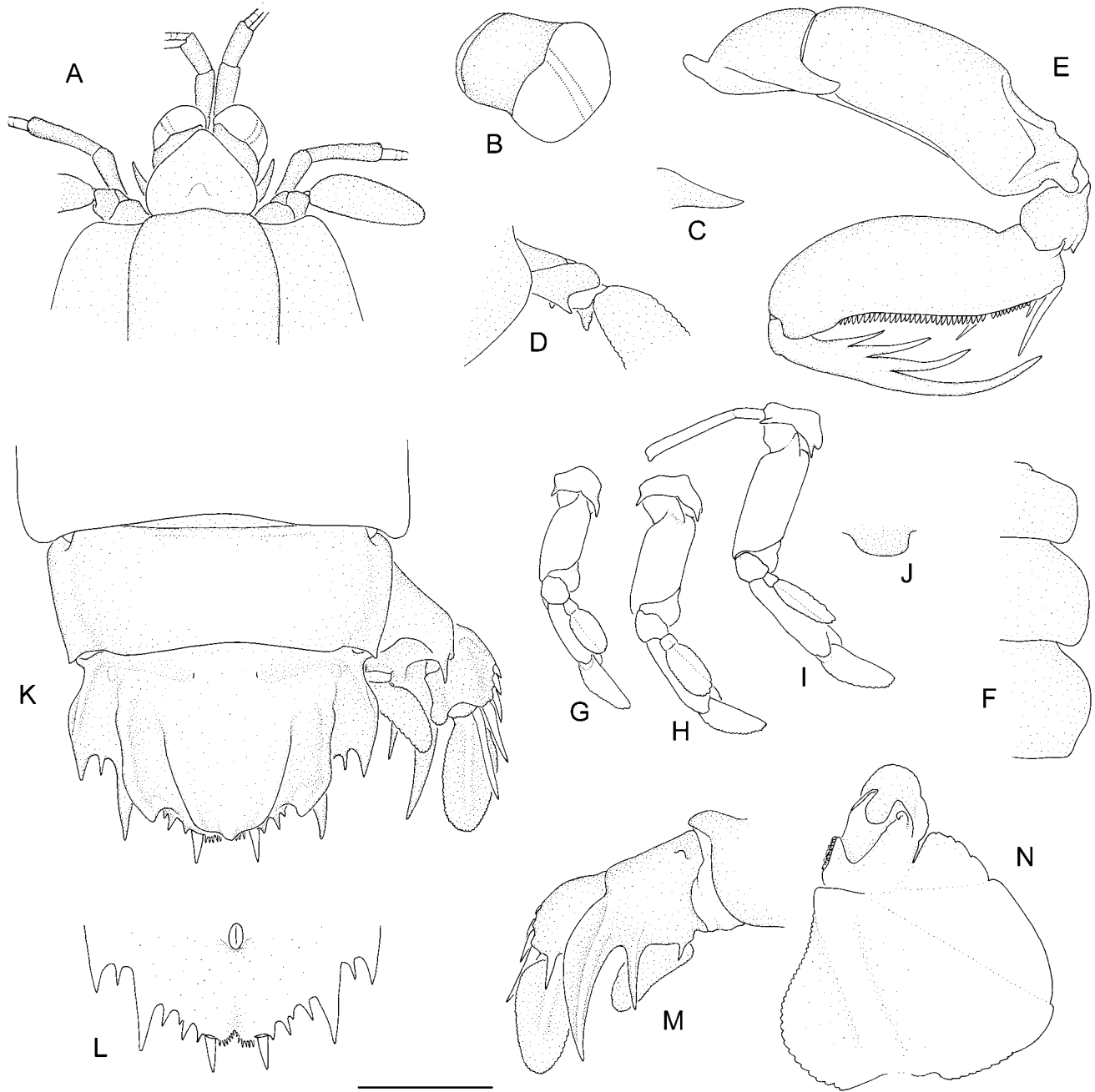


Figure 31. *Heterosquilla tridentata* (Thomson, 1882), male neotype, TL 58 mm, Port Ross, Auckland Island (NIWA 23973). A, anterior cephalothorax; B, right eye; C, right dorsal process of antennular somite, lateral view; D, right antennal protopod, lateral view; E, right raptorial claw; F, TS6-8, right dorsal view; G-I, right pereopods 1-3, posterior view; J, TS8 sternal keel, right lateral view; K, AS5-6, telson and right uropod, dorsal view; L, telson, ventral view; M, right uropod, ventral view; N, right pleopod 1 endopod, anterior view. Scale A, E-I, K-M = 4.0 mm; B-D, J, N = 1.9 mm.

plate wider than long, widest in advance of base, margins straight distally; apex bluntly angular. Raptorial claw dactylus with 4 (occasionally 5) teeth; propodus shorter than carapace. Pereopods 1-3 basal segment with inner and outer, ventrolaterally directed spine. AS6 posterolateral angle produced to short angular tooth. Telson length slightly exceeding half width;

surface between dorsal median elevation and anterior submedian carina smooth, unarmed; median elevation apex blunt, without long spine, lateral margins not anteriorly continuous with submedian carinae. Uropodal protopod inner spine half length of inner margin of outer spine.

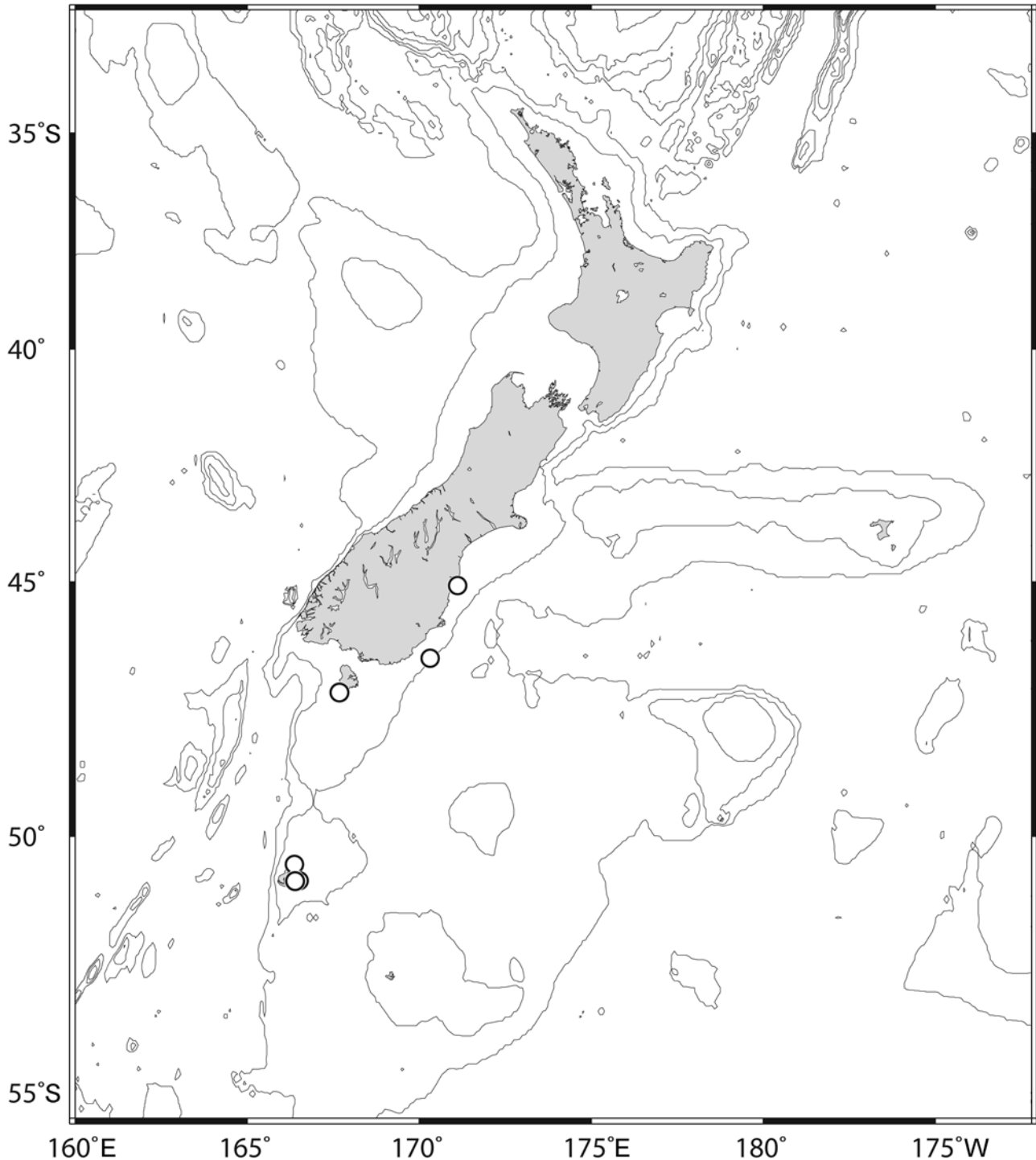


Figure 32. New Zealand distribution of *Heterosquilla tridentata* (Thomson, 1882).

DESCRIPTION. Eye not extending beyond antennular peduncle segment 2; cornea broadened, inclined laterally on stalk, stalk largely concealed by rostral plate. Ophthalmic somite anterior margin flattened. Ocular scales fused into rounded plate.

Antennular peduncle length 0.47–0.53CL. Antennular somite dorsal processes with acute apices, spiniform directed anterolaterally. Antennal protopod dorsally unarmed; with small ventrodistal tooth and 2

ventral papillae. Antennal scale length 2.94–3.92 width, 0.31–0.35CL.

Rostral plate triangular, slightly wider than long, widest in advance of base, lateral margins evenly convex proximally, straight distally, apex rounded, with faint median sulcus. Carapace anterolateral angles rounded, anterior margins straight to slightly concave.

Raptorial claw dactylus with 4 or 5 (usually 4) teeth, outer margin broadly curved to faintly sinuous, proximal margin with indistinct basal notch. Carpus dorsal margin terminating in short tooth, directed ventrally. Propodus with 3 movable spines proximally, distal margin unarmed; inferodistal margin broadly rounded; propodus length shorter than carapace; PI 116–121 (male), 115–125 (female). Ischium about one-third merus length.

Mandibular palp 3-segmented. Maxillipeds 1–5 with epipod. Maxilliped 5 basal segment without ventrally directed spine.

Pereopods 1–3 basal segment with inner and outer, ventrolaterally directed spine; endopod distal segments oval elongate, slenderest on pereopod 3.

Male pleopod 1 endopod with slight lateral lobe of distal 'endite', demarcated by small marginal notch.

TS5 lateral process obsolete, without ventrally directed spine. TS6–8 lateral process broadly rounded. TS8 sternal keel subquadrate to rounded.

AS1–5 smooth; posterior margin unarmed; posterolateral angles rounded, unarmed. AS6 smooth, lacking longitudinal carinae or dorsal spines; posterolateral angle produced to short angular tooth; with blunt, obtuse projection anterior to uropodal articulation; sternum posterior margin unarmed.

Telson thick, length slightly exceeding half width; submedian teeth slender, curved, separated by shallow fissure; with 6–10 minute submedian denticles in arcuate row either side of midline; with 4 acute 'intermediate' denticles, second and fourth from midline longer than first and third; lateral denticle spiniform. Dorsal surface with broad, flat, median elevation, anterior submedian carina and marginal carina; surface between median elevation and anterior submedian carinae smooth, unarmed. Median elevation flat, smooth medially, margins converging posteriorly, posterolaterally rounded, apex blunt; not anteriorly continuous with anterior submedian carina. Anterior submedian carina terminating posteriorly in blunt angular tooth; inner distal surface with low, rounded swelling. Marginal carina low, reaching posteriorly to or slightly beyond midlength of margin of lateral tooth. Ventral surface without post-anal carina or spine.

Uropodal protopod outer spine flattened, outer margin broadly curved, tapering to sharp apex, ventrally carinate; inner spine slender, faintly carinate ventrally, half length of inner margin of outer spine; with short slender ventral spine at endopod articulation. Uropodal exopod proximal segment with low, round, distal lobe on inner margin and slender distal spine; outer margin with 5 graded movable spines, distalmost reaching beyond midlength but not exceeding apex of distal segment. Exopod distal segment longer than proximal segment. Endopod reniform, length 2.87–3.33 width.

COLOUR IN LIFE. Not known; faded in preservative.

MEASUREMENTS. Male ($n = 6$) TL 38–64 mm, female ($n = 7$) TL 36–81 mm. Other measurements of neotype: CL 10.7 mm, antennular peduncle length 5.5 mm, antennal scale length 3.6 mm, raptorial claw propodus length 8.9 mm.

HABITAT. *Heterosquilla tridentata* burrows in sandy-mud substrates; 23–181 m. At the Auckland Islands, *H. tridentata* has been found in sympatry with *H. laevis*, the decapod crustaceans *Callinassa filholi* (A. Milne-Edwards) and *Munida* sp., the bivalve molluscs *Tawera bollonsi* Powell and *Austrovenus stutchburyi* (Wood) (as *Chione aucklandia* Powell), and the polychaetes *Branchiomma serratibranchis* (Grube) and *Arabella iricolor* (Montagu) (see Luckens 1991).

REMARKS. Thomson (1882) described *Heterosquilla tridentata* (as *Squilla tridentata*) based on a juvenile from Port Pegasus, Stewart Island. Most previous workers (e.g., Chilton 1891; Kemp 1913; Holthuis 1967) treated *H. tridentata* as a junior synonym of *H. tricarinata* (as *Lysiosquilla spinosa*). Manning (1966), however, tentatively retained *H. tridentata* in the synonymy of *H. tricarinata*, but noted that it was probably a valid species. Ahyong (2001) formally removed *H. tridentata* from the synonymy of *H. tricarinata*. Thomson's original account of the species is poor and based on a juvenile, but he did note that the dactylus of the raptorial claw was "furnished with three spines" (Thomson 1882: 230) (excluding the terminal spine), and that the species otherwise closely resembled *Squilla indefensa*, a junior synonym of *Heterosquilla tricarinata*. Unfortunately, the holotype of *H. tridentata* is now lost (Schram & Müller 2004) and two species are known from New Zealand that could apply to Thomson's (1882) minimal account (see also account of *Heterosquilla trifida* sp. nov.). Thus, the identity of *H. tridentata* is ambiguous, requiring a neotype designation. Suitable specimens of *H. tridentata* from the original type locality are not presently available, so a specimen from the Auckland Islands is herein selected as the neotype (NIWA 23973, male, TL 58 mm) to fix the identity of the species.

Heterosquilla tridentata most closely resembles *H. trifida* sp. nov. from northern New Zealand and *H. pentadactyla* Ahyong, 2001, from south-eastern Australia. They share a similar (or at least overlapping) number of teeth on the dactylus of the raptorial claw and in this respect differ from all other congeners, which have at least seven dactylar teeth. *Heterosquilla trifida* and *H. tridentata* differ from *H. pentadactyla* in having an inner and outer spine on the basal segment of pereopod 3 (rather than an outer spine only) and in usually having four instead of five teeth on the dactyli of the raptorial claws. *Heterosquilla pentadactyla* has five

teeth on the dactylus of the raptorial claw whereas *H. tridentata* and *H. trifida* usually have four teeth, occasionally with a fifth small dactylar tooth on one of the claws (perhaps as a result of regeneration after damage). *H. tridentata* further differs from *H. pentadactyla* in having an inner and outer spine on the basal segment of pereopod 3 (rather than an outer spine only) and rounded instead of triangular ocular scales. Characters distinguishing *H. tridentata* from *H. trifida* are given under the account of the latter.

DISTRIBUTION. Presently known only from South Island, New Zealand, off Oamaru, south to the Auckland Islands.

***Heterosquilla trifida* sp. nov.** (Figs 33, 34)

Lysiosquilla sp. – Calman, 1917: 143–144.

TYPE MATERIAL. *Holotype:* NIWA 55762, male holotype (TL 31 mm), off Kahurangi Shoals, north-west of Kahurangi Point, Tasman Peninsula, South Island, 40°40.00'S, 172°08.99'E, 77–80 m, NZOI stn B642, 21 Oct 1962.

OTHER MATERIAL EXAMINED. *Northland:* NIWA 55761, 1 male (TL 56 mm), Bay of Islands, 34°26.38–26.23'S, 173°07.77–07.41'E, 115–110 m, dredge, TAN0906/181, 15 Jan 2009.

Auckland: USNM 1156985, 1 male (TL 30 mm), Greater Omaha Bay, 14 m, sand, Stn C7, coll. R. Taylor, 9 May 1995; USNM 1156986, 1 female (TL 31 mm), Greater Omaha Bay, 36°20.20'S, 174°47.95'E, 14 m, sand, C14, coll. R. Taylor, 15 May 1995.

DIAGNOSIS. Ocular scales fused into rounded plate. Antennal protopod with 2 ventral papillae. Rostral plate wider than long, widest in advance of base, margins straight distally; apex bluntly angular. Raptorial claw dactylus with 4 (occasionally 5) teeth; propodus shorter than carapace. Pereopods 1–3 basal segment with inner and outer, ventrolaterally directed spine. AS6 posterolateral spine prominent, elongated. Telson slightly longer than half width; with short accessory carina between dorsal median elevation and anterior submedian carina; median elevation terminating in long blunt spine, lateral margins anteriorly continuous with anterior submedian carinae via low sinuous ridge. Uropodal protopod inner spine half length of inner margin of outer spine.

DESCRIPTION. Eye not extending beyond antennular peduncle segment 2; cornea broadened, inclined laterally on stalk, stalk largely concealed by rostral plate. Ophthalmic somite anterior margin flattened. Ocular scales fused into rounded plate.

Antennular peduncle 0.47–0.51CL. Antennular somite dorsal processes with acute apices, spiniform directed anterolaterally. Antennal protopod dorsally unarmed; with small ventrodorsal tooth and 2 ventral papillae. Antennal scale length 2.80–3.00 width, 0.31–0.36CL.

Rostral plate triangular, slightly wider than long, widest slightly in advance of base, lateral margins evenly convex, proximally, straight distally, apex rounded, with faint median sulcus. Carapace anterolateral angles rounded, anterior margins straight.

Raptorial claw dactylus with 4 or 5 (usually 4) teeth, outer margin broadly slightly sinuous, proximal margin with indistinct basal notch. Carpus dorsal margin terminating in short tooth, directed ventrally. Propodus with 3 movable spines proximally, distal margin unarmed; outer inferodistal margin broadly rounded; propodus length shorter than carapace, PI 115–118 (male), 119 (female). Ischium shorter than one-third merus length.

Mandibular palp 3-segmented. Maxillipeds 1–5 with epipod. Maxilliped 5 basal segment without ventrally directed spine.

Pereopods 1–3 basal segment with inner and outer, ventrolaterally directed spine; endopod distal segments oval elongate, slenderest on pereopod 3.

TS5 lateral process obsolete, without ventrally directed spine. TS6–8 lateral process broadly rounded. TS8 sternal keel rounded.

Male pleopod 1 endopod with slight lateral lobe of distal 'endite', demarcated by small marginal notch.

AS1–5 smooth; posterior margin unarmed; posterolateral angles rounded, unarmed. AS6 smooth, lacking longitudinal carinae or dorsal spines; posterolateral spine prominent, elongated; with blunt, obtuse projection anterior to uropodal articulation; sternum posterior margin unarmed.

Telson thick, length slightly exceeding half width; submedian teeth slender, curved, separated by shallow fissure; with 5 or 6 minute submedian denticles in arcuate row either side of midline; with 4 acute 'intermediate' denticles, second and fourth from midline longer than first and third; lateral denticle spiniform. Dorsal surface with broad, median elevation, anterior submedian carina, marginal carina and short accessory carina between median elevation and anterior submedian carina. Median elevation faintly carinate medially, terminating in long blunt spine; laterally margins cristate, posteriorly terminating in short, blunt angular lobe; lateral margin anteriorly continuous with anterior submedian carina via low sinuous ridge. Anterior submedian carina terminating posteriorly in angular tooth. Marginal carina reaching posteriorly to about midlength of margin of lateral tooth. Ventral surface without post-anal carina or spine.

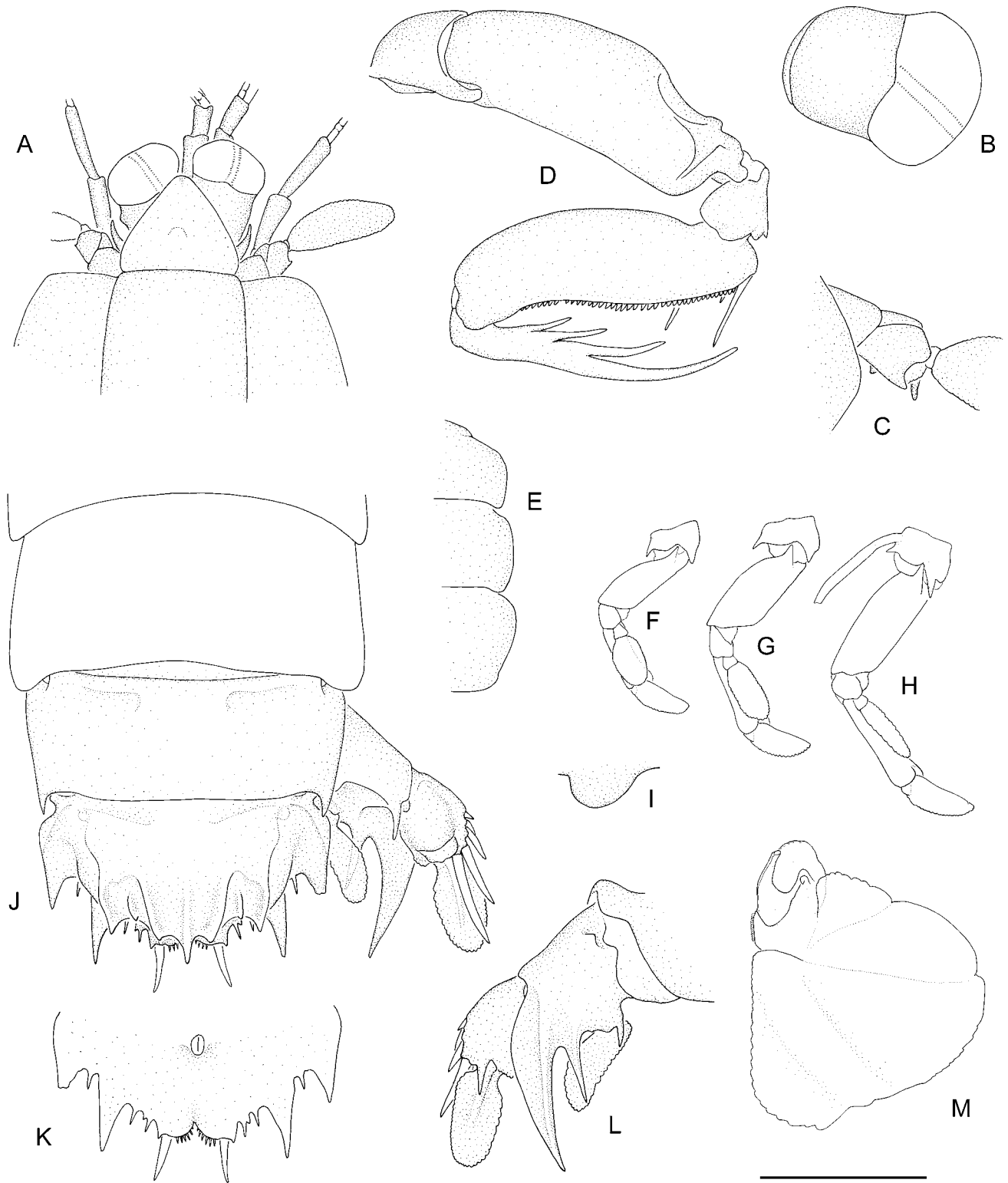


Figure 33. *Heterosquilla trifida* sp. nov., male holotype, TL 31 mm, off Kahurangi Shoals, Tasman Peninsula (NIWA 55762). A, anterior cephalothorax; B, right eye; C, right antennal protopod, lateral view; D, right raptorial claw; E, TS6-8, right dorsal view; F-H, right pereopods 1-3, posterior view; I, TS8 sternal keel, right lateral view; J, AS4-6, telson and right uropod, dorsal view; K, telson, ventral view; L, right uropod, ventral view; M, right pleopod 1 endopod, anterior view. Scale A, D-H, J-M = 3.0 mm; B-C, I = 1.5 mm.

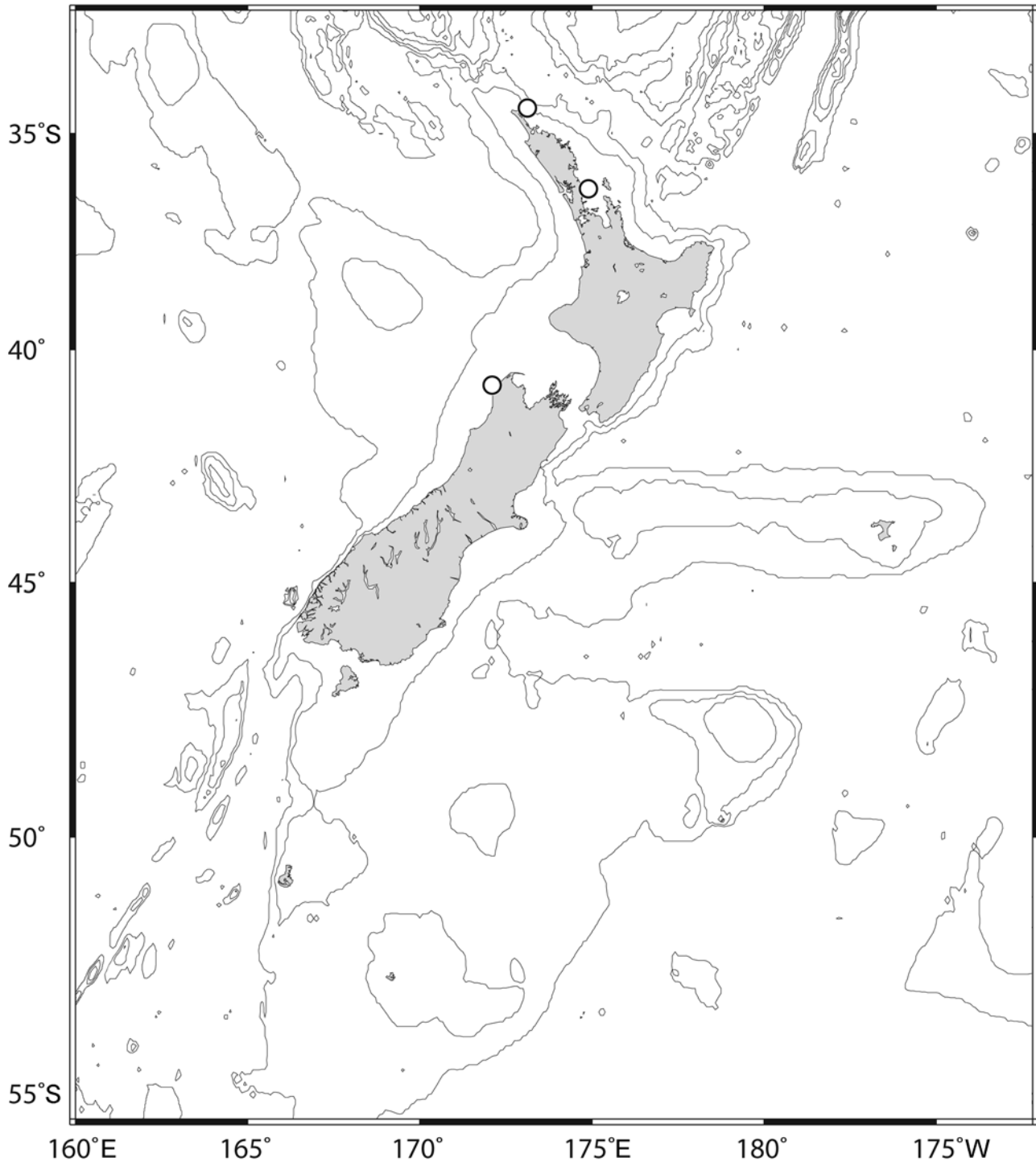


Figure 34. New Zealand distribution of *Heterosquilla trifida* sp. nov.

Uropodal protopod outer spine flattened, outer margin broadly curved, tapering to sharp apex, ventrally carinate; inner spine slender, faintly carinate ventrally, half length of inner margin of outer spine; with short slender ventral spine at endopod articulation. Uropodal exopod proximal segment with low, round, distal lobe on inner margin and slender distal spine; outer margin with 5 or 6 graded movable spines, distalmost reaching apex of distal segment. Exopod

distal segment longer than proximal segment. Endopod reniform, length 3.00–3.16 width.

COLOUR IN LIFE. Not known. In preservative, dorsum covered with scattered brown chromatophores giving evenly mottled appearance. Telson surface on posterior half black between median elevation and anterior submedian carinae. Movable spines on outer margin of uropodal exopod black.

MEASUREMENTS. Male ($n = 3$) TL 30–56 mm; female ($n = 1$) TL 31 mm. Other measurements of holotype: CL 6.3 mm, antennular peduncle length 3.0 mm, antennal scale length 2.0 mm, raptorial claw propodus length 5.3 mm.

ETYMOLOGY. The specific epithet alludes to the trifid appearance of the posteromedian elevation of the telson.

HABITAT. Burrows in soft level sandy substrates; 14–115 m. One specimen of *H. trifida* (NIWA 55761) was collected together with *Anchisquilloides mcneilli* from the Bay of Islands.

REMARKS. *Heterosquilla trifida* sp. nov. most closely resembles *H. tridentata* Thomson, 1882 (southern New Zealand) and *H. pentadactyla* Ah Yong, 2001 (southeastern Australia). *Heterosquilla trifida* differs from *H. pentadactyla* in having an inner and outer spine on the basal segment of pereopod 3 (rather than an outer spine only), in usually having four instead of five teeth on the dactyli of the raptorial claws, and in having rounded instead of triangular ocular scales. *Heterosquilla tridentata* and *H. trifida* differ in the ornamentation of AS6 and the telson, being more strongly ornamented in the latter. In *H. trifida*, the posterolateral angles form a prominent elongated spine, rather than a short angular tooth as in *H. tridentata*. In *H. trifida*, the median boss has a long, blunt median posterior spine and the lateral margins of the boss each terminate in a blunt angle posteriorly and anteriorly form a low curved ridge that turns laterally to meet the anterior submedian carina. A short longitudinal carina is present on each side between the median boss and anterior submedian carina. In *H. tridentata*, however, the short carina between the median boss and anterior submedian carina is lacking, the median boss lacks the long posterior projection and is not anterolaterally continuous with the anterior submedian carinae. The ranges of the two species are not yet known to overlap, each species occurring on either side of the subtropical convergence, *H. tridentata* to the south and *H. trifida* to the north.

The specimens in the present series exhibit little morphological variation apart from the TL 31 mm female (USNM) having four teeth on the dactylus of one raptorial claw and five on the other. All males examined have well developed penes and fully modified pleopod 1 endopods.

Calman (1917) reported larval and postlarval '*Lysio-squilla*' from Spirits Bay and from near Three Kings Islands that bear four teeth on the dactyli of the raptorial claws; they are probably referable to *H. trifida*.

DISTRIBUTION. Presently known only from northern half of New Zealand from the Bay of Islands, North Island,

south to the Tasman Peninsula, South Island.

Pariliacantha gen. nov.

DIAGNOSIS. Eye with cornea bilobed, set slightly obliquely on stalk. Antennal protopod with 1 ventral papilla. Rostral plate as long as wide or slightly longer than wide; with slender anterior spine; ventral spine absent. Raptorial claw dactylus with 12–17 teeth; propodus with 4 movable spines proximally; ischium with prominent distoventral spine. Mandibular palp present. Pereopod 1 endopod distal segment subcircular. Pereopod 2 endopod distal segment ovate. Pereopod 3 endopod distal segment slender. Male pleopod 1 endopod with prominent lateral lobe on distal 'endite'. AS6 with posterolateral spine; submedian and intermediate carinae or spines absent. Telson submedian teeth with movable apices; with 4 'intermediate' and 1 lateral denticles; dorsal surface with broad, flat, posteriorly trispinous median elevation. Telson ventral surface with post-anal spine. Uropodal protopod with 2 terminal spines, inner longer than outer; with ventral spine anterior to endopod articulation; endopod spade-shaped, articulation at anterior margin.

TYPE SPECIES. *Pariliacantha georgeorum* gen. et sp. nov., by present designation.

ETYMOLOGY. A combination of the Latin *parilis*, like, similar, and *acantha*, thorn, spine, alluding to the close relationship with *Acaenosquilla*, *Heterosquilloides* and *Kasim*, each of which also have a post-anal spine on the telson. Gender: feminine.

COMPOSITION. Monotypic.

REMARKS. *Pariliacantha* gen. nov. probably forms a clade with three other closely related tetrasquillid genera, *Acaenosquilla* Manning, 1991, *Heterosquillopsis* Moosa, 1991, and *Kasim* Manning, 1995, which share a post-anal spine, a spine on the uropodal protopod anterior to the endopod articulation and a prominent lateral lobe on the posterior 'endite' of the male pleopod 1 endopod (Ah Yong & Harling 2000). Of these genera, *Pariliacantha* is most similar to *Acaenosquilla* in telson ornamentation, rostral proportions and the pair of 'eyespots' on the AS5 pleura. *Pariliacantha* differs from each of these genera by having significantly more teeth on the dactylus of the raptorial claw (12 or more versus 8 or fewer), a distoventral spine on the ischium of the raptorial claw (unarmed in all others), and a rostral plate that is widest basally rather than in advance of the base. The presence of the ischial spine in *Pariliacantha* is noteworthy, being otherwise present only in the nannosquillids *Austrosquilla* Manning, 1966 and *Pullosquilla* Manning, 1978b.

Pariliacantha georgeorum gen. et sp. nov.
(Figs 35, 36, Frontispiece 1D)

Lysiosquilla brazieri. — Chilton, 1911a: 139. [Not *L. brazieri* Miers, 1880].

Acaenosquilla brazieri. — Webber *et al.*, 2010: 135, 218. [Not *A. brazieri* (Miers, 1880)].

Squilla armata. — Morton & Miller, 1968: 458–459, fig. 169. [Not *S. armata schizodontia* Richardson, 1953].

TYPE MATERIAL. *Holotype*: NIWA 68024, male (TL 48 mm), Plimmerton, 41°05.146'S, 174°51.997'E, sand beach, low tide, 0.1 m, yabby pump, coll. S. Ah Yong, 11 Jan 2009.

Paratypes: NIWA 68023, 5 females (TL 46–54 mm), type locality; AM P87898, 1 male (TL 51 mm), 2 females (TL 52–55 mm), type locality; AM P87899, 1 male (TL 50 mm), Ivey Bay, Mana, 41°06.13'S, 174°52.32'E, from burrow in intertidal sandy-mud flat, yabby pump, coll. S. & R. Ah Yong, 6 Feb 2008; AM P87900, 1 female (TL 21 mm), Castlepoint Beach, Castlepoint, 40°53.729'S, 176°13.178'E, ocean beach in front of caravan park, low intertidal burrow, yabby pump, coll. S. Ah Yong, 26 Apr 2007; AM P87901, 2 males (TL 65–71 mm), Deliverance Cove, Castlepoint, 40°54.286'S, 176°13.627'E, 0.3 m, sand flat, low tide, yabby pump, coll. S. & R. Ah Yong, O. & A. George, 7 Feb 2010.

OTHER MATERIAL EXAMINED. *Northland*: NIWA 56470, 2 males (TL 47 mm; 1 broken, CL 8.7 mm), 34°22.21–22.17'S, 173°01.77–01.41'E, 91–88 m, TAN0906/152, 14 Jul 2009; AWMM 77962, 1 male (TL 42 mm), 1 female (TL 31 mm), Ngatehe Point, Parengarenga Harbour, Northland, 34°31.4'S, 172°58.1'E, intertidal burrows in sand beach, coll. A. Stephenson, 17 Oct 1992; NIWA 50656, 1 female (TL 21 mm), 1 fragmented specimen, Waipu Cove, 36°00.00'S, 174°32.69'E, 20 m, grab, NZOI Stn C779, 21 Feb 1962.

Auckland & Coromandel: USNM 1098991, 1 male (TL 27 mm), Greater Omaha Bay, 10 m, sand, stn C29, coll. R. Taylor, 23 May 1995; USNM 1098988, 1 female (TL 60 mm), Greater Omaha Bay, 4 m, sand, Stn C9, coll. R. Taylor, 9 May 1995; USNM 1098989, 1 female (TL 52 mm), Greater Omaha Bay, 7 m, sand, Stn C2, coll. R. Taylor, 10 Mar 1995; USNM 98990, 1 female (TL 36 mm), Greater Omaha Bay, 36°19.77'S, 174°47.61'E, 11 m, sand, stn C32, coll. R. Taylor, 25 May 1995; AM P87902, 1 male (TL 58 mm), Matatua Point, Kawau Bay, 36°22.80'S, 174°49.2'E, 4 m, muddy sand, coll. R. Taylor, 1 Jan 2004; AM P87903, 1 male (TL 56 mm), 2 females (TL 55–57 mm), Karamuroa Point, Omaha Bay, 36°20.70'S, 174°47.75'E, 9 m, muddy sand, coll. R. Taylor, 22 Jan 2004; AM P72351, 1 male (TL 40 mm), 1 female (TL 47 mm), Comet Rocks, Tawharanui, 36°21.8'S, 174°49.6'S, 1.2 m, coll. R. Taylor, 10 Nov 2001; AM P87904, 2 males (TL 62–67 mm), Stanmore Bay,

Whangaparaoa Peninsula, 36°37.5'S, 174°44.3'E, sand, low intertidal, coll. R. Taylor, 10 Jan 2004; AWMM 8355, 1 male (TL 62 mm), Cheltenham Beach, Auckland Harbour, 36°49'S, 174°49'E, coll. Cosgrove, Sep 1921; NMNZ, 1 female (TL 58 mm), Mercury Bay, Coromandel Peninsula, 36°48'S, 175°42'E, 27–37 m, sand or silty sand, Tarakihi stomach, coll. B. Godfriaux, 17 Sep 1969; NMNZ Cr12526, 1 male (damaged; CL 7.0 mm), off Slipper Island, 37°S, 176°E, 37–51 m, from Tarakihi stomach (#2239), on gravelly sand to silty sand, coll. B. Godfriaux, 19 May 1970.

Bay of Plenty: NIWA 50655, 1 male (TL 21 mm), Tauranga, 37°40.00'S, 176°15.30'E, 19 m, grab, NZOI C799, 24 Feb 1962.

Taranaki: NMNZ, 2 males (TL 31–42 mm), New Plymouth Power Station, 39°29.4'S, 174°01.2'E, from intake, coll. G. Hardy, Apr 1985.

Wellington: NIWA 61490, 1 male (TL 32 mm), 3 females (TL 56–57 mm), Paekakariki, 40°59.0'S, 174°56.6'E, 14–15 m, from stomach of gurnard, coll. R. Stewart, 25 Jan 2010; NIWA 61491, 2 males (TL 46–58 mm), 1 female (TL 52 mm), Paekakariki, 40°59.0'S, 174°56.6'E, 14–15 m, from stomach of gurnard, coll. R. Stewart, 6 Feb 2010; NIWA 61493, 5 males (TL 52–67 mm), 1 female (TL 81 mm), Paekakariki, 40°59.0'S, 174°56.6'E, 14–15 m, from stomach of gurnard, coll. R. Stewart, 25 Jan 2010; NIWA 4107, 2 females (TL 49–62 mm), Paekakariki, 40°59.0'S, 174°56.6'E, 14–15 m, from fish stomach, coll. R. Stewart, 2010.

DIAGNOSIS. As for genus.

DESCRIPTION. Eye not extending beyond antennular peduncle segment 2; cornea slightly broadened, inclined laterally on stalk, not concealed by rostral plate. Ophthalmic somite anterior margin faintly convex. Ocular scales small, rounded, separate.

Antennular peduncle 0.46–0.53CL. Antennular somite dorsal processes with acute apices, spiniform, directed almost anteriorly. Antennal protopod dorsally unarmed; with small ventrodorsal tooth and 1 ventral papilla. Antennal scale length 3.00–3.56 width, 0.42–0.53CL.

Rostral plate subpyriform with slender anterior spine; about as wide long; widest basally; anterior lateral margins sinuous; dorsum smooth; ventral surface with low carina, unarmed.

Carapace anterolateral angles broadly rounded.

Raptorial claw dactylus with 12–17 (usually 14 or 15) teeth, outer margin broadly curved, with shallow proximal notch. Carpus dorsal margin terminating in short spine tooth, directed ventrally. Propodus with 3 proximal movable spines; inferodorsal angle blunt, rounded, approximating a right angle; length usually shorter than carapace, PI 98–109 (male), 95–109 (females). Ischium about half merus length.

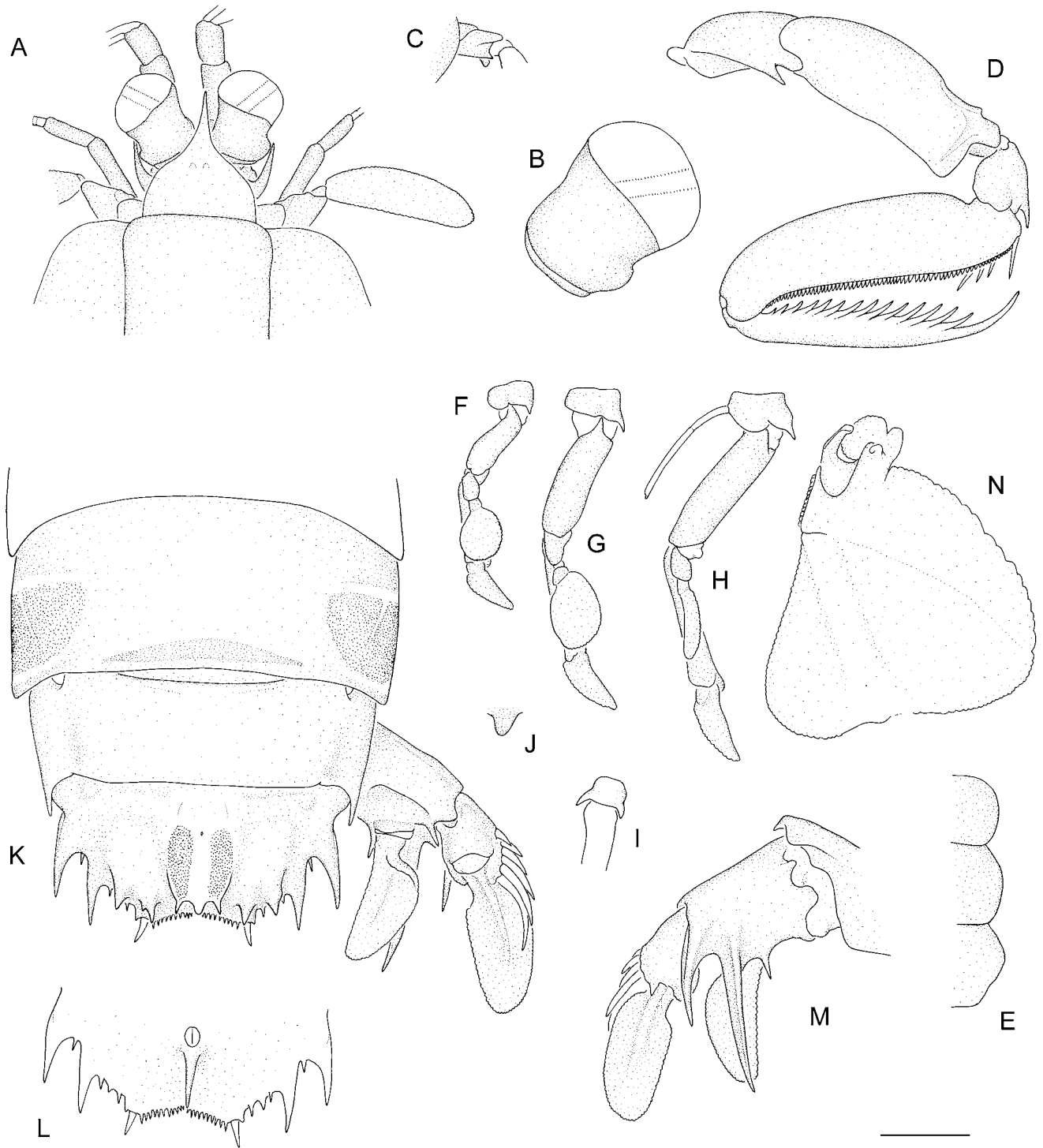


Figure 35. *Pariliacantha georgeorum* gen. et sp. nov., male holotype, TL 48 mm, Plimmerton (NIWA 68024). A, anterior cephalothorax; B, right eye; C, right antennal protopod, lateral view; D, right raptorial claw; E, TS6-8, right dorsal view; F-H, right pereopods 1-3, posterior view; I, right pereopod 2 basal segment, lateral view; J, TS8 sternal keel, right lateral view; K, AS4-6, telson and right uropod, dorsal view; L, telson, ventral view; M, right uropod, ventral view; N, right pleopod 1 endopod, anterior view. Scale A, C-I, K-M = 2.5 mm; B, J, N = 1.25 mm.

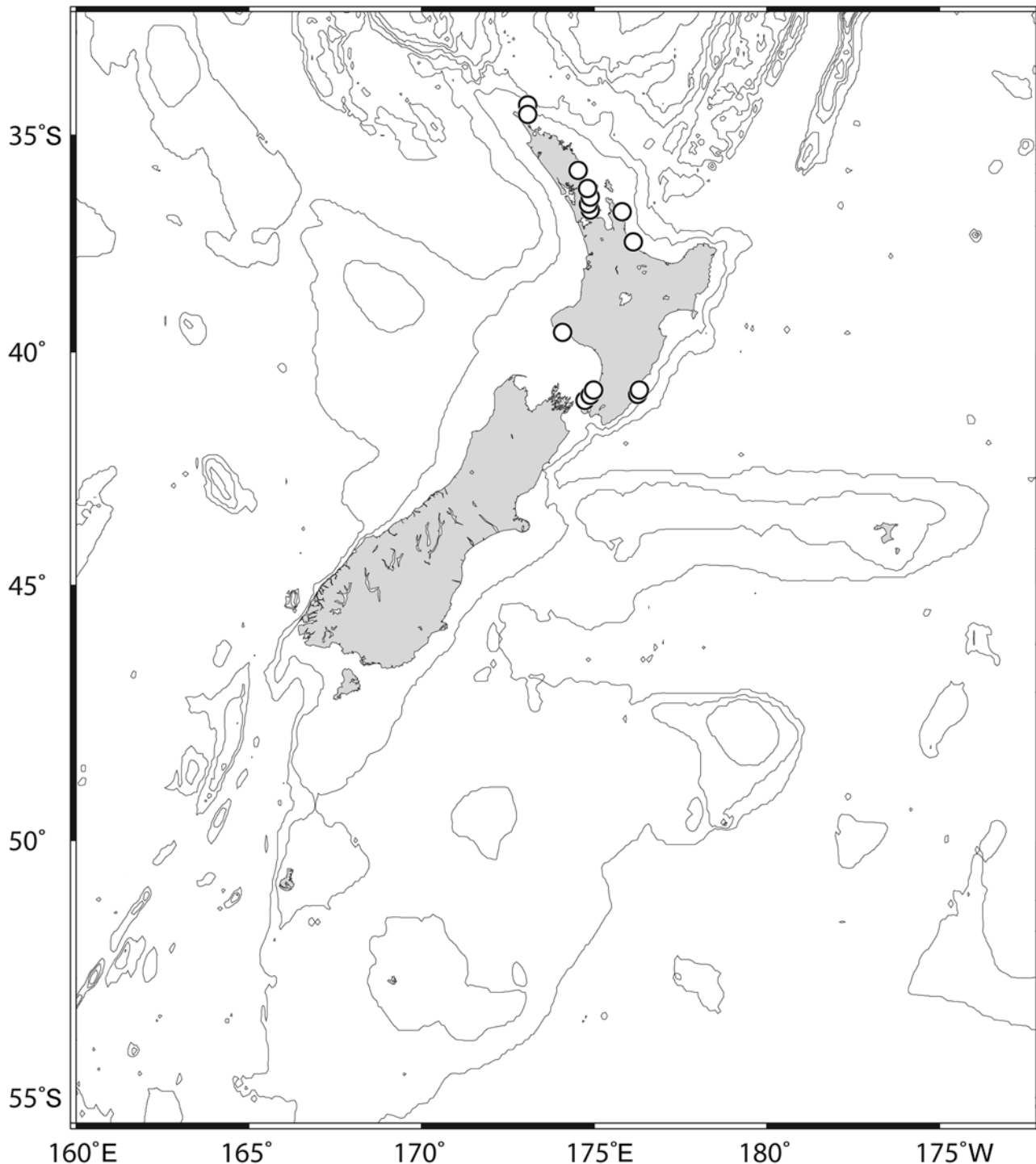


Figure 36. New Zealand distribution of *Pariliacantha georgeorum* gen. et sp. nov.

Mandibular palp 3-segmented in adults. Maxillipeds 1–5 with epipod. Maxilliped 5 basal segment without ventrally directed spine.

Pereopods 1–3 basal segment with anterior and posterior spine on outer margin; inner margin unarmed. Pereopod 1 endopod distal segment subcircular. Pereopod 2 endopod distal segment ovate. Pereopod 3 endopod distal segment slender, elongate.

Male pleopod 1 endopod with distinct lateral lobe on distal 'endite'. Hook process short, squat, distinctly shorter than tube process.

TS5 lateral process obsolete, lacking ventrally directed spine. TS6–8 lateral process broadly rounded. TS8 sternal keel rounded.

AS1–5 smooth; posterior margin unarmed; postero-lateral corners angular, unarmed. AS6 smooth, lacking

carinae; posterolateral spine prominent, elongated; with short spine and blunt, obtuse projection anterior to uropodal articulation; sternum posterior margin unarmed, slightly concave.

Telson thick, about twice as wide as long; submedian teeth slender, curved; with 7–12 spiniform submedian denticles; with 4 acute ‘intermediate’ denticles, second and fourth from midline more slender than first and third; lateral denticle spiniform. Posterodorsal surface with broad, trispinous median elevation, flanked by two prominent spines, occasionally secondarily bifid. Median elevation flat, margins converging posteriorly; median tooth blunt; slender lateral spines. Post-anal spine prominent, reaching posteriorly beyond midpoint between anal pore and posterior margin of telson.

Uropodal protopod terminal spines slender, ventrally carinate, outer spine about half length of inner spine; with slender ventral spine anterior to endopod articulation. Uropodal exopod proximal segment with low, round, distal lobe on inner margin and slender distal spine; outer margin with 5 or 6 movable spines, distalmost slightly exceeding midlength of distal segment. Exopod distal segment longer than proximal segment. Endopod length 2.11–3.07 times width.

COLOUR IN LIFE. (Cover and Frontispiece 1D) Overall pale gray-brown with dark brown transverse bands. AS1 and 5 with black post-erolateral ‘eye-spot’. Posterior margin of AS5–6 with dark brown transverse line. Telson with posteromedian pair of elongate, black spots separated by whitish or pale yellow line. Antennules, antennae, raptorial claw, pereopods and uropods with scattered brown chromatophores.

MEASUREMENTS. Male ($n = 11$) TL 27–71 mm, female ($n = 11$) TL 21–81 mm. Other measurements of holotype: CL 8.9 mm, cornea width 1.9 mm, antennular peduncle length 4.7 mm, antennal scale length 4.3 mm, raptorial claw propodus length 8.7 mm.

ETYMOLOGY. Named *georgeorum*, after my good friends Owain and Angharad George, who helped collect some of the type material.

HABITAT. *Pariliacantha georgeorum* gen. et sp. nov. Burrows on exposed or semi-exposed clean to muddy fine-sand beaches from the lowest tide level to about 50 m depth. Burrows of *P. georgeorum* are usually found at or below the lowest spring-tide level, in contrast to *Heterosquilla tricarinata* and the decapod *Callinassa filholi* (A. Milne-Edwards), whose burrows can also be found higher up in the intertidal zone. At Greater Omaha Bay, *P. georgeorum* occupied burrows in clean sand at a density of at least 0.5 individuals/m² (R. Taylor, pers. com.). During the course of this study,

at Plimmerton, near Wellington, *P. georgeorum* could sometimes be found at densities of 2 individuals/m², but the distribution along the shoreline was highly uneven, with the species absent in some parts of the beach that appeared to be suitable habitat. Burrows of *P. georgeorum* appear to have a single entrance with an initial vertical shaft of three to four body lengths after which the burrow may change direction. Morton & Miller (1968) reported burrows of *P. georgeorum* (misidentified as *Squilla armata*) to a depth of about 1 m. All specimens were found singly, rather than in pairs.

Pariliacantha georgeorum was sympatric with *Heterosquilla laevis* at Kawau Bay and *Heterosquilla tricarinata* at Deliverance Cove, Castlepoint.

REMARKS. *Pariliacantha georgeorum* gen. et sp. nov. is relatively common around North Island, New Zealand, but has not been recognised as new to science until now. Morton & Miller (1968) noted the presence of *P. georgeorum* from sand beaches near Auckland, albeit misidentified as *Squilla armata* (= *Pterygosquilla schizodontia*).

Chilton’s (1911a) tentative record of *Lysiosquilla brazieri* (= *Acaenosquilla brazieri*) from Otaki, the only published record of the species from New Zealand, is almost certainly based on *P. georgeorum*. Unfortunately, Chilton’s (1911a) account is brief and his material was in poor condition, apparently now lost (pers. com., S. Black, Whanganui Regional Museum). His material, collected from numerous specimens washed ashore after a storm at Otaki, is fully consistent with the intertidal or shallow subtidal habitat of *P. georgeorum*. In contrast, *Acaenosquilla brazieri* is known only from depths of 36 m or greater (Ahyong 2001). Moreover, Otaki is well within the range of *P. georgeorum* and only about 40 km north of the type locality. *Pariliacantha georgeorum* is similar to *A. brazieri* and *A. latifrons* in telson structure and colour pattern but differs significantly by bearing many more teeth on the dactylus of the raptorial claw (12–16 versus 6–8), in having a narrower cornea and narrower rostral plate with a long rostral spine, and an outer distal spine on the ischium of the raptorial claw.

Morphological variation is slight, the most significant being in the number of teeth on the dactylus of the raptorial claw, ranging from 12–17, but most frequently 14 or 15. The propodus of the raptorial claw is usually slightly shorter than the carapace, and does not appear to be sexually dimorphic, the PI of both sexes being similar. The pleopod 1 endopod of males is fully modified by TL 40–42 mm.

DISTRIBUTION. Presently known only the east and west coasts of North Island, New Zealand, as far south as Mana, near Porirua, in the west, and Castlepoint in the east.

SQUILLOIDEA Latreille, 1802

DIAGNOSIS. Cornea with 2 rows of hexagonal mid-band ommatidia. Maxillipeds 3–4 with propodi ovate, neither ribbed nor beaded ventrally. Body depressed, articulation compact. Raptorial claw with terminal ischiomerall articulation; dactylus not inflated basally. Telson with distinct median carina; submedian teeth with movable or fixed apices, other primary teeth with fixed apices. Uropodal protopod with at most two primary spines; articulation of exopod segments terminal.

COMPOSITION. Squillidae Latreille, 1802

REMARKS. Squilloidea includes the single family, Squillidae. Harpiosquillidae Manning, 1980 and the Cretaceous Ursquillidae Hof, 1998, have been recognised by some authors, but Ah Yong (2005) showed through cladistic analysis that both of these nominal families are deeply nested within Squillidae and thus synonymous. Although Ursquillidae exhibits multiple dorsal carinae on the telson, a relatively uncommon (but not unusual) feature in squillids, the telson is subquadrate, prelateral lobes are present, and submedian teeth are fixed. From a purely phenetic perspective, the aforementioned features of *Ursquilla* would ally it to genera such as *Squilla*, *Erugosquilla* and *Oratosquilla*. Cladistic analysis, however, shows that the subquadrate telson, presence of prelateral lobes fixed submedian teeth are derived features. *Squilla*, *Oratosquilla* and allies, including *Ursquilla*, form a clade that is deeply nested within the Squillidae (Ah Yong 2005). The telson of *Ursquilla* exhibits neither phylogenetically nor taxonomically unusual features. *Ursquilla* cannot be justifiably placed in a separate family from Squillidae and thus Ursquillidae is not recognised as valid. Likewise, Harpiosquillidae is also deeply nested among other squillids and although it possesses several distinct autapomorphies, such as the excavated posterolateral margin of the carapace and spinose occlusal margin of the propodus of the raptorial claw, it is nevertheless closely related to the 'core' group of squillid genera such as *Squilla* and *Oratosquilla* (Ah Yong 2005).

Ah Yong & Harling (2000) established the phylogenetic position of the Squilloidea as sister to Eurysquilloidea + Parasquilloidea. Schram & Müller (2004) proposed merging squilloids with eurysquilloids and parasquilloids into a single expanded superfamily, Squilloidea. The squilloids, eurysquilloids and parasquilloids, however, are each morphologically and ecologically distinct (Ah Yong 2005; Ah Yong *et al.* 2008). Moreover, Squilloidea sensu stricto uniquely share the presence of four or more (rather than two or fewer) intermediate telson denticles and the alima larva (rather than pseudozoea). The flattened body form of eurysquilloids is morphologically convergent

with that of lysiosquilloids and the subcylindrical gonodactyloid-body form of parasquilloids is probably plesiomorphic; neither is similar to the depressed squilloid body form. Schram & Müller (2004) united the squilloids, eurysquilloids and parasquilloids into Squilloidea sensu lato on the basis of the double row of mid-band ommatidia in the cornea, proposed as an 'underlying' synapomorphy. Parasquilloids, however, have two or three mid-band ommatidial rows and eurysquilloids have two or six (but almost always six). Only squilloids (sensu stricto) consistently have two rows of mid-band ommatidia. Although a two-row ommatidial mid-band may prove to be part of the 'ground-pattern' of the clade containing Eurysquilloidea + Parasquilloidea + Squilloidea sensu stricto, it is not an effective synapomorphy that can diagnose Squilloidea sensu Schram & Müller (2004). Other suggested synapomorphies, such as the absence of anterior submedian carinae on the telson are not reliable: they are absent in most eurysquilloids, present or absent in parasquilloids, and present or absent in squilloids. Thus, no single consistent (or near consistent) synapomorphy unites Eurysquilloidea + Parasquilloidea + Squilloidea because stem characters that support this clade, although retained as plesiomorphies in the 'basal' or near 'basal' clades within each superfamily are further modified or lost further 'up-tree'. Schram & Müller (2004) certainly provide thoughtful character argumentation and rightly recognise the unity of the Eurysquilloidea + Parasquilloidea + Squilloidea clade, but translating this into a workable classification is more difficult. Unfortunately, their revised, enlarged concept of Squilloidea is not taxonomically effective because it can neither be diagnosed by consistent synapomorphies nor by combinations of plesiomorphies. As a result, a better alternative is to retain three independent superfamilies, Eurysquilloidea, Parasquilloidea and Squilloidea sensu stricto; this has the dual advantage of retaining taxa that are both monophyletic and that have consistent character support enabling effective diagnosis.

SQUILLIDAE Latreille, 1802

Squillares Latreille, 1802: 36.

Squillinae. – Giesbrecht, 1910: 148.

Squillidae. – Manning, 1968c: 109, 113.

Harpiosquillidae Manning, 1980: 367, 369.

Ursquillidae Hof, 1998: 92–93.

DIAGNOSIS. As for superfamily.

COMPOSITION. *Alima* Leach, 1817; *Alimopsoides* Moosa, 1991; *Alimopsis* Manning, 1977b; *Anchisquilla* Manning, 1968c; *Anchisquilloides* Manning, 1977b; *Anchisquillopsis* Moosa, 1986; *Areosquilla* Manning, 1976; *Belosquilla*

Ahyong, 2001; *Busquilla* Manning, 1978b; *Carinosquilla* Manning, 1968c; *Clorida* Eydoux & Souleyet, 1842; *Cloridina* Manning, 1995; *Cloridopsis* Manning, 1968c; *Crenatosquilla* Manning, 1984b; *Dictyosquilla* Manning, 1968c; *Distosquilla* Manning, 1977b; *Erugosquilla* Manning, 1995; *Fallosquilla* Manning, 1995; *Fennerosquilla* Manning & Camp, 1983; *Gibbesia* Manning & Heard, 1997; *Harpiosquilla* Holthuis, 1964; *Humesosquilla* Manning & Camp, 2001; *Kaisquilla* Ahyong, 2002b; *Kempella* Low & Ahyong, 2010; *Leptosquilla* Miers, 1880; *Lenisquilla* Manning, 1977b; *Levisquilla* Manning, 1977b; *Lophosquilla* Manning, 1968c; *Meiosquilla* Manning, 1968c; *Miyakea* Manning, 1995; *Natosquilla* Manning, 1978c; *Neclorida* Manning, 1995; *Neoanchisquilla* Moosa, 1991; *Oratosquilla* Manning, 1968c; *Oratosquillina* Manning, 1995; *Paralimopsis* Moosa, 1991; *Parvosquilla* Manning, 1973; *Pontiosquilla* Manning, 1995; *Pterygosquilla* Hilgendorf, 1890; *Quollastria* Ahyong, 2001; *Rissoides* Manning & Lewinsohn, 1982; *Schmittius* Manning, 1972; *Squilla* Fabricius, 1787; *Squilloides* Manning, 1968c; *Tuleariosquilla* Manning, 1978b; *Visaya* Ahyong, 2004.

REMARKS. Squillidae is the most diverse stomatopod family, currently containing 46 genera (Ahyong 2001, 2002b, 2004). *Kempina* Manning, 1978c, recently shown to be preoccupied, was replaced by *Kempella* Low & Ahyong, 2010. Three squillid genera are represented in New Zealand.

KEY TO GENERA OF SQUILLIDAE FROM NEW ZEALAND

1. Lateral processes of TS5–7 bilobed .. ***Oratosquilla***
 - Lateral processes of TS5–7 undivided, not bilobed2
2. Rostral plate with pointed apex and median carina. Ocular scales rounded. Lateral process of TS5 recurved anteriorly ***Anchisquilloides***
 - Rostral plate with rounded apex; median carina absent. Ocular scales spiniform. Lateral process of TS5 directed laterally ***Pterygosquilla***

***Anchisquilloides* Manning, 1977**

Anchisquilloides Manning, 1977: 421. [Type species: *Squilla mcneilli* Stephenson, 1953b, by original designation and monotypy. Gender: masculine].

DIAGNOSIS. Eye with cornea strongly bilobed, width less than 0.3CL. Antennular somite dorsal processes with short slender apices, directed anterolaterally. Carapace with anterolateral spines; with median, reflected marginal, and reduced lateral carinae; median posterior margin straight or slightly concave; posterolateral margin rounded. Raptorial claw dactylus with 5 or 6

teeth; carpus with short undivided dorsal carina and distal tooth; merus without outer inferodistal spine. Mandibular palp present. Maxillipeds 1–4 with epipod. Pleopod 1 endopod in adult males with posterior ‘endite’; hook process blunt distally. TS6–8 with distinct submedian and intermediate carinae. TS5–7 lateral process single. AS1–5 with median, submedian, intermediate, lateral and marginal carinae. AS6 with submedian, intermediate, lateral carinae. Telson triangular; dorsolateral surface with curved rows of shallow pits and low submedian swelling; submedian teeth with movable apices; prelateral lobe present; ventrolateral stridulatory carinae present. Uropodal protopod inner margin crenulate.

COMPOSITION. *A. mcneilli* Stephenson, 1953; *A. michelae* Moosa, 1986.

REMARKS. *Anchisquilloides* Manning, 1977, forms a clade with *Anchisquillopsis* Moosa, 1986, and *Kaisquilla* Ahyong, 2002b, sharing the combination of a low obtuse swelling on the dorsal submedian surface of the telson, a distally blunt hook process on the endopod of male pleopod 1, a triangular telson with movable submedian teeth and ventrolateral stridulatory carinae (Ahyong 2005). Species of *Anchisquilloides* have an anti-tropical western Pacific distribution, with *A. michelae* occurring in the Philippines and *A. mcneilli* in New Zealand and eastern Australia.

KEY TO SPECIES OF ANCHISQUILLOIDES

1. TS5 lateral process directed anteriorly or slightly inclined ventrally. Lobe on outer margin of inner spine of uropodal protopod distinctly wider than adjacent spine..... ***A. mcneilli***
 - TS5 lateral process directed almost ventrally. Lobe on outer margin of inner spine of uropodal protopod narrower than or as wide as adjacent spine ***A. michelae***

***Anchisquilloides mcneilli* (Stephenson, 1953)** (Figs 37, 38)

Squilla armata. – Whitelegge, 1900: 199.
Squilla mcneilli Stephenson, 1953: 213–218, fig. 4 [type locality: off coast between Merimbula and Tathra, New South Wales, Australia].
Anchisquilloides mcneilli. – Manning, 1977b: 421. – Ahyong, 2001: 199–200, fig. 97.

TYPE MATERIAL. *Holotype*: AM P8808, female (TL 90 mm), off coast between Merimbula and Tathra, New South Wales, Australia, 36°49’S, 150°05’E, 73 m, coll. M. Ward, Mar 1927.



OTHER MATERIAL EXAMINED. *Northland*: NIWA 73406, 1 female (TL 66 mm), Cape Reinga, 34°26.96–27.05'S, 172°20.41–20.61'E, 120–117 m, beam trawl, TAN1105/63, 30 Mar 2011; NMNZ, 1 male (TL 45 mm), 1 female (TL 32 mm), North Cape, 34°22'S, 173°00'E, 119 m, 21 Apr 1966; NIWA 56834, 1 female (TL 54 mm), north of Cavalli Islands, 34°24.12–23.83'S, 174°08.28–08.17'E, 145–149 m, TAN0906/164, 14 Jul 2009; NIWA 57161, 1 male (TL 60 mm), off North Cape, 34°26.38–26.23'S, 173°07.77–07.41'E, 115–110 m, dredge, TAN0906/181, 15 Jan 2009; NMNZ Cr9381, 1 male (TL 47 mm), north-east of Cape Karikari, 34°42.59'S, 173°31.20'E, 163–168 m, dredge, NZOI O613, RV *Tangaroa*, 27 Jan 1981; NIWA 56320, 1 female (TL 67 mm), north-east of Cape Karikari, 34°42.42–42.60'S, 173°18.57–18.54'E, 77–72 m, TAN0906/143, 13 Jul 2009; NIWA 55873, 1 male (TL 39 mm), north-east of Cape Karikari, 34°43.74–43.89'S, 173°40.83–40.05'E, 201–191 m, TAN0906/116, 10 Jul 2009; NMNZ, 1 male (TL 40 mm), 12 miles off Flat Point, Doubtless Bay, 34°45'S, 173°39'S, 150–159 m, 16 Jun 1963; NIWA 23966, 1 female (TL 32 mm), west of Ninety Mile Beach, 34°52.50'S, 172°34.39'E, 155–163 m, NZOI stn P64, 7 Feb 1977; NIWA 55441, 1 female (TL 39 mm), 34°52.74–52.59'S, 173°55.02–54.75'E, 115–112 m, TAN0906/81, 8 Jul 2009; NIWA 55377, 1 female (TL 59 mm), 34°54.45–54.45'S, 174°00.06'S–173°59.67'E, 149–143 m, TAN0906/78, 8 Jul 2009; NIWA 57323, 1 female (TL 66 mm), north of Cavalli Islands, 34°57.39–57.51'S, 174°05.25–05.65'E, 174–147 m, TAN0906/232, 19 Jul 2009; NIWA 57581, 4 males (TL 46–55 mm), north of Cavalli Islands, 35°04.50–04.89'S, 174°01.09–01.23'E, 67–72 m, TAN0906/245, 19 Jul 2009; NIWA 55090, 1 male (TL 53 mm), 2 females (TL 45–50 mm), east of Cavalli Islands, 35°06.07–06.09'S, 174°17.10–17.35'E, 125–126 m, TAN0906/52, 7 Jul 2009; NIWA 55032, 1 male (TL 45 mm), 35°12.87–12.54'S, 174°29.13–29.07'E, 136–144 m, TAN0906/43, 6 Jul 2009; NIWA 55026, 1 female (TL 46 mm, photo), 35°12.87–12.54'S, 174°29.13–29.07'E, 136–144 m, TAN0906/43, 6 Jul 2009; NIWA 55764, 1 raptorial claw, off Northland, 35°22.00'S, 174°51.49'E, 260–263 m, F906, 10 Oct 1968; NMNZ, 1 female (TL 62 mm), north-east of Whangarei, 35°29'S, 175°02'E, 256–269 m, beam trawl, BS366, RV *Acheron*, 14 Feb 1974; NMNZ Cr9365, 1 male (TL 80 mm), south-east of Poor Knights Islands, 35°40.60'S, 174°51.25'E, 126–145 m, J06/34/81, RV *James Cook*, coll. G.S. Hardy, 20 Apr 1981; NIWA 23947, 3 males (TL 31–40 mm), 4 females (TL 30–34 mm), 35°47.80–47.20'S, 175°36.6–39.19'E, 257–287 m, NZOI stn I6, 3 May 1975; NIWA 23944, 1 female (TL 38 mm), 35°47.99–45.59'S, 174°50.20–52.30'E, 122–129 m, NZOI stn I2, 2 May 1975; NIWA 23945, 11 males (TL 29–76 mm), 21 females (TL 29–84 mm), east of Whangarei, 35°47.80–49.3'S, 175°13.00–17.39'E, 151–153 m, NZOI Stn I4, 2 May 1975.

Auckland & Coromandel: NIWA 23951, 1 male (TL 37 mm), 1 female (TL 51 mm), north-west of Little Barrier

Island, 35°58.69–56.20'S, 175°25.00–23.59'E, 114–132 m, NZOI stn I51, 10 May 1975; NIWA 23934, 1 male (TL 63 mm), off Great Barrier Island, 36°00.00'S, 175°45.79'E, 188 m, NZOI Stn C783, 21 Feb 1962; USNM 1156987, 1 male (TL 88 mm), off Alderman Islands, 36°00–02.41'S, 175°55.02–58.84'E, 237–223 m, KAH9401/4, RV *Kaharoa*, 4 Jan 1994; NMNZ Cr20165, 3 males (TL 60–83 mm), Craddock Channel, between Little Barrier Island and Great Barrier Island, 36°11'S, 175°12'E, 29 Jun 1965; NIWA 23954, 4 males (TL 47–78 mm), 6 females (TL 40–81 mm), east of Great Barrier Island, 36°12.00–12.59'S, 176°00.59'E–175°55.39'E, 193–169 m, NZOI Stn I65, 12 May 1975; NMNZ Cr9347, 1 female (TL 80 mm), Auckland district; NMNZ Cr18649, 1 male (TL 100 mm), off Kaipara Bar, 36°30'S, 174°00'E, 183 m, prawn trawl, FV *Sandra*, NZ Marine Department, 1955; NMNZ Cr595, 1 male (TL 76 mm), off Kaipara Bar, 36°30'S, 174°00'E, prawn trawl, FV *Sandra*, NZ Marine Dept, 1955; NIWA 23985, 1 female (TL 96 mm), Mercury Islands, 36°38.77–41.61'S, 176°10.96–12.21'E, 288–298 m, NZOI Stn Z9022, KAH9801/38, 24 Jan 1998; USNM 1156988, 1 female (TL 76 mm), Mercury Islands, 36°55.06–52.06'S, 176°16.42–16.39'E, 349–352 m, from scampi trawl, KAH 9604/10, coll. R. Taylor, 9 April 1996; NMNZ Cr9343, 1 male (TL 79 mm), between Alderman Islands and Red Mercury Island, 183 m, haul 7, coll. R. Pike, 26 Sep 1962; USNM 1156988, 1 male (TL 100 mm), Alderman Islands, 36°59.23'–37°02.05'S, 176°14.38–13.12'E. 269–275 m, scampi trawl, KAH9604/13, coll. R. Taylor, 10 April 1996; NMNZ Cr9346, 1 female (TL 71 mm), south of Manukau Heads, 37°00'S, 174°30'E, 55 m, from dogfish, 2 May 1954; NMNZ, 1 female (broken; CL 16.7 mm), Slipper Island, 37°S, 176°E, 55 m, stn N4, coll. B.L. Godfriaux, 17 Sep 1969; NMNZ, 1 male (TL 80 mm), Slipper Island, 37°S, 176°E, 37 m, sand, anchor dredge, coll. B.L. Godfriaux, 8 Apr 1970; NMNZ, 1 male (TL 57 mm), 1 female (TL 77 mm), south-east of Alderman Islands, 37°00.49'S–36°59.40'S, 176°12.70–13.09'E, 202–207 m, mud, NZOI Stn O595, RV *Tangaroa*, 24 Jan 1981.

Bay of Plenty: NMNZ Cr9370, 1 male (TL 70 mm), 1 female (TL 68 mm), Motiti Island, 37°39'S, 176°25'E, 55 m, sand, coll. B.L. Godfriaux, 10 Mar 1969; NMNZ, 1 male (broken, CL 18.2 mm), Motiti Island, 37°39'S, 176°25'E, 70 m, silty sand, anchor dredge, coll. B.L. Godfriaux, 4 Nov 1969; NMNZ, 1 female (broken, CL 14.6 mm), Motiti Island, 37°39'S, 176°25'E, 70 m, silty sand, Agassiz trawl, stn I36, coll. B.L. Godfriaux, 4 Nov 1969; NMNZ, 1 male (TL 73 mm), Motiti Island, 37°39'S, 176°25'E, 70 m, Agassiz trawl, stn I16, coll. B.L. Godfriaux, 25 May 1969; NMNZ, 4 females (TL 79–106 mm), off Motiti Island, 403 m, coll. T. Bonnevie, Mar 1972; NMNZ Cr639, 2 females (TL 76–80 mm), Bay of Plenty, 237 m, trawl, NZ Marine Department, 7 Jun 1955; NMNZ Cr641, 1 male (TL 80 mm), Bay of Plenty, 110 m, trawled, 10 Jul 1955; NMNZ Cr9382, 2 females (TL ca. 40–61 mm), Bay of Plenty, coll. B.L. Godfriaux;

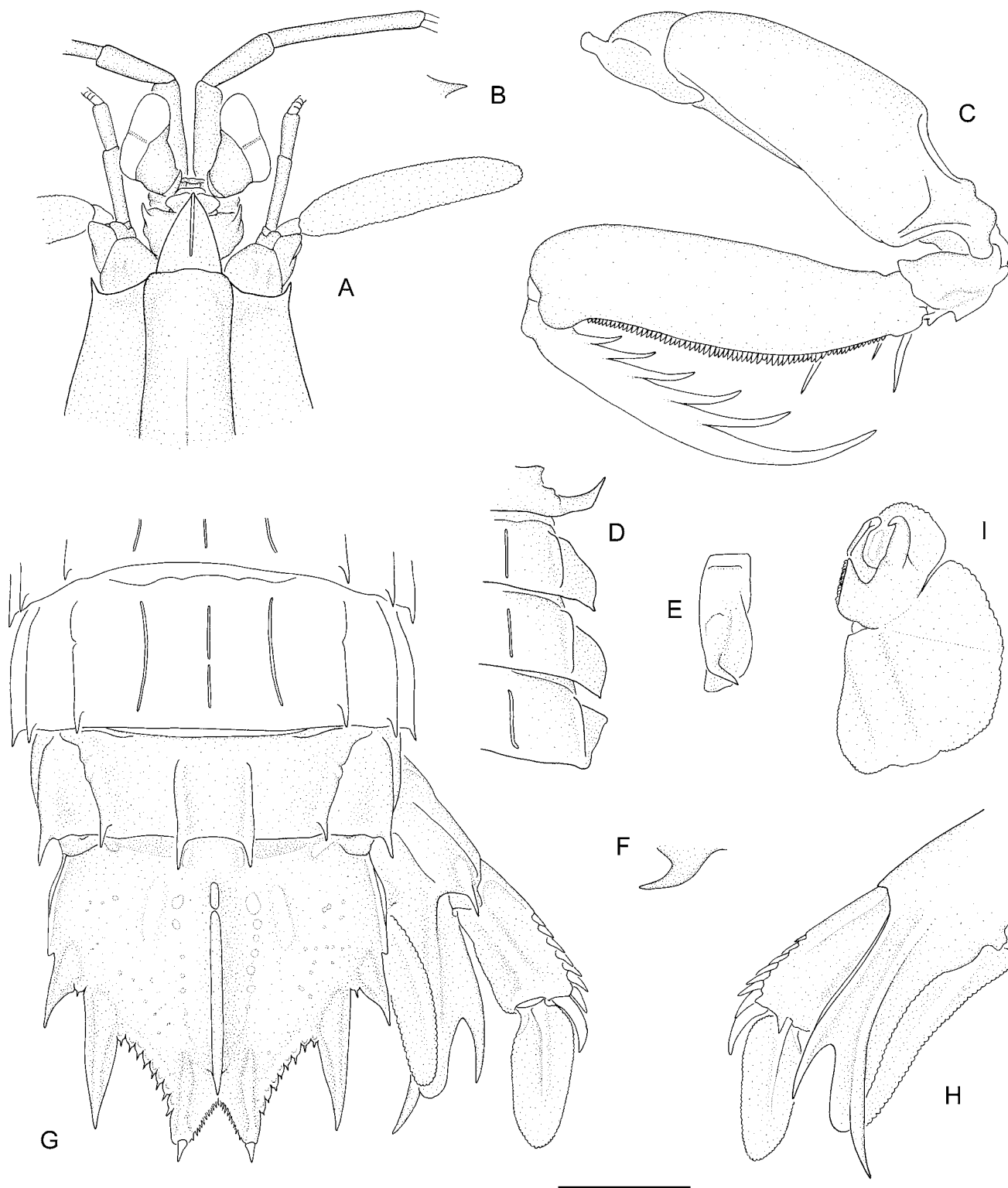


Figure 37. *Anchisquilloides mcneilli* (Stephenson, 1953), male, TL 73 mm, Motiti Island, Bay of Plenty (NMNZ). A, anterior cephalothorax; B, right dorsal process of antennular somite, lateral view; C, right raptorial claw; D, TS6-8, right dorsal view; E, TS5, right lateral view; F, TS8 sternal keel, right lateral view; G, AS4-6, telson and right uropod, dorsal view; H, right uropod, ventral view; I, right pleopod 1 endopod, anterior view. Scale A, C-E, G-H = 5.0 mm; B, F, I = 2.5 mm.

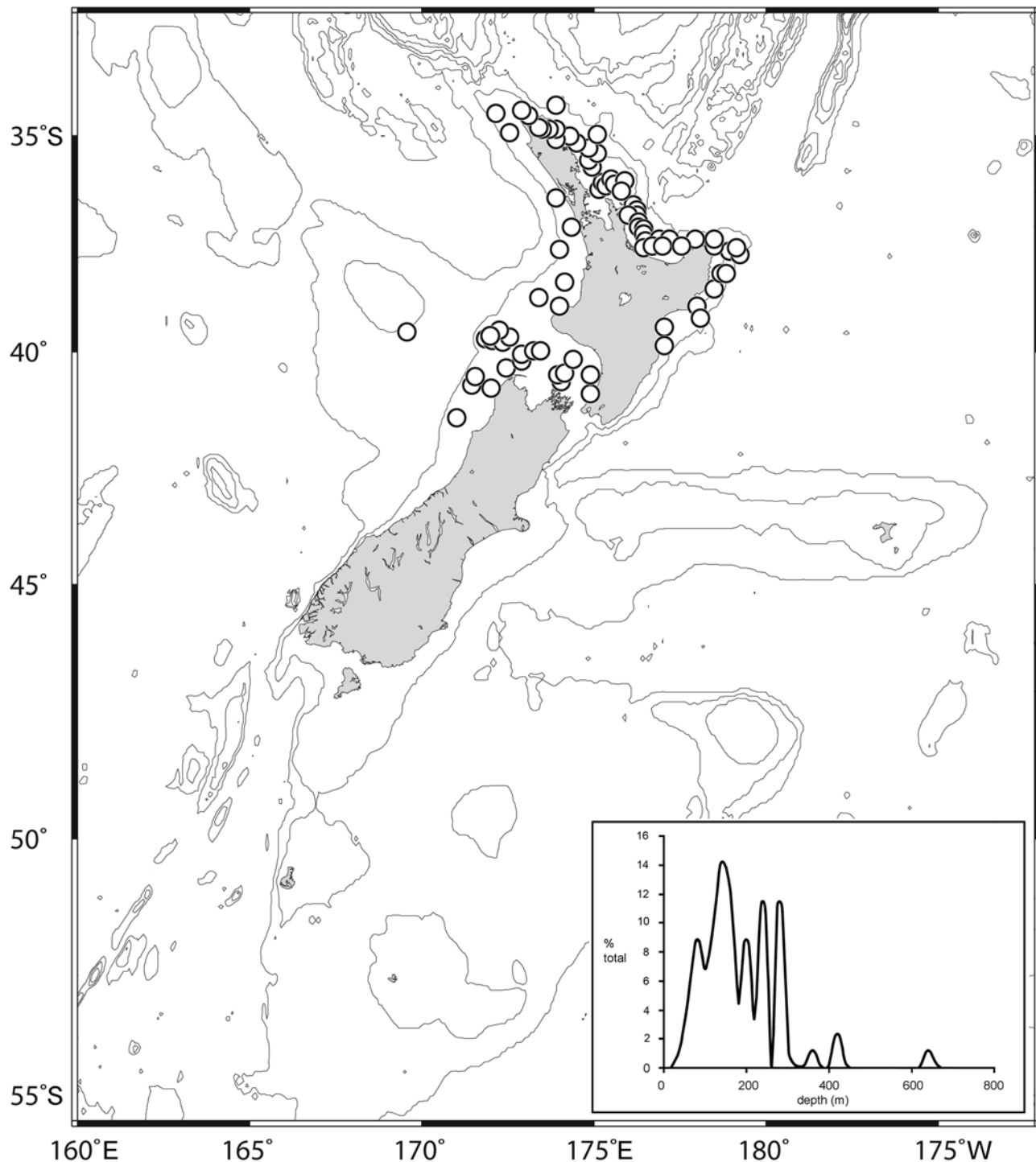


Figure 38. New Zealand distribution of *Anchisquilloides mcneilli* (Stephenson, 1953).

NMNZ Cr9367, 6 males (TL 48–100 mm), 1 female (TL 48 mm), about 11 km north-west of Mayor Island, 37°11.5–10.3'S, 176°10.0–11.5'E, 198–273 m, mud, NZOI stn R108, RV *Tangaroa*, 22 Jan 1979; NMNZ Cr12522, 1 male (TL 90 mm), off Mayor Island, 37°14'S, 176°20'E, 402 m, green mud; NIWA 23935, 1 male (broken, CL 19.6 mm), 37°20.09'S, 176°19.00'E, 201–177 m, NZOI stn C798, 23 Feb 1962; NMNZ, 1 female (TL 66 mm),

ca. 9 km south-east of Mayor Island, 37°21.90'S, 176°20.89'E, 203–248 m, mud, NZOI R101, BS743, RV *Tangaroa*, 22 Jan 1979; NIWA 13868, 1 male (broken; CL 12.3 mm), Tumokemoke Seamount, 37°27.69–27.87'S, 176°54.81–54.85'E, 294–247 m, TAN0413/170, 16 Nov 2004; NIWA 13866, 1 male (TL 66 mm), Tumokemoke Seamount, 37°28.00–28.16'S, 176°54.91–54.87'E, 225–210 m, TAN0413/164, 15 Nov 2004; NIWA

13865, 1 male (TL 48 mm), Tumokemoke Seamount, 37°28.02–28.13'S, 176°55.13–54.98'E, 232–218 m, TAN0413/161, 15 Nov 2004; NIWA 13867, 1 female (TL 47 mm), 37°28.19–28.33'S, 177°13.20–12.94'E, 200–175 m, TAN0413/74, 12 Nov 2004; NIWA 4122, 1 female (TL 60 mm), 37°28.21–28.09'S, 177°07.03–06.46'E, 220–320 m, KAH9907/49; NMNZ, 1 male (TL 41 mm), ca. 30 km north of Motuhora Island, 37°35.09–37.59'S, 176°59.50–59.59'E, 248–213 m, mud, NZOI R80, BS722, RV *Tangaroa*, 20 Jan 1979; NMNZ, 1 male (TL 44 mm), ca. 28 km north of Motuhora Island, 37°35.89–37.60'S, 176°59.50–59.80'E, 139–179 m, mud, BS723 (NZOI R81), RV *Tangaroa*, 20 Jan 1979; NMNZ, 1 male (TL 100 mm), 37°36.69–37.93'S, 176°39.33–42.79'E, 226–235 m, KAH9301/14, 3 Jan 1993; NMNZ Cr12357, 2 males (TL 71–87 mm), east of Motiti Island and north of Plate Island, 37°37'S, 176°34'E, 55–73 m, stn L-14, RV *Ikatere*, coll. C. Voorich, 23 Sep 1968; NMNZ, 1 male (TL 100 mm), south-east of White Island, 37°37.03–36.92'S, 177°21.24–25.02'E, 227–245 m, scampi trawl, KAH 9301/62, RV *Kaharoa*, 19 Jan 1993; NMNZ Cr9363, 1 female (TL 90 mm), Plate Island, 37°40'S, 176°34'E, 183 m, sandy-mud, triangular dredge, coll. B. L. Godfriaux, 10 Mar 1969; NMNZ, 1 female (broken, CL 16.2 mm), Plate Island, 37°40'S, 176°34'E, 146 m, Agassiz trawl, stn I65, coll. B.L. Godfriaux, 9 Jun 1970; NMNZ Cr6096, 1 male (TL 75 mm), Bay of Plenty, 37°35.3'S, 176°24.2'E, 165 m, stn J16/28/84, RV *James Cook*, 22 Sep 1984; NMNZ, 1 female (TL mm), ca. 9 km north-north-west of Orete Point, Cape Runaway, 37°32.20–32.50'S, 177°52.00–51.79'E, 144–137 m, mud, NZOI R124, BS766, RV *Tangaroa*, 25 Jan 1979.

Gisborne: NIWA 75581, 1 female (TL 66 mm), northern Ranfurly Bank, 37°28.14–28.23'S, 178°51.77–51.79'E, 117–106 m, epibenthic sled, TAN1108/253, 1 Jun 2011; NMNZ, 1 male (TL 78 mm), off Matakaoa Point, Hicks Bay, 37°30.49'S, 178°19.90'E, 134–159 m, mud, NZOI R44, BS686, RV *Tangaroa*, 17 Jan 1979; NMNZ, 1 male (TL 60 mm), 1 female (TL 60 mm), off Matakaoa Point, 37°32.40'S, 178°19.90'E, 99–102 m, mud, NZOI R43, BS685, RV *Tangaroa*, 17 Jan 1979; NMNZ, 4 males (TL 55–70 mm), off Matakaoa Point, 37°32.89'S, 178°19.00'E, 64–68 m, mud, NZOI R42, BS684, RV *Tangaroa*, 17 Jan 1979; NMNZ, 1 male (TL 33 mm), 3 miles north-east of Hick's Bay, 37°34'S, 178°20'E, 183–220 m, 4 Apr 1963; NMNZ, 1 female (TL 59 mm), 37°34.99–34.50'S, 178°51.60–53.50'E, Ranfurly Bank, East Cape, 39–50 m, hard substrate, NZOI R38, BS680, RV *Tangaroa*, 17 Jan 1979; USNM 138321, 1 male (TL 84 mm), 2 females (TL 55–77 mm), east of East Cape, 37°35–37'S, 178°46–47'E, 128–146 m, blake trawl, 28 May 1966; NIWA 75299, 9 males (TL 30–91 mm), 22 females (TL 33–92 mm), Tokomaru Bay, 38°14.71–14.45'S, 178°41.65–41.72'E, 137–136 m, beam trawl, TAN1108/206, 30 May 2011; NMNZ Cr9366, 10 males (TL 44–67 mm), 3 females

(TL 45–67 mm), about 30 km east-north-east of Tolaga Bay, 38°15.2'S, 178°38.6'E, 139 m, mud, NZOI Stn R31, BS673, RV *Tangaroa*, 16 Jan 1979; NIWA 75519, 1 male (TL 61 mm), 3 females (TL 59–67 mm), central-southern Ranfurly Bank, 37°38.75–38.82'S, 178°56.66–56.93'E, 158–160 m, beam trawl, TAN1108/249, 1 Jun 2011; NIWA 75282, 1 male (TL 72 mm), 1 female (TL 83 mm), Ariel Bank, 38°41.32–41.29'S, 178°28.00–27.75'E, 240–175 m, beam trawl, TAN1108/203, 30 May 2011.

Hawkes Bay: NIWA 75130, 1 male (TL 53 mm), Cabbage Patch, Table Cape, 39°01.58–01.55'S, 178°10.99–0.59'E, 120–113 m, epibenthic sled, TAN1108/187, 29 May 2011; NMNZ, 3 males (TL 48–78 mm), 2 females (TL 66–70 mm), east of Portland Island, Mahia Peninsula, 39°18.70–21.70'S, 178°04.60–03.79'E, 127–134 m, mud, NZOI R131, BS773, RV *Tangaroa*, 27 Jan 1979; NMNZ, 1 male (TL 78 mm), 1 female (TL 75 mm), ca. 17 km east of Portland Island, Mahia Peninsula, 39°18.70–21.70'S, 178°04.60–03.79'E, 127–134 m, mud, NZOI R131, BS773, RV *Tangaroa*, 27 Jan 1979; NMNZ Cr9362, 1 male (TL 88 mm), off Napier, 39°30'S, 177°00'E, coll. A.G. Clark, Sep 1953; NMNZ Cr9344, 1 male (TL 63 mm), north-east of Cape Turnagain, 40°S, 177°E, 146 m, RV *James Cook*.

Waikato: NMNZ Cr9383, 1 male (TL 38 mm), between Manukau and Raglan Harbours, 37°32.50'S, 174°05.29'E, 231 m, NZOI O567, RV *Tangaroa*, 12 Jan 1981; NMNZ, 3 females (TL 48–53 mm), south-west of Kawhia Harbour, 38°21.49'S, 174°17.80'E, 83 m, NZOI O571 BS826, RV *Tangaroa*, 13 Jan 1981.

Taranaki: NMNZ, 1 male (TL 63 mm), 1 female (TL 21 mm), west-north-west of Cape Egmont, 38°48.79'S, 173°29.59'E, 146 m, sand, NZOI O534 BS791, RV *Tangaroa*, 9 Jan 1981; NMNZ Cr12523, 1 male (TL 83 mm), off New Plymouth, 39°S, 174°E, from scorpion fish stomach, Dept of Conservation, coll. Williams, Sep 2000; NMNZ Cr9345, 1 female (TL 71 mm), 48–64 km south of New Plymouth, 73 m, FV *Admiral*, coll. A. Dickinson, Aug 1957.

Challenger Plateau: NMNZ Cr9369, 2 males (TL 45–80 mm), 7 females (TL 40–77 mm), west of Cape Egmont, 39°29'S, 172°28'E, 132 m, J2/73/69; NMNZ Cr9384, 2 males (TL 83–86 mm), west of Cape Egmont, 39°30.00'S, 172°40.00'E, J07/37/80, RV *James Cook*, 7 Apr 1980; NIWA 23928, 2 males (TL 25–51 mm), 39°37.00'S, 171°58.20'E, 271 m, NZOI stn C166, 3 Sep 1959; NMNZ, 1 male (TL 60 mm), Challenger Plateau, 39°26'S, 169°36'E, 612–630 m, Granton trawl, J15/008/76, 23 Sep 1976; NIWA 33232, 1 female (TL 55 mm), east of Taranaki, 39°38.54–38.75'S, 172°08.86–08.78'E, 266–267 m, TAN0707/140, 7 Jun 2007; NIWA 33233, 2 females (TL 30 mm; 1 broken, CL12.5 mm), east of Taranaki, 39°38.54–38.75'S, 172°08.86–08.78'E, 266–267 m, TAN0707/140, 7 Jun 2007; NIWA 23929, 1 female (TL 72 mm), east of Taranaki, 39°40.00'S, 172°25.00'E,

234 m, NZOI stn C169, 3 Sep 1959; NIWA 4125, 1 male (broken; CL 18.3 mm), Egmont, 39°40.0'S, 172°00'E, 170 fathoms [273 m], C167, 3 RV *Viti*, Sep 1959.

Manawatu: NIWA 23932, 3 males (TL 18–22 mm), South Taranaki Bight, 39°49.99'S, 173°31.00'E, 95 m, NZOI stn C184, 6 Sep 1959; NIWA 23933, 2 males (TL 26–35 mm), South Taranaki Bight, 39°49.99'S, 173°18.00'E, 115 m, NZOI stn C185, 6 Sep 1959; NMNZ, 1 male (TL 81 mm), south of Egmont, 40°03.70–05.60'S, 172°55.48–58.70'E, 109–111 m, J19/25/78, 14 Dec 1978; NMNZ Cr9368, 5 males (47–76 mm), 10 females (TL 50–89 mm), about 29 km south of Waverley (Waitotara River mouth), 40°09.5'S, 174°36'E, 82 m, Stn 76488, BS488; NMNZ, 1 male (TL 48 mm), ca. 11 miles south-west of Manawatu River mouth, 40°33.5'S, 174°59.5'E, 86–88 m, RV *Acheron*, 2 Mar 1976.

Wellington: NMNZ, 1 male (TL 82 mm), Kapiti, 41°S, 175°E, from cod gut, coll. L.J. Paul, Mar 1966.

Tasman-Nelson: NIWA 55763, 1 female (broken; CL 5.3 mm), north-east of Cape Farewell, 40°00.00'S, 173°00.00'E, 117 m, B646, 22 Oct 1962; NIWA 23927, 1 male (TL 52 mm), 1 female (TL 30 mm), north of Cape Farewell, 40°16.00'S, 172°32.29'E, 126–127 m, NZOI stn B686, 28 Oct 1962; NMNZ, 1 female (TL 52 mm), 30 miles north-west of Kahurangi Point, west of Cape Farewell, 40°27'S, 171°44'E, 258–263 m, BS529, 10 Mar 1976; NMNZ Cr9364, 1 male (TL 74 mm), west of Kahurangi Point, north-west of Nelson, 40°40.00'S, 171°39.00'E, 208–264 m, J15/11/76, RV *James Cook*, 24 Sep 1976; NMNZ, 1 male (broken, CL 9.3 mm), off Kahurangi Shoals, ca. 7 miles north-west of Kahurangi Point, 40°42.5'S, 172°07'E, 91 m, BS533, 10 Mar 1976.

Marlborough: NMNZ, 1 female (TL 49 mm), ca. 15 miles north-east of Stephens Island, 40°31'S, 174°15'E, 117–119 m, BS507, RV *Acheron*, 4 Mar 1976; NMNZ, 1 male (TL 25 mm), 9 miles off Stephens Island, 40°33'S, 174°07'E, 132 m, mud, BS 509, 4 Mar 1976; NMNZ, 1 female (TL 58 mm), ca. 10 miles east of Stephens Island, 40°38.5'S, 174°12'E, 128 m, BS506, RV *Acheron*, 4 Mar 1976.

West Coast: NIWA 23979, 1 male (TL 42 mm), 1 female (TL 52 mm), east of Waimarie, 41°26.4'S, 171°07.7'E, 179–178 m, NZOI stn S395, 8 Feb 1983.

DIAGNOSIS. TS5 lateral process directed anteriorly of slightly inclined ventrally. Lobe on outer margin of inner spine of uropodal protopod distinctly wider than adjacent spine. Intermediate carinae on AS2 and usually AS1 posteriorly, with posterior spine.

DESCRIPTION. Dorsal integument smooth, polished.

Eye not extending beyond antennular peduncle segment 1; cornea strongly bilobed, set obliquely on stalk; CI 365–507. Ophthalmic somite anterior margin faintly biconcave. Ocular scales separate, rounded to subtruncate.

Antennular peduncle length 0.88–1.03CL. Antennular somite dorsal processes with spinular apices, directed anteriorly. Antennal scale length 0.48–0.63CL.

Rostral plate triangular to peltate, longer than wide, apex acute, often with small point; lateral margins usually convex, occasionally straight; dorsal surface with distinct median carina.

Carapace anterior width 0.42–0.48CL; anterolateral spines not extending to base of rostral plate; surface smooth; median carina without anterior bifurcation; lateral carinae extending anteriorly to about level of cervical groove; reflected marginal carinae distinct; posterior margin straight or weakly concave.

Raptorial claw dactylus with 5 or 6 (rarely 7 or 8) teeth, outer margin broadly rounded, outer proximal margin with distinct notch; carpus dorsal carina divided into 2 triangular teeth; propodus distal margin unarmed; merus outer inferodistal angle rounded.

Mandibular palp 3-segmented. Maxilliped 5 basal segment without ventrally directed distal tooth. Pereopod 1–3 basal segments unarmed; endopod slender, 2-segmented.

TS5–8 submedian and intermediate carinae distinct. Median carina absent on TS5, indistinct on TS6–7, distinct on TS8. TS5 lateral process a slender spine, recurved anteriorly, slightly inclined ventrally; ventral spine absent. TS6–7 lateral process rounded, inclined posteriorly, with short posterolateral spine in adults. TS8 anterolateral margin triangular, apex blunt; sternal keel a posteriorly directed falcate spine.

Pleopod 1 endopod with posterior 'endite'; tube process about as long as hook process; hook process apex blunt.

AS1–5 with distinct median and submedian carinae distinct; submedian carinae outwardly curved, posteriorly divergent. AS6 with distinct submedian, intermediate and lateral carinae; minute ventral spine anterior to uropodal articulation; posterior margin of sternum unarmed. Abdominal carinae spined as follows: submedian 6, intermediate (1–2)3–6, lateral (1–2)3–6, marginal (1)2–5.

Telson flattened, subtriangular, about as long as wide; dorsal carina of submedian, intermediate and lateral teeth short, distinct, swollen in adult males; movable apices of submedian teeth conical. Dorsolateral surface with few curved, shallow grooves or pits; proximally with low swelling either side of median carina. Median carina interrupted proximally; posterior spine slender. Submedian denticles minute, spinular. Intermediate and lateral denticles rounded with spiniform apices; submedian 10–17, intermediate 6–10, lateral 1. Telson ventrolateral carina short, extending to base of lateral tooth; post-anal carina absent or indistinct.

Uropodal protopod terminal spines divergent, inner about twice length of outer; lobe on outer margin

of inner spine rounded, distinctly wider than adjacent spine, margin smooth, straight to concave; with blunt lobe anterior to endopod articulation; protopod outer margin smooth, inner margin crenulate. Uropodal exopod proximal segment longer than distal segment; with distoventral spine and 7–9 movable spines on outer margin, distal spine not reaching midlength of distal segment.

COLOUR IN LIFE. Overall dorsal colour light straw-brown, with carinae and grooves yellow and dark brown. Telson with median carina yellow with dark brown patch below posterior spine, extending laterally along posterior margins. Uropodal protopod dark brown basally; exopod distal segment dark brown.

MEASUREMENTS. Male ($n = 132$) TL 18–100 mm, female ($n = 135$) TL 29–106 mm. Ahyong (2001) recorded specimens to TL 110 mm.

HABITAT. Silty-sand and mud substrates, often taken in scampi trawls; 37–630 m, but usually from 100–250 m. Ahyong (2001) reported a bathymetric range of 14–308 m for Australian *A. mcneilli*. One specimen of *A. mcneilli* (NIWA 57161) was collected together with *Heterosquilla trifida* at the Bay of Islands.

REMARKS. *Anchisquilloides mcneilli*, previously known only from Australia, is reported from New Zealand for the first time. The New Zealand specimens of *A. mcneilli* agree well with Australian material (Ahyong 2001) but have a much more uniform number of teeth on the dactylus of the raptorial claw. Almost all New Zealand specimens have six teeth on the dactylus of both raptorial claws (except in one specimen bearing five teeth on the dactylus of one claw and six teeth on the other, and in two specimens, each with a regenerating claw bearing seven and eight dactylar teeth, respectively). Australian specimens exhibit a similar range of variation in raptorial claw armature but usually have five teeth on one or both claws (75% of specimens examined by Ahyong (2001)). These proportional meristic differences in raptorial claw armature possibly reflect a degree of population differentiation between Australian and New Zealand populations of the species. However, in the absence of stable morphological differences or population genetic data, the New Zealand specimens are referred to *A. mcneilli* sensu stricto. Abdominal spination of New Zealand *A. mcneilli* (submedian 6, intermediate (1–2)3–6, lateral 1–6, marginal 1–5) is as documented for Australian material. The pleopod 1 endopod of males is fully developed by TL 37–39 mm and the posterolateral spine on the lateral process of TS6–7 is not developed in specimens smaller than TL 55–60 mm.

Anchisquilloides mcneilli differs little from its Philippine congener, *A. michelae*, and apparent differences in

carapace proportions identified by Moosa (1986) are based on a misinterpretation of Stephenson's original account of *A. mcneilli* (see Ahyong 2001). The two species differ in the orientation of the lateral process of TS5 (directed anteriorly or only slightly inclined ventrally in *A. mcneilli* versus directed almost ventrally in *A. michelae*) and in the size of the lobe between the terminal spines of the uropodal protopod in adults (distinctly wider than the adjacent spine in *A. mcneilli* versus distinctly narrower in *A. michelae*). Additionally, the intermediate carinae of AS1–2 are always unarmed in *A. michelae*. In most specimens of *A. mcneilli* above TL 60 mm, and all specimens larger than TL 82 mm, the intermediate carinae are armed on AS2 and usually also AS1.

Of the New Zealand squillids, *Anchisquilloides mcneilli* is most similar to *Pterygosquilla armata* in its undivided lateral processes of TS5–7. *Anchisquilloides mcneilli* is readily distinguished from *P. armata* by its rounded rather than spiniform ocular scales; distally pointed and medially carinate rather than distally rounded, smooth rostral plate; falcate rather than laterally directed lateral process of TS5; and presence of a median carina on AS1–5. From both species of New Zealand *Oratosquilla*, *A. mcneilli* is readily separated by its pointed rather than distally blunt rostral plate; undivided rather than bilobed lateral processes of TS5–7; median carina on AS1–5; and triangular rather than subquadrate telson with movable rather than fixed apices of the submedian teeth.

Anchisquilloides mcneilli is the most common squillid around the North Island, ranging south to the Tasman Peninsula, upper South Island. Other New Zealand squillids have much more limited North Island ranges. The introduced squillid *Oratosquilla oratoria* currently has a limited range in the Kaipara area, and *Oratosquilla fabricii* has been recorded only from Auckland. *Pterygosquilla schizodontia* primarily occurs from Cook Strait (including Wellington Harbour) southwards, and although it has been recorded as far north as the Gisborne region, it is not common there.

DISTRIBUTION. Coral Sea, Queensland, south to Tasmania and the Perth area, Western Australia; and for the first time from New Zealand, ranging from Northland south to the Tasman Peninsula.

Oratosquilla Manning, 1968

Oratosquilla Manning, 1968c: 120, 133. [Type species: *Squilla oratoria* De Haan, 1844, by original designation. Gender: feminine].

DIAGNOSIS. Dorsal integument variously pitted. Eye with cornea strongly bilobed, distinctly broader than and set obliquely on stalk, cornea width less

than 0.3CL. Ocular scales separate. Carapace with anterolateral spines; with median, lateral, marginal and reflected marginal carinae; median carina distinct, usually uninterrupted at base of anterior bifurcation (variable in *O. fabricii*); 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 present. Maxillipeds 1–4 with epipod. Pleopod 1 endopod in adult males with posterior ‘endite’; hook process blunt distally. TS6–8 with submedian and intermediate carinae. TS5–6 lateral processes bilobed. AS1–5 with submedian, intermediate, lateral and marginal carinae. Telson submedian teeth with fixed apices; prelateral lobe present; dorsolateral surface with curved rows of shallow pits; without supplementary longitudinal carinae; ventrolateral stridulatory carinae present. Uropodal protopod inner margin crenulate.

COMPOSITION. *Oratosquilla fabricii* (Holthuis, 1941); *O. kempii* (Schmitt, 1931); *O. mauritiana* (Kemp, 1913); *O. oratoria* (De Haan, 1844).

REMARKS. Two species of *Oratosquilla* are recorded from New Zealand, of which *O. oratoria* has been recently introduced.

KEY TO SPECIES OF *ORATOSQUILLA*

1. Raptorial claw merus without outer inferodistal spine *O. kempii*
 - Raptorial claw merus with outer inferodistal spine 2
2. Submedian carinae of AS4–6 each with posterior spine 3
 - Submedian carinae of AS4 unarmed ... *O. oratoria*
3. Dorsum smooth, not punctate. Anterior lobe of lateral process of TS7 blunt *O. mauritiana*
 - Dorsum distinctly punctate. Anterior lobe of lateral process of TS7 pointed to blunt *O. fabricii*

Oratosquilla fabricii (Holthuis, 1941) (Figs 39, 40)

Squilla nepa. – Heller, 1865: 124. – Miers, 1876: 89. – Filhol, 1885b: 435. – Chilton, 1891: 60. [Not *Squilla nepa* Latreille, 1828].

Squilla affinis. – Chilton, 1911a: 137–138, fig. 3. [Not *Squilla affinis* Berthold, 1845].

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

Squilla calumnia Townsley, 1953: 410, figs 8, 9 [type locality: Hilo, Hawaii].

Oratosquilla calumnia. – Manning, 1971b: 4–6, fig. 1. – Moosa, 1991: 210–211. – Ahyong & Norrington, 1997: 107.

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

TYPE MATERIAL. *Holotype*: ZMA, female (TL 128 mm), Telok Dalam, Nias, Indonesia, coll. Kleiweg de Zwaan.

OTHER MATERIAL EXAMINED. *Auckland*: NHMW 1850, 1 female (TL 119 mm), Auckland, ‘Novara’, Zelebor.

DIAGNOSIS. Dorsal integument pitted, rugose. Rostral plate slightly wider than long but appearing elongate; apex rounded. Carapace with median carina interrupted or uninterrupted at base of anterior bifurcation; branches of anterior bifurcation distinct. Raptorial claw merus outer inferodistal angle acute. TS6 lateral process anterior lobe triangular. TS7 lateral process anterior lobe short, triangular or rounded. AS4 submedian carinae with posterior spine. Telson prelateral lobe shorter than margin of lateral tooth. Uropodal protopod with lobe on outer margin of inner spine rounded, narrower than adjacent spine.

DESCRIPTION. Dorsal integument distinctly pitted, rugose. Eye extending beyond midlength but not apex of antennular peduncle segment 1; cornea strongly bilobed, set obliquely on stalk; CI 397–448. Ophthalmic somite anterior margin faintly emarginate. Ocular scales truncate, separate. Antennular peduncle 0.83–0.84CL. Antennular somite with dorsal processes trianguloid, directed anterolaterally, apices pointed but blunt. Antennal scale 0.61–0.63CL.

Rostral plate trapezoid to linguiform, slightly wider than long but appearing elongate; apex rounded; median carina absent. Carapace anterior width 0.49CL; anterolateral spines not extending beyond base of rostral plate; median carina distinct, interrupted or uninterrupted at base of anterior bifurcation; branches of anterior bifurcation distinct, opening anterior to dorsal pit; posterior median projection distinct, obtuse.

Raptorial claw dactylus with 6 teeth, outer margin sinuous, proximal margin without basal notch; carpus dorsal carina tuberculate; propodus distal margin unarmed; merus with outer inferodistal tooth.

Mandibular palp 3-segmented. Maxilliped 5 basal segment with small ventrally directed spine. Pereopod 1–3 basal segments unarmed; endopod segments fused, slender.

TS5 lateral process bilobed; anterior lobe a slender spine directed anteriorly; posterior lobe short, directed laterally. TS6 lateral process anterior lobe elongate,

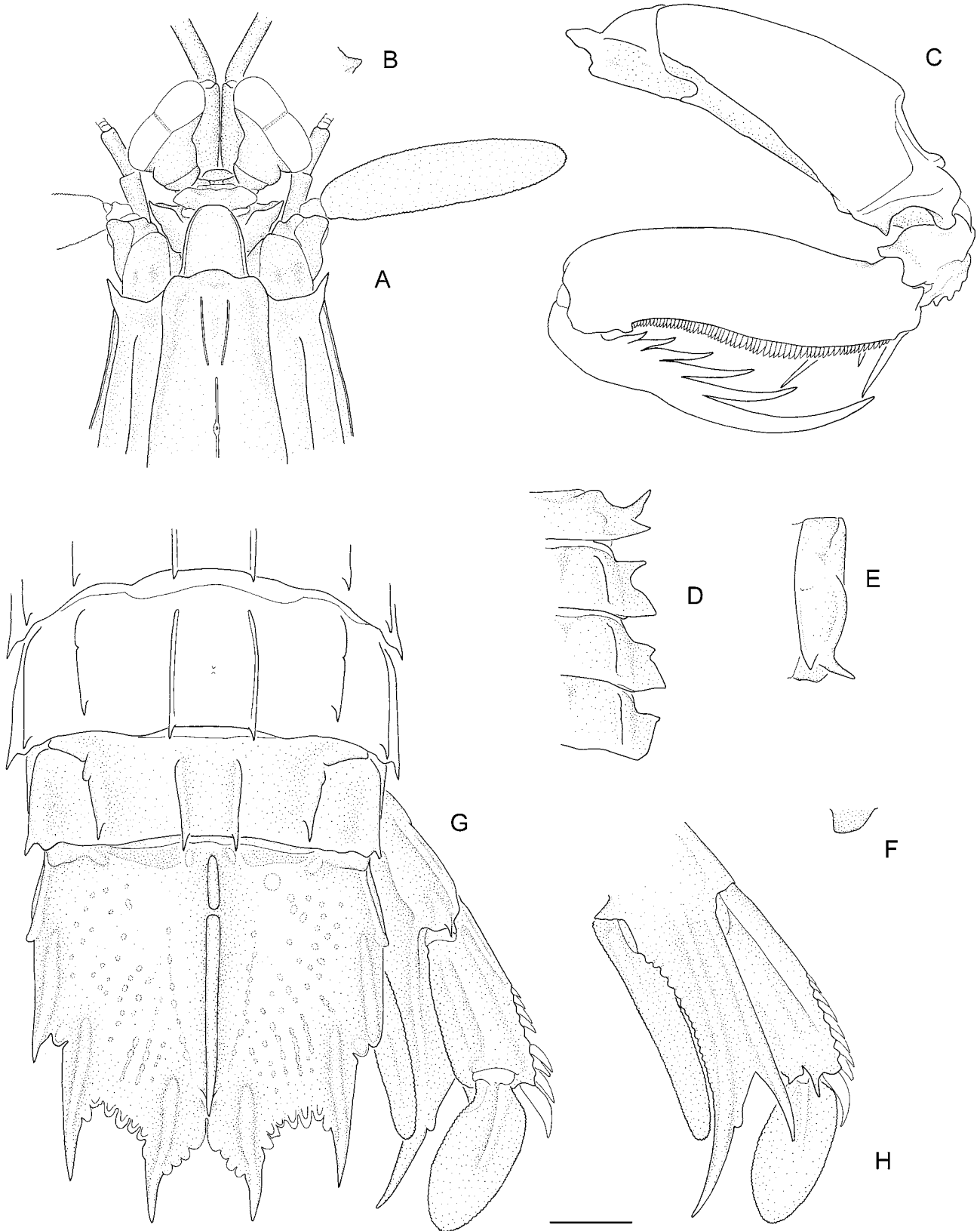


Figure 39. *Oratosquilla fabricii* (Holthuis, 1941), female, TL 119 mm, Auckland (NHMW 1850). A, anterior cephalothorax; B, right dorsal process of antennular somite, lateral view; C, right raptorial claw; D, TS6-8, right dorsal view; E, TS5, right lateral view; F, TS8 sternal keel, right lateral view; G, AS4-6, telson and right uropod, dorsal view; H, left uropod, ventral view. Scale = 5.0 mm.

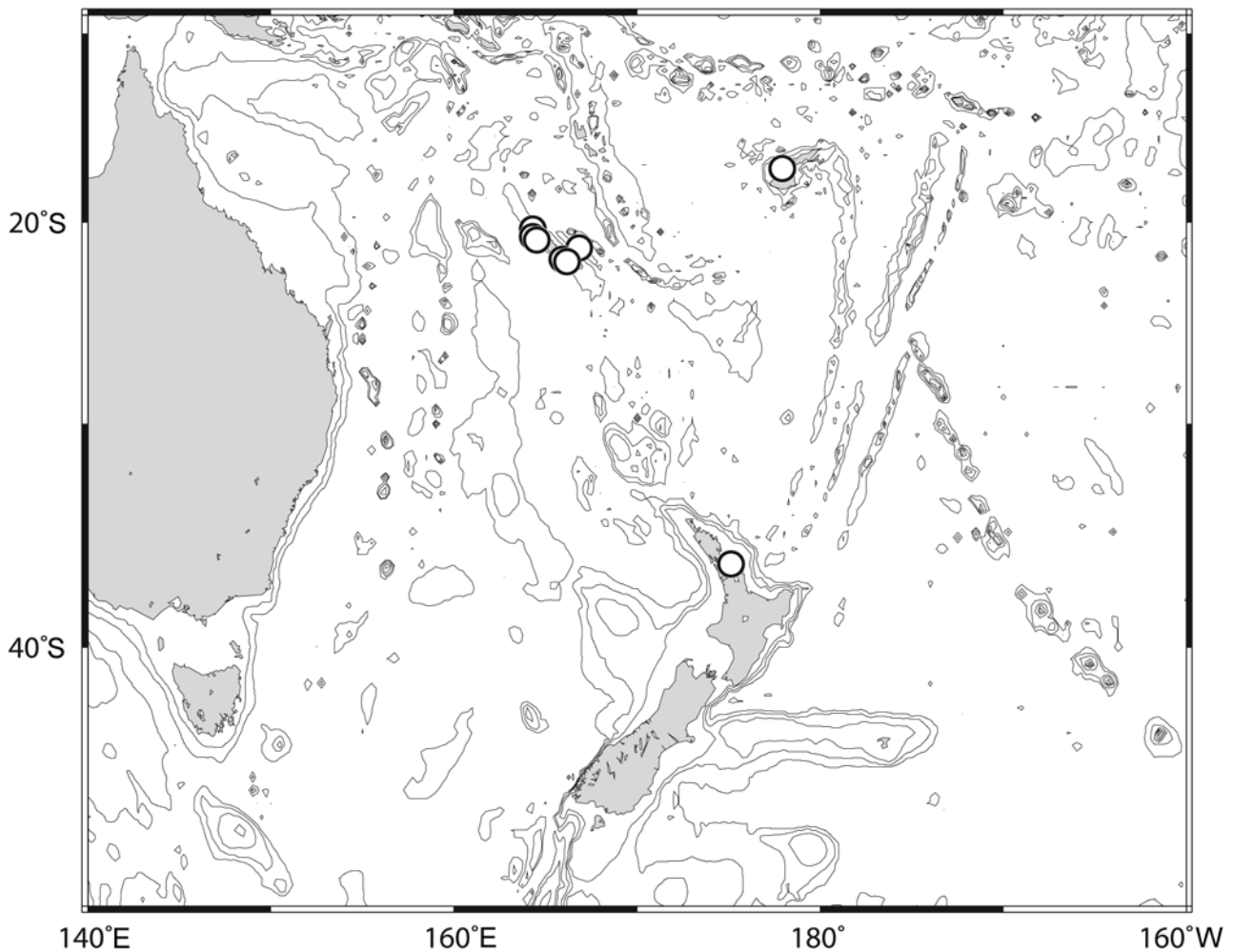


Figure 40. South-western Pacific distribution of *Oratosquilla fabricii* (Holthuis, 1941).

triangular, smaller than broad, triangular posterior lobe. TS7 lateral process with small triangular anterior lobe, apex pointed to blunt, and broad, triangular posterior lobe. TS8 anterolateral margin triangular, apex sharp; sternal keel rounded to bluntly angular.

AS1–5 with distinct submedian, intermediate, lateral and marginal carinae. Submedian carinae parallel on AS1–5. A56 with small ventral spine anterior to uropodal articulation; sternum posterior margin unarmed; lacking transverse carinae. Abdominal carinae spined as follows: submedian (3)4–6, intermediate (1)2–6, lateral 1–6, marginal 1–5.

Telson flattened, subquadrate, slightly broader than long; submedian, intermediate and lateral teeth each with dorsal carina; prelateral lobe shorter than margin of lateral tooth; median carina interrupted proximally, with short posterior spine; dorsolateral surface with curved rows of shallow pits; denticles rounded, each with dorsal tubercle, submedian 4, intermediate 7–8, lateral 1. Telson post-anal carina extending posteriorly beyond midpoint between anal pore and posterior margin of telson; ventrolateral

carina short, not extending posteriorly as far as base of lateral denticle.

Uropodal protopod terminating in 2 slender spines, with lobe on outer margin of inner spine rounded, narrower than adjacent spine, margin concave; with minute ventral spine anterior to endopod articulation; protopod inner margin crenulate. Uropodal exopod proximal segment shorter than distal segment; with 2 distoventral spines, outer longer; with 8 or 9 movable spines on outer margin.

COLOUR IN LIFE. Overall pale gray with diffuse, darker mottling; carinae of carapace and submedian carinae of abdomen dark red. AS2 with dark, diffuse transverse bar medially. Telson with red-maroon patch at anterior end of median carina, dark brown patch at posterior; telson carinae dark blue-green. Uropodal exopod with distal half of proximal segment and inner two-thirds of distal segment blue; outer half of distal segment yellow. Raptorial claw merus dusky; propodus, carpus and dactylus white.

MEASUREMENTS. Female ($n = 2$) TL 119–128 mm. Ahyong *et al.* (2008) recorded a maximum TL 149 mm.

HABITAT. Sand and mud substrates in sheltered waters such as embayments and estuaries; 5–50 m (Ahyong *et al.* 2008).

REMARKS. The present specimen of *Oratosquilla fabricii* is the basis of Heller's report of *Squilla nepa* Latreille, 1828, from New Zealand. The specimen agrees well with the recent redescription of the holotype (Ahyong 2000) but differs chiefly in having the anterior bifurcation of the median carina of the carapace interrupted instead of entire, a feature since found to be variable in *O. fabricii* (see Ahyong 2002c). As indicated by Ahyong (2002c), the condition of the anterior bifurcation of the median carina of the carapace, whether interrupted or entire, is the single character presently distinguishing *Oratosquilla* from *Oratosquillina*, indicating that the concepts of both genera require revision.

Oratosquilla fabricii has not been recorded from New Zealand since Heller's (1865) report, but as with Heller's other records of warm-water Stomatopoda from New Zealand waters, the record of *O. fabricii* in Auckland appears to be reliable. *Oratosquilla fabricii* is common in tropical waters to the north of New Zealand, such as New Caledonia and Fiji; it is likely that pelagic larvae occasionally successfully recruit in northern New Zealand waters.

Oratosquilla fabricii closely resembles *O. oratoria* (De Haan, 1844), recently established in northern New Zealand, but is easily distinguished by having armed submedian carina on AS4.

DISTRIBUTION. Pacific Ocean from Hawaii, French Polynesia, Taiwan, the Philippines, Indonesia, Guam, Fiji, New Caledonia, and now from New Zealand.

Oratosquilla oratoria (De Haan, 1844)

(Figs 41, 42, Frontispiece 2C)

Squilla oratoria De Haan, 1844 (atlas): pl. 51, fig. 2 [type locality: Japan]; 1849 (text): 223. — Kemp, 1913: 3, 10, 23, 66, pl. 5, figs. 54–56 (part).

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

Oratosquilla oratoria. — Manning, 1971b: 4, 6–8, fig. 2. — Manning, 1995: 25, 224, figs. 136a, b, 137. — Ahyong, 2001: 283–285, fig. 138. — Ahyong, 2010c: 11–12, unnumbered colour figure. — Ahyong & Wilkens, 2011: 477, tab. 1, 2. — Webber *et al.*, 2010: 136, 218.

MATERIAL EXAMINED. *Northland*: NIWA-MITS 69691, 2 males (TL 130–132 mm), 6 females (TL 129–155 mm), between Rawene and Kohukohu, Hokianga, 35°23'S, 173°31'E, muddy bottom, shallow water, in flounder nets, coll. M. Pinkney, 11 May 2010; AM P87905, 1

male (TL 131 mm), 1 female (TL 133 mm), between Rawene and Kohukohu, Hokianga, 35°23'S, 173°31'E, muddy bottom, shallow water, in flounder nets, coll. M. Pinkney, 11 May 2010; NIWA-MITS 69701, 2 males (TL 132–135 mm), 1 female (TL 141 mm), Arapaoa River, Kaipara Harbour, 36°14'S, 174°18'E, coll. C. Yardley, 11 Jun 2010; NIWA-MITS, 1 male (TL 151 mm), Port Albert arm, Kaipara, 36°17.506–17.345'S, 174°23.931–22.676'E, 5.0–4.2 m, trawl, site EA8S, coll. M. Lowe *et al.*, 28 Apr 2010; NIWA-MITS 69606, 1 male (TL 135 mm), Kaipara Harbour, 36°35.493–35.708'S, 174°23.08–23.039'E, 7.0–7.7 m, SH4S, trawl 60, coll. M. Smith & M. Lowe, 13 Apr 2010.

DIAGNOSIS. Dorsal integument pitted, rugose. Rostral plate trapezoid, wider than long, appearing squat; apex truncate to slightly curved. Carapace with median carina uninterrupted at base of anterior bifurcation; branches of anterior bifurcation distinct. Raptorial claw merus with outer inferodistal tooth. TS6 lateral process anterior lobe slender, blunt. TS7 lateral process anterior lobe short, triangular. AS4 submedian carinae unarmed posteriorly. Telson prelateral lobe as long as or longer than margin of lateral tooth. Uropodal protopod with lobe on outer margin of inner spine rounded, narrower than adjacent spine.

DESCRIPTION. Dorsal integument distinctly pitted, rugose. Eye extending beyond midlength but not apex of antennular peduncle segment 1; cornea strongly bilobed, set obliquely on stalk; CI 503–544. Ophthalmic somite anterior margin faintly emarginate. Ocular scales truncate, separate. Antennular peduncle 0.89–0.96CL. Antennular somite with dorsal processes trianguloid, directed anterolaterally, apices blunt. Antennal scale 0.64–0.70CL.

Rostral plate trapezoid, broader than long, apex truncate to slightly rounded; median carina absent. Carapace anterior width 0.53–0.57CL; anterolateral spines not extending beyond base of rostral plate; median carina distinct, uninterrupted at base of anterior bifurcation; branches of anterior bifurcation distinct, opening anterior to dorsal pit; posterior median projection distinct, obtuse.

Raptorial claw dactylus with 6 teeth, outer margin sinuous, proximal margin without basal notch; carpus dorsal carina tuberculate; propodus distal margin unarmed; merus with outer inferodistal tooth.

Mandibular palp 3-segmented. Maxilliped 5 basal segment with small ventrally directed spine. Pereopod 1–3 basal segments unarmed; endopod segments fused, slender.

TS5 lateral process bilobed; anterior lobe a slender spine directed anteriorly; posterior lobe short, directed laterally. T56 lateral process anterior lobe elongate, slender, blunt; posterior lobe broad, triangular. TS7

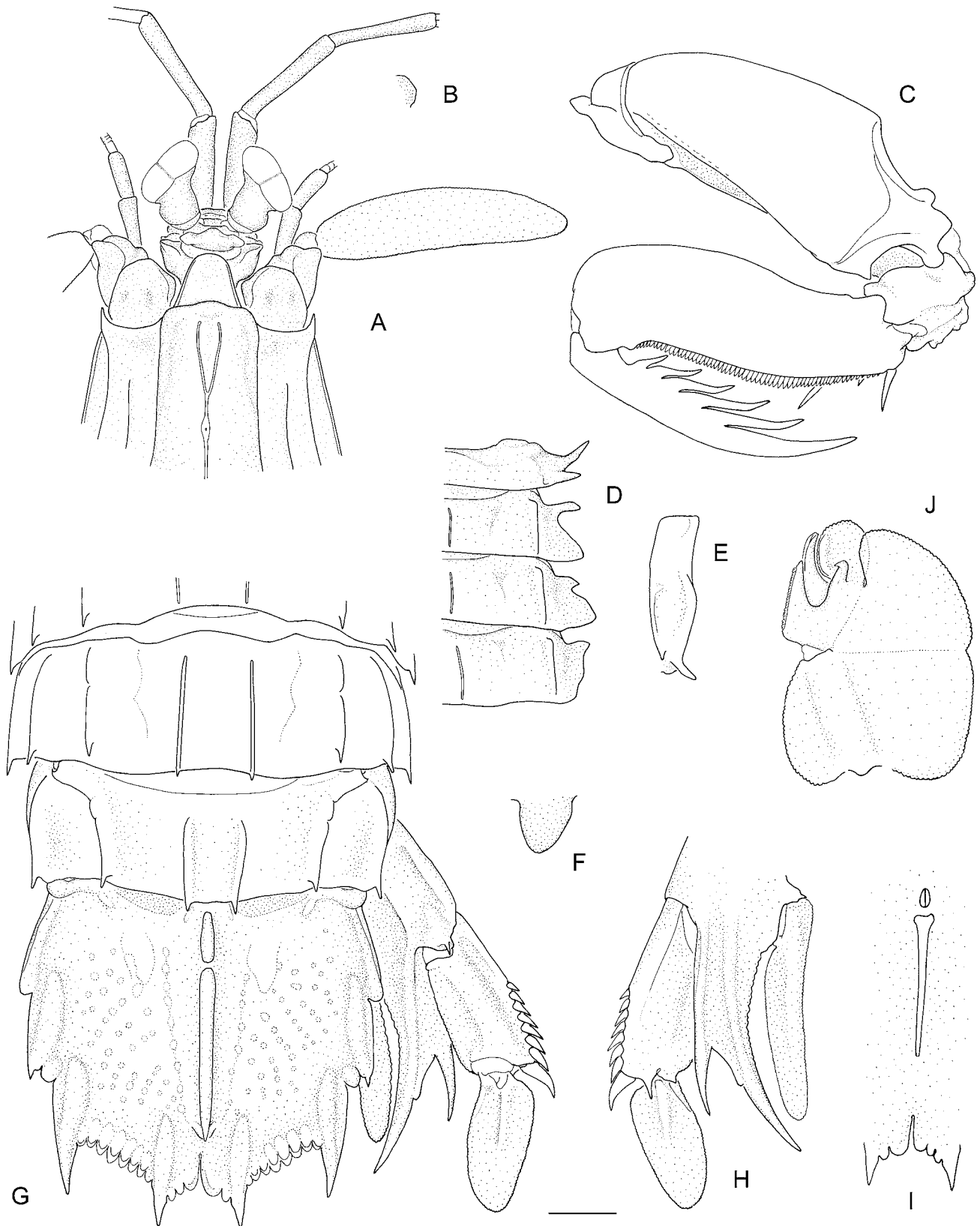


Figure 41. *Oratosquilla oratoria* (De Haan, 1844). Male, TL 135 mm, Kaipara Harbour (NIWA-MITS 69606). A, anterior cephalothorax; B, right dorsal process of antennular somite, lateral view; C, right raptorial claw; D, TS6-8, right dorsal view; E, TS5, right lateral view; F, TS8 sternal keel, right lateral view; G, AS4-6, telson and right uropod, dorsal view; H, right uropod, ventral view; I, post-anal carina; J, right pleopod 1 endopod, anterior view. Scale: A-E, G-I = 5.0 mm, F, J = 2.5 mm.

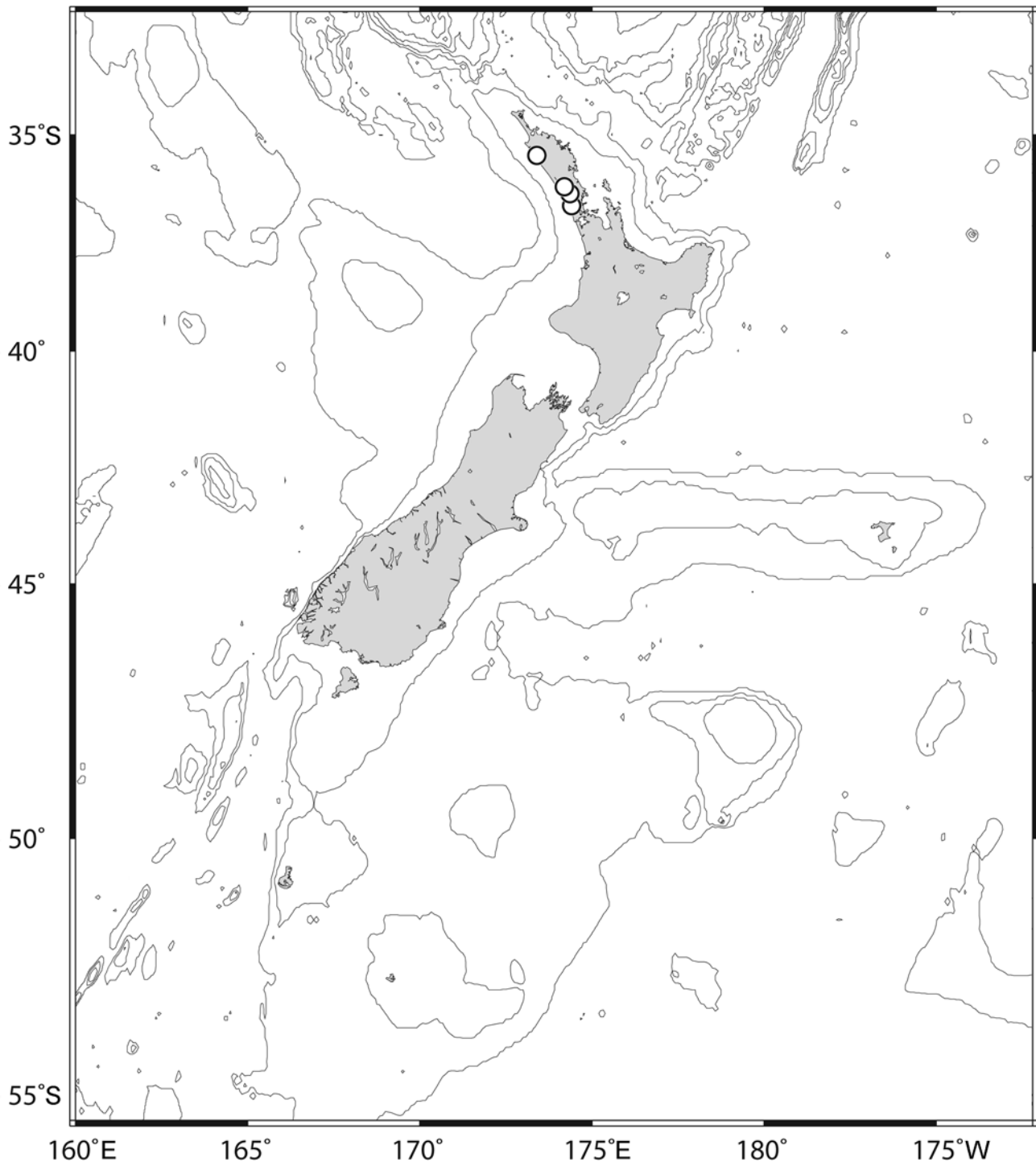


Figure 42. New Zealand distribution of *Oratosquilla oratoria* (De Haan, 1844).

lateral process with small triangular anterior lobe and broad, triangular posterior lobe. TS8 anterolateral margin triangular, apex sharp; sternal keel rounded to bluntly angular.

AS1–5 with distinct submedian, intermediate, lateral and marginal carinae. Submedian carinae parallel on AS1–5. AS6 with small ventral spine anterior to uropodal articulation; sternum posterior margin

unarmed; lacking transverse carinae. Abdominal carinae spined as follows: submedian 5–6, intermediate (2)3–6, lateral (1)2–6, marginal 1–5.

Telson flattened, subquadrate, slightly broader than long; submedian, intermediate and lateral teeth each with dorsal carina; prelateral lobe longer than or occasionally as long as margin of lateral tooth; median carina interrupted proximally, with short posterior

spine; dorsolateral surface with curved rows of shallow pits; denticles rounded, each with dorsal tubercle, submedian 2–4, intermediate 6–9, lateral 1. Telson post-anal carina extending posteriorly beyond midpoint between anal pore and posterior margin of telson; ventrolateral carina short, not extending posteriorly as far as base of lateral denticle.

Uropodal protopod terminating in 2 slender spines, with lobe on outer margin of inner spine rounded, narrower than adjacent spine, margin concave; with minute ventral spine anterior to endopod articulation; protopod inner margin crenulate. Uropodal exopod proximal segment shorter than distal segment; with 2 distoventral spines, outer longer; with 7–9 movable spines on outer margin.

COLOUR IN LIFE. (Frontispiece 2C) Overall dorsal colour light grey to light brown in large males. Carinae and grooves of carapace, submedian and intermediate carinae of thorax and abdomen dark red. Posterior margins of thoracic and abdominal somites dark green. Median carina, tubercles and carinae of primary teeth of telson dark brown-green; apices of primary teeth red. Uropodal protopod with transparent red terminal spines. Uropodal exopod with proximal segment dark blue distally; distal segment yellow with dark inner margin. Raptorial claw merus dusky; propodus, carpus and dactylus white.

MEASUREMENTS. Male ($n = 7$) TL 130–151 mm, female ($n = 7$) TL 129–155 mm. Ah Yong (2001) recorded specimens to TL 185 mm.

HABITAT. Muddy or sandy-mud substrates; 10–20 m.

REMARKS. *Oratosquilla oratoria* is native to the north-western Pacific (Korea, Japan, Taiwan, China and Vietnam) where it is a significant commercial species. It was introduced to the Sydney region, Australia, probably in the early to mid-1980s where it successfully colonised disturbed and impacted habitats, mostly in the upper reaches of Sydney Harbour and in Botany Bay (Ah Yong 2001). The presence of *O. oratoria* in New Zealand waters is almost certainly also the result of recent human introduction. The species has not been collected in any previous biosecurity surveys throughout New Zealand, and long-term commercial fishers, Peter and Christine Yardley, who have worked the Kaipara area since 1973, note that the species first appeared in their catch in November 2009 (Ah Yong 2010c).

The New Zealand specimens agree in all respects with those reported by Ah Yong (2001) from Japan and Australia, including colour in life. One specimen has a regenerating raptorial claw with only five instead of six teeth on the dactylus (male, TL 132 mm, NIWA-MITS

69691). The originating source of the New Zealand population of *O. oratoria* remains to be determined, whether from East Asia or eastern Australia.

Chilton (1891) suggested that Heller's record of *Squilla nepa* from Auckland was based on *Squilla affinis* Berthold, 1845 (= *Oratosquilla oratoria* (De Haan, 1844)) on the basis of an unlabelled specimen in the collections of the Dominion Museum, assumed to originate from New Zealand waters. Chilton's specimen of *O. oratoria*, an incomplete dry specimen now in the collections of the Canterbury Museum, Christchurch, lacks locality data but almost certainly did not originate from New Zealand waters. The specimen probably originated from collections of the Indian Museum, Calcutta, which holds numerous specimens of the species (Kemp 1913), and which exchanged material with several Australian and New Zealand museums in the late 1800s and early 1900s. As shown above, Heller's (1865) Auckland *Squilla nepa* is referable to *Oratosquilla fabricii*, which is morphologically similar to *O. oratoria*. *Oratosquilla oratoria* is readily separated from *O. fabricii* by its unarmed submedian carina on AS4. In *O. fabricii*, the submedian carinae of AS4 and sometimes also AS3 have posterior spines. Although *Oratosquilla oratoria* is now known from isolated localities in northern New Zealand, it is the result of recent human introduction (Ah Yong 2010c).

DISTRIBUTION. North-western Pacific from Korea and Japan to China and Vietnam; introduced to south-eastern Australia and northern New Zealand (Ah Yong 2001, 2010c). In New Zealand waters, *O. oratoria* is presently known only from Hokianga and Kaipara harbours, in the north-western North Island.

Pterygosquilla Hilgendorf, 1890

Pterygosquilla Hilgendorf, 1890: 172. [Type species: *Pterygosquilla laticauda* Hilgendorf, 1890, by monotypy].

DIAGNOSIS. Eye with cornea strongly bilobed, width less than 0.3CL. Antennular somite dorsal processes with short slender apices, directed anterolaterally. Ocular scales present as short anteriorly directed spines. Carapace with anterolateral spines; dorsal carinae reduced, with reflected marginal and reduced lateral carinae; median posterior margin straight or slightly concave; posterolateral margin rounded. Raptorial claw dactylus with 6 or more teeth; carpus with short undivided dorsal carina; 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. TS5–7 lateral process single. AS1–5 with or without submedian carina; with intermediate,

lateral and marginal carina. AS6 with submedian, intermediate, lateral carinae. Telson subquadrate; dorsolateral surface with low submedian swelling; submedian teeth with movable apices; intermediate and lateral teeth distinct; prelateral lobe absent; ventrolateral stridulatory carinae absent. Uropodal protopod inner margin crenulate.

COMPOSITION. *Pterygosquilla armata* (H. Milne Edwards, 1837); *P. capensis* Manning 1969a; *P. gracilipes* (Miers, 1881); *P. schizodontia* (Richardson, 1953).

REMARKS. *Pterygosquilla* is distinctive within Squilloidea in having the combination of spiniform ocular scales, reduced carapace carinae and movable apices on the submedian teeth of the telson. It is most closely related to genera of the 'Meiosquilla' group of genera, which includes genera such as *Distosquilla* Manning, 1977b, *Meiosquilla* Manning, 1968c, *Squilloides* Manning, 1968c, and allies sharing an indistinct marginal telson carina, absence of the prelateral lobe and ventrolateral carina on the telson, reduced carapace carination, and absence of the mandibular palp (Ahyong 2005). Species of *Pterygosquilla* occur only in temperate Southern Hemisphere localities: New Zealand, southern South America and South Africa. Thus, like *Heterosquilla*, *Pterygosquilla* is one of the few stomatopod genera to range into subantarctic latitudes.

KEY TO SPECIES OF *PTERYGOSQUILLA*

1. Telson with 18 or more triangular to spinular submedian denticles. Post-anal carina absent.....
.....*P. gracilipes*
- Telson with 1 or 2 submedian denticles, developed as rounded or subquadrate lobes, occasionally with up to 10 minute spinules on margin. Post-anal carina present.....2
2. Rostral plate linguiform; apex broadly rounded. Distance between submedian carinae one-third distance between intermediate carinae.....
.....*P. schizodontia*
- Rostral plate triangular; apex rounded, narrow. Distance between submedian carinae one-fourth distance between intermediate carinae.....3
3. Submedian carinae of AS1-5 always distinct. Posterior margin of AS5 usually with 1 or more accessory spinules.....*P. armata*
- Submedian carinae of AS1-5 present in juveniles and small adults, indistinct to absent in specimens exceeding TL 90 mm. Posterior margin of AS5 usually without accessory spinules.....*P. capensis*

Pterygosquilla schizodontia (Richardson, 1953)
(Figs 43, 44, Frontispiece 2D)

Squilla armata. — Hector, 1877: 474. — Kirk, 1879b: 401. — Miers, 1880: 27, 125 [New Zealand record only]. — Filhol, 1885a: 52; 1885b: 435. — Chilton, 1891: 60-64. — Hutton, 1904: 256. — Chilton, 1911a: 135, fig. 1, 2; 1911b: 287, 306-307. — Kemp, 1913: 41, pl. 2, figs 28-29. — Thomson, 1913: 241. — Thomson & Anderton, 1921: 108. — Parisi, 1922: 93. — Anonymous, 1964: 185 [un-numbered fig.]. — Wear, 1965; 9, fig. 4D. — Manning, 1966: 90-93, fig. 2. — Yaldwyn, 1975: 362. [Not *S. armata* H. Milne Edwards, 1837].
Squilla armata var. *schizodontia* Richardson, 1953: 315, figs. 103 [type locality: Petone, Wellington Harbour, by present neotype designation].
Pterygosquilla armata schizodontia. — Manning, 1969a: 11; 1995: 26.
Pterygosquilla schizodontia. — Ahyong, 2010c: 11-12, un-numbered colour figure. — Webber *et al.*, 2010: 135, 136, 218.

TYPE MATERIAL. *Neotype*: NMNZ Cr9360, male (TL 81 mm), Petone, Wellington Harbour, 41°14'S, 174°53'E, from stomach of *Mustelus lenticulatus*, coll. R.A. Falla, 18 Sep 1950.

OTHER MATERIAL EXAMINED. *Gisborne*: NMNZ exCr9366, 2 females (TL 44-47 mm), about 30 km east-north-east of Tolaga Bay, 38°15.2'S, 178°38.6'E, 139 m, mud, NZOI Stn R31, BS673, RV *Tangaroa*, 16 Jan 1979.

Hawkes Bay: CM AQ1807, 2 males (TL 62-73 mm), 7 females (TL 46-68 mm), 5½ miles north-east of Table Cape, 39°03.0'S, 178°06.7'E, 77 m, soft sand and mud, from stomach of *Dasybatus brevicaudatus* (= *Dasyatis brevicaudatus* (Hutton)), *Nora Niven* Stn 85, 20 Aug 1907 NMNZ Cr9361, 1 male (TL 33 mm), off Napier, 39°29'S, 177°00'E, trawled, coll. A.G. Clark, Sep 1953; NMNZ Cr9358, 1 male (TL 104 mm), Haumoana, 39°37'S, 177°00'E, coll. W. Birch, Jul 1931; NMNZ Cr20001, 1 female (TL 106 mm), east of Cape Kidnappers, Hawke Bay, 39°37.30-35.71'S, 177°45.13-48.43'E, 195-213 m, trawl, KAH9501/59, RV *Kaharoa*, 17 Jan 1995.

Wellington: NMNZ Cr9342, fragments, off Petone Beach, 41°14'S, 174°53'E, from stomach of dogfish, coll. R. Brunston, 16 Nov 1954; NMNZ Cr9376, 2 females (TL 103-135 mm), Wellington Harbour; NMNZ Cr9354, 1 female (TL 109 mm), Ngauranga, Wellington Harbour, 41°15'S, 174°49'E, coll. W. Heaphy, 24 Aug 1952; NMNZ Cr9355, 1 female (TL 120 mm), Ngauranga, Wellington Harbour, 41°15'S, 174°49'E, coll. W. Heaphy, 31 Nov 1952; NMNZ Cr12525, 1 male (TL 121 mm), off Miramar wharf, Wellington Harbour, 41°19'S, 174°49'E, on hook with mussel bait, coll. C. Porebski, 23 Apr 2002; NMNZ, 1 female (TL 36 mm), off Eastbourne, 41°17'S, 174°53'E, 10-17 m, dredge, coll. M.C. Fenwick, 8 Mar



2005; NIWA 23940, 1 male (TL 76 mm), off Raumatī, 41°17.10'S, 174°52.00'E, 21 m, NZOI stn D345, 20 Nov 1964; AM P87906, 2 males (TL 105–120 mm), 1 female (TL 110 mm), Seaview terminal, Wellington Harbour, 41°15.255'S, 174°54.082'E, 8.6 m, trap, coll. K. Neill *et al.*, 26 Jun 2009; AM P87907, 1 male (TL 100 mm), Wellington Harbour, 41°17.2'S, 174°47.2'E, carapace with bryozoa (*Antarctothoa tongima*), coll. K. Neill *et al.*, 14 Jul 2009; AM P87908, 1 male (TL 104 mm), Burnham Wharf, Wellington Harbour, 41°18.7'S, 174°48.6'E, 17 m, crab trap, SVWLG 10164, coll. A. Bradley *et al.*, 13 Nov 2009; NMNZ Cr9337, 1 female (TL 119 mm), Cook Strait; NIWA 72033, 1 female (TL 69 mm), Wairarapa Canyon, 41°26.83'S, 175°01.32'E, 168–260 m, rock dredge, TAN1103/38, 16 Feb 2011; NMNZ Cr9373, 1 male (TL 91 mm), Cook Strait, caught in sardine net, coll. A.C. Kaberry, 1944; NMNZ Cr9336, 7 males (TL 114–120 mm), 6 females (TL 80–120 mm), Cook Strait, trawled, c. 1956; NMNZ Cr18269, 1 female (TL 45 mm), Cook Strait, trawl, Dec 1956.

Tasman-Nelson: NMNZ Cr4813, 1 female (TL 81 mm), Tasman Bay, scallop dredge, Oct 1976; NIWA 28035, 1 male (TL 67 mm), 2 females (TL 66–68 mm), Karamea Bight, 41°15.60–18.22'S, 171°54.33–52.57'E, 70–67 m, KAH0704/016, RV *Kaharoa*, 29 Mar 2007; NIWA 23992, 1 female (TL 97 mm), north-east of Separation Point, 40°45.66–47.70'S, 173°24.49–27.36'E, 52–53 m, KAH9701/70, NZOI stn Z10904, RV *Kaharoa*, 6 Apr 1997.

Marlborough: NMNZ, 1 female (TL 54 mm), ca. 9 miles north-east of Stephens Island, 40°33'S, 174°07'E, 132 m, RV *Acheron*, 4 Mar 1976; NIWA 23938, 1 male postlarva (TL 19 mm), Pelorus Sound, 40°55.39'S, 174°07.69'E, 25 m, NZOI stn C937, 11 Feb 1963; NMNZ, 2 males (TL 32–41 mm), 1 female (TL 32 mm), Cloudy Bay, 41°26.20'S, 174°15.89'E, 59–64 m, mud, NZOI R134, BS776, RV *Tangaroa*, 28 Jan 1979; NMNZ, 1 female (TL 70 mm), north-east of Cape Campbell, 41°40'S, 174°30'E, 110 m, coll. F. Abernathy, Mar 1957; NMNZ Cr9356, 1 female (TL 97 mm), off Cape Campbell, 41°42'S, 174°00'E, 73 m, coll. F. Abernathy, 4 Nov 1952; NMNZ Cr9357, 1 male (TL 94 mm), off Cape Campbell, 41°42'S, 174°00'E, 73 m, coll. F. Abernathy, 4 Nov 1952; NMNZ Cr12538, 1 male (TL 60 mm), off Cape Campbell, 41°42'S, 174°00'E, 119 m, 6 Dec 1956.

Chatham Rise: NMNZ Cr4842, 1 male (TL 75 mm), north of Chatham Islands, 43°30.0'S, 176°11.0'W, 210 m, FV *Oyang*, coll. C.D. Roberts, 24 May 1987; NMNZ Cr4843, 2 females (TL 90–106 mm), north of Chatham Islands, 43°33.0'S, 176°02.0'W, 239 m, FV *Oyang*, coll. C.D. Roberts, 26 May 1987.

Canterbury: NIWA 23921, 1 female (broken, CL 6.5 mm), off Kekerengu, 42°01.30'S, 174°06.40'E, 58 m, NZOI stn B528, 13 Feb 1962; NMNZ Cr9377, 1 male (TL 124 mm), off mouth of Clarence River, 42°10'S, 173°57'E, 46 m, FV *Antares*, coll. L.D. Bowring, 10 Aug

1967; NIWA 4128, 11 damaged females, 42°14.0'S, 173°56.0'S, 64 m, from fish stomachs, otter trawl, NZOI stn G167, 18 Nov 1967; NMNZ Cr3925, 1 male (TL 95 mm), Kaikoura, from Ling stomach, coll. L.D. Bowring, 1967; NMNZ Cr8950, 1 male (broken, TL 100+ mm), off Kaikoura, 43°17.8–16.2'S, 173°23.2–25.6'E, 78–186 m, 16 Aug 1985; NIWA 23943, 1 female (TL 98 mm), east of Montanau, 42°58.00'S, 173°30.00'E, 110–128 m, NZOI stn G156, 13 Nov 1967; NIWA 23976, 1 female (TL 45 mm), off Cheviot, 42°45.19'S, 173°30.10'E, 79 m, NZOI stn S208, 4 Nov 1979; NMNZ Cr3742, 1 male (TL 70 mm), 1 female (TL 71 mm), off Akaroa, 43°47'S, 173°18'E, 73 m, from fish stomachs, 1942; NMNZ, 1 male (TL 46 mm), 10 miles off Oamaru, 45°S, 171°E, RV *Acheron*; NMNZ Cr3909, 1 male (TL 104 mm), Pegasus Bay, North Canterbury, 43°20'S, 173°00'E, coll. T. Gorman, Oct/Nov 1991; AWMM 6480, 1 female (TL 112 mm), 10 miles off Banks Peninsula, Canterbury, 43°36'S, 173°21'E, 71 m, 3 Apr 1986; CM AQ3237, 5 males (TL 85–107 mm), off Akaroa, from stomach of fish, coll. E.W. Bennett, Oct 1927; CM AQ439, 1 male (TL 92 mm), Canterbury, coll. P. Feron *et al.*, Aug 1966; NMNZ Cr16751, 1 male (TL 100 mm), Canterbury Bight, 44°15.54–17.25'S, 171°49.30–50.74'E, 42–48 m, KAH9809/69, RV *Kaharoa*, 31 Dec 1998; NIWA 76525, 1 female (TL 103 mm), Canterbury Bight, 44°23.14–23.97'S, 171°57.04–54.49'E, 64–63 m, KAH9809/70, RV *Kaharoa*, 31 Dec 1998; NIWA 23988, 1 male (TL 120 mm), south of Banks Peninsula, 44°16.12–16.24'S, 172°28.60–31.38'E, 70–74 m, KAH0014/104, NZOI stn Z10661, RV *Kaharoa*, 3 Jan 2001.

Otago: NMNZ Cr9359, 1 female (TL 89 mm), between Moeraki and Oamaru, 45°14'S, 170°56'E, 73–110 m, coll. J.M. Moreland, Nov 1952; NMNZ Cr9371, 1 male (TL 96 mm), north Otago, 25F zone 2, coll. J. Graham, 1962; OM, 1 male (TL 95 mm), Otago Harbour, 46°S, 170°E, 20 Jul 1994; OM, 1 male (TL 120 mm), Dunedin Harbour, 1 Sep 1982.

West Coast: NIWA 50532, 1 male (TL 51 mm), south-west of Kahurangi Point, 41°13.15–15.51'S, 172°00.42–171°57.91'E, 50–52 m, KAH0503/027, RV *Kaharoa*, 29 Mar 2005;

NIWA 23977, 1 male (TL 91 mm), west of Ross, 42°57.4–57.9'S, 170°02.3–02.9'E, 180–171 m, NZOI stn S371, 28 Jan 1983; NIWA 23978, 1 female (TL 32 mm), off Greymouth, 42°19.6'S, 171°01.0'E, 124 m, NZOI stn S382, 2 Feb 1983; NIWA 4126, 1 female (TL 94 mm), west of Ross, 43°25.74–24.42'S, 169°25.57–29.34'E, 127–133 m, KAH004/35, 24 Mar 2000; NIWA 4121, 1 male (TL 75 mm), 5 miles west of Otarokua Point, 43°25'S, 169°48'E, 20 fm [37 m], trawl, Z1907, 24 Jan 1964.

Southland: AM P87909, 1 female (TL 124 mm), Bluff Harbour, coll. M. Rodrigue, 2 Nov 2011; NMNZ, 1 male (TL 147 mm), Sylvan Cove, Port Pegasus, Stewart Island, 47°13.8'S, 167°34.8'E, 6 m, silt/weed bottom, coll. P. & I. Tait on scuba, Sep 1998.

Auckland Islands: NIWA 23959, 1 female (TL 54 mm), Musgrave Harbour, Auckland Island, 50°47.89'S, 166°01.20'E, 39 m, NZOI stn J529, 12 Dec 1973.

No specific locality: USNM 112415, 2 males (TL 113–115 mm), 1 female (TL 120 mm), New Zealand, from L.R. Richardson.

DIAGNOSIS. Rostral plate linguiform; apex broadly rounded. Abdominal submedian carinae distinct; distance between submedian carinae about one-third distance between intermediate carinae in specimens exceeding TL 90 mm. Posterior margin of AS5 usually with 1 or more accessory spinules. Telson with post-anal carina; adults with single rounded or subquadrate submedian denticle.

DESCRIPTION. Dorsal integument finely rugose.

Eye extending beyond midlength but not to apex of antennular peduncle segment 1; cornea strongly bilobed, set obliquely on stalk; CI 352–592. Ophthalmic somite anterior margin faintly concave. Ocular scales spiniform, occasionally with small accessory spine laterally.

Antennular peduncle length 0.89–1.06CL. Antennular somite dorsal processes with spinular apices, directed anterolaterally. Antennal scale length 0.46–0.62CL.

Rostral plate linguiform, slightly longer than wide to slightly wider than long, apex broadly rounded, lateral margins sinuous; dorsal surface smooth.

Carapace anterior width 0.47–0.61CL; anterolateral spines extending almost to base of rostral plate; surface smooth, lateral carinae extending anteriorly to about level of cervical groove; reflected marginal carinae low. Carapace posterior margin with low, triangular, median projection.

Raptorial claw dactylus with 6–9 (usually 8) teeth, outer margin broadly rounded, outer proximal margin with distinct notch; carpus dorsal carina entire, terminating in angular point; propodus distal margin unarmed; merus outer inferodistal angle rounded.

Maxilliped 5 basal segment without ventrally directed distal tooth. Pereopod 1–3 basal segments unarmed; endopod slender, 2-segmented.

TS5–8 submedian and intermediate carinae distinct. TS5 lateral process slender, straight, apex acute, directed laterally; with short, triangular, ventrally directed spine. TS6–7 lateral process rounded, inclined posteriorly, usually with short posterolateral spine. TS8 anterolateral margin triangular, apex rounded; sternal keel slender, directed ventrally apex blunt to pointed.

Pleopod 1 endopod with posterior 'endite'; tube process about as long as hook process; hook process apex sharp.

AS1–5 submedian carinae distinct, subparallel to slightly divergent posteriorly, distance between submedian carinae about one-third distance between intermediate carinae. AS5 posterior margin with 0–6 spinules (usually 2 or 3) between submedian and intermediate carinae. AS6 submedian carinae subparallel; posterior margin between submedian and intermediate spines rarely with accessory spinule; minute ventral spine or denticle anterior to uropodal articulation; posterior margin of sternum unarmed. Adult males with swollen pleura between intermediate and marginal carinae. Abdominal carinae spined as follows: submedian 6, intermediate (1–3)4–6, lateral (1–3)4–6, marginal (1)2–5.

Telson flattened, subquadrate, wider than long; dorsal carina of submedian, intermediate and lateral teeth short, distinct; movable apices of submedian teeth small blunt. Dorsolateral surface finely rugose, with few curved, shallow grooves or pits; median carina with posterior spine. Submedian denticle blunt, often with minute secondary spinules in juveniles. Intermediate denticles frequently with bifurcate apices; submedian 1–2, intermediate 7–13, lateral 1. Telson ventral ventrolateral carina absent; post-anal carina distinct, reaching posteriorly to or slightly beyond midpoint between anal pore and median posterior margin.

Uropodal protopod terminal spines divergent, inner about twice length of outer; lobe on outer margin of inner spine rounded, narrower than to wider than adjacent spine, margin uneven, straight to concave; with minute spine or denticle anterior to endopod articulation; protopod outer margin smooth, inner margin crenulate. Uropodal exopod proximal segment longer than distal segment; with distoventral spine and 7–9 movable spines on outer margin, distal spine almost reaching midlength of distal segment.

COLOUR IN LIFE. (Frontispiece 2D) Overall dusky pale gray-brown. Post-erolateral margins of AS5–6 dark red, extending onto intermediate and lateral carinae on AS6. Telson margins dull yellow-orange. Uropodal protopod dirty white; proximal half with diffuse reddish highlights dorsally. Uropodal exopod distal segment and distal half of endopod yellow. Raptorial claw merus white with diffuse brown dorsal mottling; carpus white with light pink lateral surface and dark red articulation with merus; propodus and dactylus white.

MEASUREMENTS. Male ($n = 49$) TL 19–147 mm; female ($n = 57$) TL 32–135 mm. Other measurements of the neotype: CL 17.3 mm, antennular peduncle 16.8 mm, antennal scale 9.5 mm, cornea width 3.7 mm, anterior carapace width 9.5 mm. The present series includes the largest known specimens of the species.

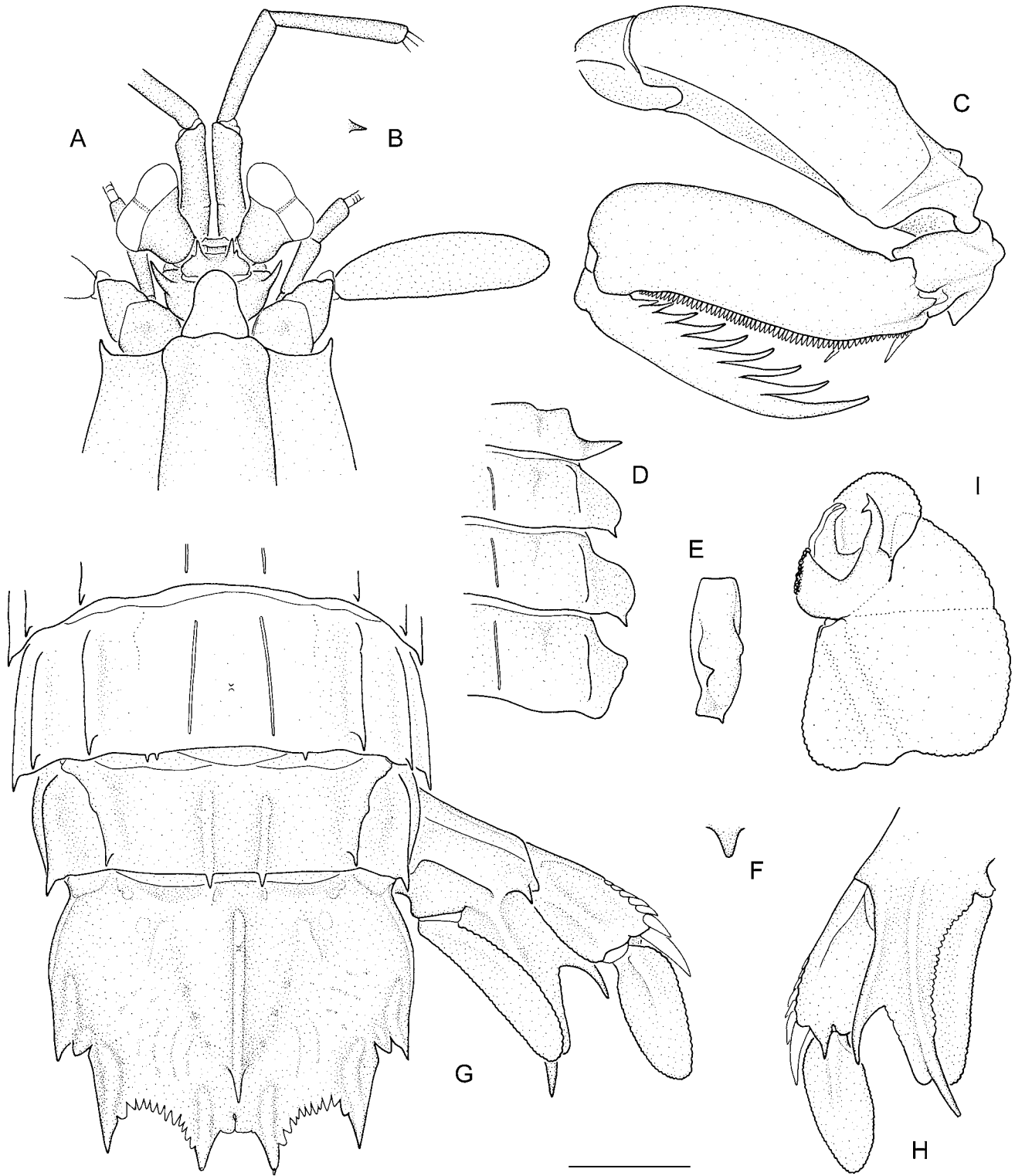


Figure 43. *Pterygosquilla schizodontia* (Richardson, 1953), male neotype, TL 81 mm, Petone, Wellington Harbour (NMNZ Cr9360). A, anterior cephalothorax; B, right dorsal process of antennular somite, lateral view; C, right raptorial claw; D, TS6–8, right dorsal view; E, TS5, right lateral view; F, TS8 sternal keel, right lateral view; G, AS4–6, telson and right uropod, dorsal view; H, right uropod, ventral view; I, right pleopod 1 endopod, anterior view. Scale A–H = 5.0 mm; I = 2.5 mm.

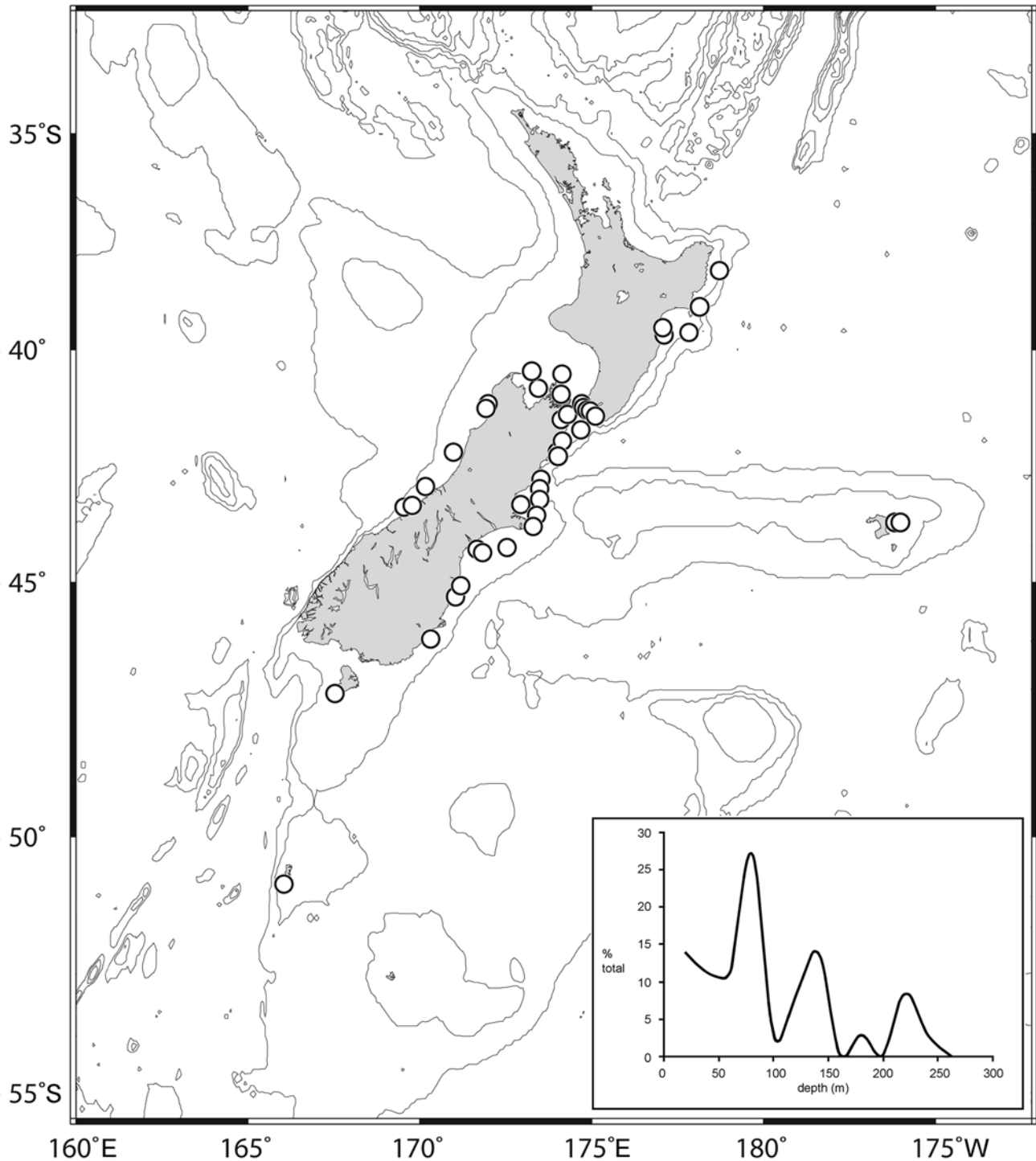


Figure 44. New Zealand distribution of *Pterygosquilla schizodontia* (Richardson, 1953).

HABITAT. Inshore and shallow shelf waters, especially embayments and sheltered sites with level sandy-mud or mud substrates suitable for burrowing; 6–213 m depth, but usually between 50 and 100 m. Morton & Miller (1968) indicated that *P. schizodontia* (as *Squilla armata*) may occur intertidally, but their observation was based on misidentified *Pariliacantha georgeorum*.

Likewise, the photo caption in Anonymous (1964) indicating an intertidal to 100 fathom bathymetric range of *P. schizodontia* (as *Squilla armata*) is probably erroneous for the intertidal. Several specimens were taken from fish stomachs including those of the chondrichthyans, *Mustelus lenticulatus* Phillipps (Triakidae) and *Dasyatis brevicaudata* (Hutton) (Dasyatidae).

REMARKS. Manning (1969a) recognised three subspecies of *Pterygosquilla armata*: *P. a. armata* (H. Milne Edwards, 1837), *P. a. capensis* Manning 1969a, and *P. a. schizodontia* (Richardson, 1953). Characters originally used by Richardson (1953) to distinguish *P. a. schizodontia* from the nominate subspecies, the sometimes bifid telson denticles and spinular posterior margins of AS5, are unreliable, being shared by both forms (Manning 1966). Manning (1969a), however, proposed other distinguishing features for specimens TL 100 mm or larger: the distinctness of the abdominal submedian carinae, the distance between the abdominal submedian carinae and the size of the lobe between the terminal spines of the uropodal protopod. The utility of first two morphological features is corroborated herein, but the third feature is not reliable. The lobe on the outer margin of the inner spine of the uropodal protopod is present in many squilloids and its proportional width relative to the protopodal spine typically decreases with increasing body size. Thus, the size and shape of the uropodal lobe typically varies predictably and is often a useful diagnostic character providing the range of variation given body size is considered. Manning (1969a) distinguished *armata* sensu stricto from *schizodontia* and *capensis* of TL 100 mm and larger by the size of the uropodal lobe, being low with a straight or convex margin in the former, being prominent and rounded with a concave margin in the latter two. Whilst adults with the largest the uropodal lobes are always of *schizodontia* (prominent and wider than the adjacent spine), the lobe size ranges down to being slightly narrower than the adjacent spine. In *armata*, the uropodal lobe may be extremely low, almost obsolete, but in its upper range, the lobe can be rounded and slightly narrower than the adjacent spine. Thus, lobe size at the lower end of variation in *schizodontia* overlaps the upper end of variation in *armata*. In *capensis*, the size of the lobe between the uropodal protopodal spines is somewhat intermediate between those of *armata* and *schizodontia*. The size of the uropodal lobe remains a useful taxonomic character in *Pterygosquilla* if used carefully in conjunction with other characters. An additional feature identified here that may distinguish *schizodontia* from *armata* and *capensis* is the shape of the rostral plate, being relatively wide anteriorly, with a broadly rounded apex. In *armata* and *capensis*, the rostral plate is more strongly triangular, with a narrow, rounded apex. Of the three *armata*-like species, *P. schizodontia* is morphologically most similar to *P. armata*, sharing distinct abdominal submedian carinae and posterior spinules on AS5.

The large series of *Pterygosquilla* examined herein corroborates the stability of most diagnostic characters of the var. *schizodontia* identified by Manning (1969a). Distinctions between the three nominal subspecies of *P. armata* appear consistent and each has a discrete and limited distribution, with *schizodontia* known only from

New Zealand, *capensis* known only from South Africa, and *armata* known only from southern South America. Therefore, in view of the discrete morphologies and distributions of the nominal subspecies of *P. armata*, each is recognised as a separate species. Four species of *Pterygosquilla* are recognised: *P. armata*, *P. capensis*, *P. gracilipes*, and *P. schizodontia*.

Distinctions between *P. armata* and *P. schizodontia* are subtle and Richardson (1953) did not specify a holotype or type series for *P. schizodontia*, but his listed specimens are syntypes by default. Unfortunately, all specimens reported by Richardson (1953) are now lost. Some specimens examined by Richardson during the 1950s and 60s are still extant in the NMNZ and USNM but these do not include any of the original syntypes. They neither fit morphologically nor with collection data of the type material (Richardson 1953). Schram & Müller (2004) listed a female (NHM 45.69) from Laurie Harbour, Auckland Islands, as a type specimen of *P. schizodontia*, but this attribution is not correct. All type specimens were collected from either Cook Strait or Napier. Therefore, a neotype male (TL 81 mm, NMNZ Cr9360) is herein selected from Wellington Harbour, on Cook Strait, in order to fix the identity of *P. schizodontia*.

Morphological variation in *P. schizodontia* is marked, particularly in the number of teeth on the dactylus of the raptorial claw (6–9, usually 7 or 8); the number of accessory spinules on the posterior margin of AS5; and the condition of the intermediate denticles of the telson. The posterior accessory spinulation of AS5 ranges from 0–6 on each side, usually 2 or 3, the number generally correlating with body size. Specimens smaller than about TL 40 mm lack accessory spinules; larger specimens almost invariably have one or more accessory spinules, often varying from left to right. Only one specimen larger than TL 40 mm lacked any trace of accessory spinules on either side (male, TL 120 mm, AM P87906, Frontispiece 2D). Accessory spinules are usually distinct, but may be incipient, represented by a small bump on the somite margin. As in *P. armata* sensu stricto, one or more intermediate denticles of the telson of *P. schizodontia* are frequently secondarily bifurcated, particularly in large adults. The distribution of bifurcate denticles follows no obvious pattern, however, varying between left and right sides. Other minor variation is as follows: the rostral plate is about as long as wide, ranging from being slightly longer to slightly wider; the posterolateral spine of the lateral processes of TS6 and 7 is occasionally bifurcate or absent; an additional small spinule is occasionally present lateral to the main spine of each ocular scale; and the apex of the TS8 sternal keel ranges from bluntly rounded to sharp.

Sexual dimorphism in *P. schizodontia* is typical of other squilloids – males have a stouter propodus on

the raptorial claw and more inflated dorsal carinae on the telson teeth. An unusual form of sexual dimorphism in large males of *Pterygosquilla* is swollen or expanded abdominal pleura between the lateral and marginal carinae, giving the body of large males a higher, deeper appearance than females. *Pterygosquilla schizodontia* might also mature at a larger size than *P. armata*. The pleopod 1 endopod of males is fully modified by TL 51 mm in *P. schizodontia* and by TL 36 mm in *P. armata* (Ahyong, unpubl.).

Larval development of *P. schizodontia* (see Pyne 1972, as *Squilla armata*) includes two propelagic and nine pelagic stages and is similar to other squillids such as *O. oratoria*. Larval duration, however, is extended. Eggs are incubated for 72–74 days, and, rather than lasting less than two months typical of warm-water squillids, larval development in *P. schizodontia* lasts approximately nine months, perhaps reflecting the colder, subantarctic habitat of the species.

Pterygosquilla schizodontia is common in inshore and shallow shelf waters on sandy-mud or mud substrates

from Wellington Harbour, Cook Strait, and around the South Island. It ranges south to at least the Auckland Islands and is occasionally found as far north as East Cape, North Island, where it can be sympatric with *Anchisquilloides mcneilli*, the dominant North Island squilloid. Reports of *P. schizodontia* (as *Squilla armata*) from southern Australia (Whitelegge 1900; Anonymous 1964) are based on misidentified *A. mcneilli*.

Pterygosquilla schizodontia is frequently preyed on by demersal fishes such as dogfish and ling. The carapace of one specimen (AM P87907) is partially encrusted by the bryozoan, *Antarctothoa tongima* (Ryland & Gordon), and represents the first record of a bryozoan-stomatopod association.

DISTRIBUTION. Presently known only from New Zealand, from the Gisborne region to Wellington, Cook Strait, the Chatham Islands, Dunedin, Otago, and the Auckland Islands.

DISCUSSION

Twenty species of Stomatopoda in 13 genera and seven families are now known from New Zealand waters, more than doubling the most recent previous estimate (Webber *et al.* 2010). The New Zealand Stomatopoda comprises a widespread tropical component (nine species or 45%) and a temperate-water component of which eight species (40%) are endemic, one is introduced (5%) and two species (10%) are shared with eastern Australia. The tropical component comprises widespread tropical Indo-West Pacific species that occur along the Norfolk and Kermadec Ridges south to northern New Zealand at the southern end of their ranges in the southwestern Pacific. These species are primarily gonodactyloids (*Gonodactylaceus falcatus*, *Gonodactylellus viridis*, *Gonodactylellus osheai*, *Gonodactylus platysoma*, *Odontodactylus scyllarus*, *O. hawaiiensis*, and *Haptosquilla helleri*), but also include a squilloid (*Oratosquilla fabricii*) and a bathysquilloid (*Bathysquilla microps*). A parallel situation obtains on the Australian East coast for stomatopods common on the Great Barrier Reef and coastal tropical Queensland, but which range south into temperate southeastern Australia, such as *Gonodactylaceus falcatus*, *Gonodactylus chiragra*, *Gonodactylus smithii*, *O. scyllarus*, *Pseudosquilla ciliata*, and numerous squilloids including species of *Harpioquilla* and *Erugosquilla* (Ahyong 2001).

In both eastern Australia and northern New Zealand, penetration of tropical species into temperate waters is facilitated by warm currents originating in the north such as the East Australian Current and Tasman Front. The Tasman Front significantly influences North Island hydrography via the West Auckland Current along the north-west coast and the East Auckland Current along the north-east coast (Carter & Garlick 1998; Gordon *et al.* 2010). Only four of nine warm-water stomatopod species from New Zealand, however, also occur in north-eastern Australia (*Gonodactylaceus falcatus*, *Gonodactylus platysoma*, *Odontodactylus scyllarus* and *Bathysquilla microps*). In the south-western Pacific, *Odontodactylus hawaiiensis*, *Oratosquilla fabricii* and *Gonodactylellus viridis* occur only as far west as New Caledonia (although *G. viridis* is also known from north-western Australia and *O. fabricii* from Indonesia). *Haptosquilla helleri* also occurs north of New Zealand including Tonga and the South China Sea, but is not yet known from New Caledonia or eastern Australia. Thus, the presence of tropical stomatopods in New Zealand that otherwise only occur east of the New Hebrides suggests that in addition to trans-Tasman supply, northern New Zealand probably may also receive significant tropical propagule input from the central-western Pacific. Given the cryptic habits

of stomatopods, numerous species in New Zealand waters have probably been overlooked, and further exploration of Northland habitats will almost certainly yield further tropical species.

Apart from *Hemisquilla australiensis* and *Anchisquilloides mcneilli*, which are shared with south-eastern Australia, the temperate-water New Zealand stomatopods are endemic. These endemics are dominated by tetrasquillid lysiosquilloids: the Southern Hemisphere genus *Heterosquilla* and two endemic genera *Colubrisquilla* and *Pariliacantha*. Notably, five of the eight known species of *Heterosquilla* are New Zealand endemics; the New Zealand stomatopod fauna could be said to be 'characterised' by tetrasquillids. New Zealand appears to be the 'centre of diversity' for *Heterosquilla*, but whether or not the genus evolved in the region requires further phylogenetic and biogeographic research. In contrast to the endemic tetrasquillids, the similarly diverse New Zealand gonodactyloids are primarily widespread species or species that are probably only occasional or temporary residents; only *Hemisquilla australiensis* among the gonodactyloids is limited to temperate waters. As with the brachyuran crabs (Dell 1968), this temperate component of the New Zealand Stomatopoda can be further divided into species occurring throughout mainland waters, a northern group and a southern group essentially occurring on either side of the subtropical convergence at the Chatham Rise. Three stomatopod species, all of *Heterosquilla*, *H. laevis*, *H. koning* and *H. tricarinata*, range throughout New Zealand, from Northland to the Chatham Islands, south to at least Stewart Island.

Northern temperate-water species occurring only around the North Island are *Pariliacantha georgeorum* and *Hemisquilla australiensis*. *Pariliacantha georgeorum* is recorded from around most of the North Island apart from Cook Strait and *H. australiensis* is not known south of New Plymouth in the west or East Cape in the east. *Anchisquilloides mcneilli* and *Heterosquilla trifida* are also primarily North Island species that reach to the northern tip of the South Island. *Colubrisquilla dempsey* is known only from localities between East Cape and the Chatham Rise. The introduced *Oratosquilla oratoria* is currently restricted to two upper North Island localities (Kaipara and Hokianga).

Among the southern temperate species only *H. tridentata* is apparently restricted to South Island coastal waters, ranging from Oamaru to the Auckland Islands. *Pterygosquilla schizodontia* is common around the South Island, but occasionally occurs as far north as East Cape. Five species occur on the Chatham Rise (*Colubrisquilla dempsey*, *Heterosquilla koning*, *Heterosquilla tricarinata*, *Heterosquilla laevis*, *P. schizodontia*) and three range south to the Auckland Islands (*H. laevis*, *H. tridentata*, *P. schizodontia*).

Two major marine biogeographic provinces are traditionally recognised around New Zealand (summarised by Morton 2004): a northern region influenced by subtropical water masses ranging from Northland south to East Cape in the east or Cape Egmont in the west (fide Pawson 1961), the Aupourian Province; and a southern mixed zone swept by cooler southern water masses taking in the remainder of mainland New Zealand, the Cookian Province. Smaller proposed divisions include the Kermadec Province for the Kermadec Islands fauna, the Moriorian Province for the Chatham Islands and the Antipodean Province for the subantarctic islands. The distributions of the New Zealand stomatopods only partially corroborate the traditionally recognised biogeographic provinces. Stomatopods with an exclusively Aupourian distribution include the temperate water species *Hemisquilla australiensis*, the introduced *Oratosquilla oratoria* and eight tropical Indo-West Pacific species (*Bathysquilla microps*, *Gonodactylaceus falcatus*, *Gonodactylellus viridis*, *Gonodactylus platysoma*, *Odontodactylus scyllarus*, *Oratosquilla fabricii*, *Haptosquilla helleri* and probably also *Gonodactylellus osheai*). Most of these, however, are known from only single or few records; only *H. australiensis* has a well known Aupourian range. Three stomatopod species have Cookian distributions: *Colubrisquilla dempsey*, *Heterosquilla tridentata* and *Pterygosquilla schizodontia*, although the latter two also range to the Auckland Islands in the Antipodean Province. *Odontodactylus hawaiiensis*, the only stomatopod known from the Kermadec Islands, occupies the Kermadec Province. All other New Zealand stomatopods variously span both major biogeographic provinces, some very wide-ranging such as *Heterosquilla koning*, *H. laevis* and *H. tricarinata* (Northland to at least Stewart Island), others spanning only the North Island (e.g. *Pariliacantha georgeorum*), and others embracing the North Island and upper South Island (e.g. *Anchisquilloides mcneilli*, *Heterosquilla trifida*). Although East Cape marks a biogeographic discontinuity for several temperate species (*Hemisquilla australiensis*, *Colubrisquilla dempsey*, *Pterygosquilla schizodontia*), it is clearly not a barrier for many others and overall, New Zealand stomatopod distributions do not closely reflect the traditional marine biogeographic provinces. New Zealand stomatopod distributions do, however, generally validate a northern and southern marine biota recognised by many workers (Shears *et al.* 2008), whose ranges are largely influenced by the interaction of warm northern and cool southern water masses.

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SPECIES INDEX

Principal taxonomic account is in bold font; species illustrations in bold italic.

<i>Acaenosquilla</i>	8, 47, 73	<i>Distosquilla</i>	79, 93
<i>Acaenosquilla brazieri</i>	8, 74, 77	<i>Echinosquilla</i>	42
<i>Acaenosquilla latifrons</i>	77	<i>Erugosquilla</i>	78, 79, 99
Alainosquillidae	18	<i>Eurysquilla</i>	48
<i>Alima</i>	78	Eurysquilloidea	78
<i>Alimopsis</i>	78	<i>Fallosquilla</i>	79
<i>Alimopsoides</i>	78	<i>Fennerosquilla</i>	79
<i>Allosquilla</i>	47	<i>Gibbesia</i>	79
<i>Altosquilla</i>	14	Gonodactylidae	13, 18
<i>Anchisquilla</i>	78	Gonodactyloidea	6, 13, 14, 18
<i>Anchisquilloides</i>	78, 79	Gonodactylaceus	13, 19
<i>Anchisquilloides mcneilli</i>	6, 13, 73, 79, 81, 82, 99, 100	<i>Gonodactylaceus falcatus</i>	13, 19, 20, 21, 28, 42, 99, 100
<i>Anchisquilloides michelae</i>	79, 85	<i>Gonodactylaceus glabrous</i>	19
<i>Anchisquillopsis</i>	78, 79	<i>Gonodactylaceus graphurus</i>	19
<i>Antarctothoa tongima</i>	99	<i>Gonodactylaceus gravieri</i>	19
<i>Arabella iricolor</i>	59, 69	<i>Gonodactylaceus randalli</i>	19
<i>Areosquilla</i>	78	<i>Gonodactylaceus ternatensis</i>	19
<i>Austrosquilla</i>	73	<i>Gonodactylellus</i>	19, 23
<i>Austrosquilla malayensis</i>	65	<i>Gonodactylellus affinis</i>	23
<i>Austrovenus stutchburyi</i>	59, 69	<i>Gonodactylellus annularis</i>	23
<i>Bathysquilla</i>	14	<i>Gonodactylellus barberi</i>	23, 25
<i>Bathysquilla crassispinosa</i>	14, 18	<i>Gonodactylellus bicarinatus</i>	23
<i>Bathysquilla microps</i>	4, 6, 8, 13, 14, 15, 16, 99, 100	<i>Gonodactylellus caldwelli</i>	23
Bathysquillidae	13, 14	<i>Gonodactylellus choprai</i>	23
Bathysquilloidea	6, 13, 14	<i>Gonodactylellus crosnieri</i>	23
<i>Belosquilla</i>	78	<i>Gonodactylellus demanii</i>	23, 25
<i>Belosquilla laevis</i>	7	<i>Gonodactylellus diana</i>	23, 25
<i>Branchiomma serratibranchis</i>	59, 69	<i>Gonodactylellus erdmanni</i>	23
<i>Busquilla</i>	79	<i>Gonodactylellus espinosus</i>	23
<i>Callianassa filholi</i>	59, 69, 77	<i>Gonodactylellus incipiens</i>	23
<i>Cancer falcatus</i>	19	<i>Gonodactylellus kandi</i>	23
<i>Cancer scyllarus</i>	36, 39	<i>Gonodactylellus lanchesteri</i>	23
<i>Carinosquilla</i>	79	<i>Gonodactylellus micronesicus</i>	23
<i>Chorisquilla</i>	42	<i>Gonodactylellus molyneux</i>	23, 25
<i>Clorida</i>	79	<i>Gonodactylellus osheai</i> sp. nov.	6, 13, 23, 24, 28, 99, 100
<i>Cloridina</i>	79	<i>Gonodactylellus rubriguttatus</i>	23
<i>Cloridopsis</i>	79	<i>Gonodactylellus spinosus</i>	23
<i>Coelorinchus</i>	51	<i>Gonodactylellus snidvongsi</i>	23, 25
<i>Colubrisquilla</i> gen. nov.	6, 47, 100	<i>Gonodactylellus viridis</i>	13, 19, 23, 25, 26, 27, 31, 99, 100
<i>Colubrisquilla dempsey</i> gen. et sp. nov.	6, 13, 47, 48, 49, 50, 100	Gonodactyloideus	19
Coronididae	46	<i>Gonodactylolus</i>	19
<i>Coronis spinosa</i>	7, 60	<i>Gonodactylopsis</i>	19
<i>Coronis tricarinata</i>	7, 60, 65	<i>Gonodactylus</i>	19, 29
<i>Crenatosquilla</i>	79	<i>Gonodactylus acutirostris</i>	29
<i>Dasyatis brevicaudata</i>	97	<i>Gonodactylus aloha</i>	19
<i>Dictyosquilla</i>	79	<i>Gonodactylus bleekeri</i>	39

<i>Gonodactylus botti</i>	29	<i>Heterosquilla spinosa</i>	8, 55, 60, 65
<i>Gonodactylus childi</i>	29	<i>Heterosquilla tricarinata</i>	5, 6, 8, 13, 52, 55, 59, 60, 61 , 62, 69, 77, 100
<i>Gonodactylus chiragra</i>	19, 29, 99	<i>Heterosquilla tridentata</i>	8, 13, 52, 55, 59, 60, 65, 66, 67 , 68, 73, 100
<i>Gonodactylus cultrifer</i>	36	<i>Heterosquilla trifida</i> sp. nov.	6, 13, 52, 55, 60, 66, 69, 70, 71 , 72, 100
<i>Gonodactylus elegans</i>	39	Heterosquillidae	46
<i>Gonodactylus glaber</i>	19, 43, 45, 46	<i>Heterosquilloides</i>	47, 48
<i>Gonodactylus insularis</i>	19	<i>Heterosquilloides insignis</i>	51
<i>Gonodactylus lenzi</i>	43	<i>Heterosquilloides insolita</i>	51
<i>Gonodactylus platysoma</i>	13, 28, 29, 30 , 31, 65, 99, 100	<i>Heterosquillopsis</i>	47, 73
<i>Gonodactylus pulchellus</i>	43	<i>Hoplosquilla</i>	19
<i>Gonodactylus siamensis</i>	19	<i>Hoplosquilloides</i>	19
<i>Gonodactylus smithii</i>	29, 99	<i>Humesosquilla</i>	79
<i>Gonodactylus styliferus</i>	32	Indosquillidae	14
<i>Gonodactylus takedai</i>	19	<i>Kaisquilla</i>	79
<i>Gonodactylus trispinosus</i>	7, 43, 45, 46	<i>Kasim</i>	47, 73
<i>Haptosquilla</i>	42, 43	<i>Kempella</i>	79
<i>Haptosquilla corrugata</i>	43	<i>Kempina</i>	79
<i>Haptosquilla ectypa</i>	43, 46	<i>Lenisquilla</i>	79
<i>Haptosquilla glabra</i>	43, 45, 46	<i>Leptosquilla</i>	79
<i>Haptosquilla glyptocercus</i>	43	<i>Levisquilla</i>	79
<i>Haptosquilla hamifera</i>	43	<i>Lophosquilla</i>	79
<i>Haptosquilla helleri</i> sp. nov.	6, 13, 43, 44 , 45, 99, 100	<i>Lyreidus tridentatus</i>	28
<i>Haptosquilla lenzi</i>	43	<i>Lysiosquilla</i>	7, 52, 55, 70, 73
<i>Haptosquilla moosai</i>	43	<i>Lysiosquilla brazieri</i>	7, 8, 74, 77
<i>Haptosquilla philippinensis</i>	43	<i>Lysiosquilla microps</i>	14
<i>Haptosquilla proxima</i>	43	<i>Lysiosquilla platensis</i>	51
<i>Haptosquilla pulchella</i>	43	<i>Lysiosquilla spinosa</i>	7, 52, 55, 60, 65
<i>Haptosquilla pulchra</i>	43	<i>Lysiosquilla tricarinata</i>	60
<i>Haptosquilla stoliura</i>	43	Lysiosquillidae	46
<i>Haptosquilla tanensis</i>	43	Lysiosquilloidea	6, 13, 14, 46
<i>Haptosquilla togianensis</i>	43	<i>Lysmata vittata</i>	28
<i>Haptosquilla trispinosa</i>	43, 46	<i>Meiosquilla</i>	79, 93
<i>Haptosquilla tuberosa</i>	43	<i>Miyakea</i>	79
<i>Harpiosquilla</i>	79, 99	<i>Munida</i>	59, 69
Harpiosquillidae	78	<i>Mustelus lenticulatus</i>	97
<i>Hemisquilla</i>	32	Nannosquillidae	46
<i>Hemisquilla australiensis</i>	4, 8, 13, 32, 33, 34 , 35, 100	<i>Natosquilla</i>	79
<i>Hemisquilla braziliensis</i>	32	<i>Neclorida</i>	79
<i>Hemisquilla californiensis</i>	32	<i>Neoanchisquilla</i>	79
<i>Hemisquilla ensigera</i>	32, 33	<i>Neogonodactylus</i>	19
<i>Hemisquilla ensigera australiensis</i>	8, 33	Odontodactylidae	13, 18, 36
Hemisquillidae	13, 18, 32	<i>Odontodactylus</i>	36
<i>Heterosquilla</i>	6, 7, 47, 48, 51 , 93, 100	<i>Odontodactylus brevirostris</i>	8, 36, 39
<i>Heterosquilla koning</i> sp. nov.	6, 13, 52, 53 , 54, 60, 66, 100	<i>Odontodactylus hansenii</i>	36
<i>Heterosquilla laevis</i>	6, 13, 52, 55, 57 , 58, 65, 66, 77, 100	<i>Odontodactylus havanensis</i>	36
<i>Heterosquilla pentadactyla</i>	52, 55, 60, 66, 69, 70, 73	<i>Odontodactylus hawaiiensis</i>	4, 13, 36, 37 , 38 , 99
<i>Heterosquilla platensis</i>	52, 66	<i>Odontodactylus japonicus</i>	36, 39, 42
<i>Heterosquilla polydactyla</i>	52, 66	<i>Odontodactylus latirostris</i>	36
		<i>Odontodactylus scyllarus</i>	13, 36, 39, 40 , 41, 99, 100
		<i>Oratosquilla</i>	78, 79, 85

<i>Oratosquilla calumnia</i>	86	<i>Schmittius</i>	79
<i>Oratosquilla fabricii</i>	13, 85, 86 , 87 , 88, 92, 100	<i>Scylla serrata</i>	28
<i>Oratosquilla kempii</i>	86	<i>Siamosquilla</i>	42
<i>Oratosquilla mauritiana</i>	86	<i>Siamosquilla laevicaudata</i>	46
<i>Oratosquilla oratoria</i>	5, 8, 13, 65, 85, 86, 89 , 90 , 91, 99, 100	<i>Squilla</i>	78, 79
<i>Oratosquillina</i>	79, 89	<i>Squilla affinis</i>	7, 8, 86, 89, 92
<i>Paralimopsis</i>	79	<i>Squilla armata</i>	7, 8, 74, 77, 79, 93, 97, 99
<i>Parasquilloidea</i>	78	<i>Squilla armata schizodontia</i>	7
<i>Pariliacantha</i> gen. nov.	6, 47, 73 , 100	<i>Squilla calumnia</i>	86
<i>Pariliacantha georgeorum</i> gen. et sp. nov.	4 , 6, 13, 59, 73, 74 , 75 , 76, 100	<i>Squilla chiragra</i>	29
<i>Parvisquilla</i>	79	<i>Squilla fabricii</i>	86
<i>Pontiosquilla</i>	79	<i>Squilla indefensa</i>	7, 60, 65, 69
<i>Protosquillidae</i>	13, 18, 42	<i>Squilla laevis</i>	7, 55, 65
<i>Protosquilla</i>	42	<i>Squilla mcneilli</i>	79
<i>Protosquilla trispinosa</i>	7, 8, 43	<i>Squilla nepa</i>	7, 8, 86, 89, 92
<i>Pseudosquilla ciliata</i>	99	<i>Squilla oratoria</i>	85, 89
<i>Pseudosquillidae</i>	18	<i>Squilla tridentata</i>	7, 65, 66, 69
<i>Pterygosquilla</i>	8, 79, 92	<i>Squillidae</i>	13, 78
<i>Pterygosquilla armata</i>	85, 93, 98, 99	<i>Squilloidea</i>	6, 13, 14, 78
<i>Pterygosquilla capensis</i>	93, 98	<i>Squilloides</i>	79, 93
<i>Pterygosquilla gracilipes</i>	93, 98	<i>Stenopus hispidus</i>	28
<i>Pterygosquilla laticauda</i>	92	<i>Takuidae</i>	18
<i>Pterygosquilla schizodontia</i>	5, 6, 8, 13, 77, 85 , 93 , 96 , 97, 100	<i>Tawera bollonsi</i>	59, 69
<i>Pullosquilla</i>	73	<i>Tectasquilla</i>	47
<i>Quollastria</i>	79	<i>Tetrasquilla</i>	47
<i>Raoulius</i>	36	<i>Tetrasquillidae</i>	13, 46
<i>Rayellus</i>	42	<i>Tuleariosquilla</i>	79
<i>Rissoides</i>	79	<i>Ursquillidae</i>	78
		<i>Ursquilla</i>	78
		<i>Visaya</i>	79