

ISSN: 0028-8306

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To cite this article: Barry W. M. van Bakel & Àlex Ossó (27 Feb 2024): A new 'Southern Giant Crab' from a miocene continental slope palaeoenvironment at Taranaki, North Island, New Zealand, New Zealand Journal of Geology and Geophysics, DOI: [10.1080/00288306.2024.2314472](https://doi.org/10.1080/00288306.2024.2314472)

To link to this article: <https://doi.org/10.1080/00288306.2024.2314472>



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Published online: 27 Feb 2024.



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A new 'Southern Giant Crab' from a miocene continental slope palaeoenvironment at Taranaki, North Island, New Zealand

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ABSTRACT

Large-sized extinct crab specimens recovered from Waitoetoe beach, North Island, New Zealand form the basis for a new species of 'Southern Giant Crab', *Pseudocarcinus karlraubenheimeri* n. sp. The specimens originate from the upper Miocene Urenui Formation (approximately 8.8 myr) of the Taranaki Basin, in which a series of volcanoes of the Mohakaiti Volcanic Centre erupted offshore, leading to the formation of a specific palaeoenvironment. The well-preserved, articulated specimens were found buried in sediments which include reworked volcanogenic material. The crabs inhabited a deep-marine setting. This is the first evidence that *Pseudocarcinus* inhabited the region that is now New Zealand. New Zealand Miocene environments apparently offered favourable conditions in terms of food sources, metabolic requirements, and calcium-carbonate supply for *Pseudocarcinus karlraubenheimeri* n. sp. *Pseudocarcinus* thrived on both sides of the Tasman Sea until it disappeared in New Zealand waters. *Pseudocarcinus* crabs are characterised by gigantism, which provided them with significant advantages in competition and defence. Their carnivorous nature is reflected in their exceptionally large major cheliped. The broader use of benthic dwelling gastropods and bivalves as prey seems to have led to subsequent advances in brachyuran claw engineering, and an increase of molluscivorous crabs in the Late Cretaceous and Palaeogene.

Zoobank: urn:lsid:zoobank.org:pub:B53DB047-B18C-4CA4-946F-5E9209A581F2

ARTICLE HISTORY

Received 25 September 2023
Accepted 25 January 2024

HANDLING EDITOR

Elizabeth Kennedy

KEYWORDS

Brachyura; Pseudocarcinidae; new species; Taranaki Basin; Urenui Formation; volcanic deposits

Introduction

The extant 'Southern Giant Crab' *Pseudocarcinus gigas* (Lamarck 1818) ranks amongst the largest crabs ever to have lived; at present, it is endemic to the cool-temperate southern Australian continental margin, although there is also a single record of a female individual caught off the South Island of New Zealand (Levings 2008, p. 49). Ng and Davie (2020) recognised and described the unique morphological character set of this monotypic genus and erected a new family and superfamily to accommodate it. Unfortunately, the geological history of this remarkable group of crabs is poorly known.

Fossil crab faunas from New Zealand have been studied quite extensively (e.g. Woodward 1876; Glaessner 1960, 1980; Dell 1969; Feldmann and Maxwell 1990; Feldmann and Keyes 1992; Feldmann 1993, 1998a, 1998b; Feldmann and McLay 1993; McLay et al. 1995; Feldmann and Fordyce 1996; Feldmann et al. 2006, 2008). Glaessner (1960, p. 23, 24, pl. 3, fig. 11) recorded and described a dactylus of a large claw from uppermost Miocene to lower Pliocene strata at Goldsborough, South Island, which he assigned to

Pseudocarcinus sp. Until now, this was the sole fossil record of the genus from New Zealand. In contrast, *Pseudocarcinus* fossils have been recorded from the Oligocene to Quaternary faunas of Australia (Jenkins 1972, 1974, 1985; Glaessner 1980).

Here we erect a new species of *Pseudocarcinus* from the Miocene of Taranaki, North Island (New Zealand), which originates from a highly specific palaeoenvironment.

Locality and stratigraphy

The present crabs were collected from Waitoetoe Beach, Urenui (Taranaki, North Island) (Figures 1 and 2), near Waitoetoe Campsite, just south of the mouth of Mimi stream. This is sometimes referred to as the 'Mimi Beach locality' (see e.g. King et al. 2007, p. 262; Maier et al. 2016: table 1, locality U-C-27). This locality is now registered in the New Zealand Fossil Record File, jointly managed by GNS Science and Geoscience Society of New Zealand, as Q19/f6523A (<https://doi.org/10.21420/JQQB-NK89>), and available online in the Fossil Record Electronic

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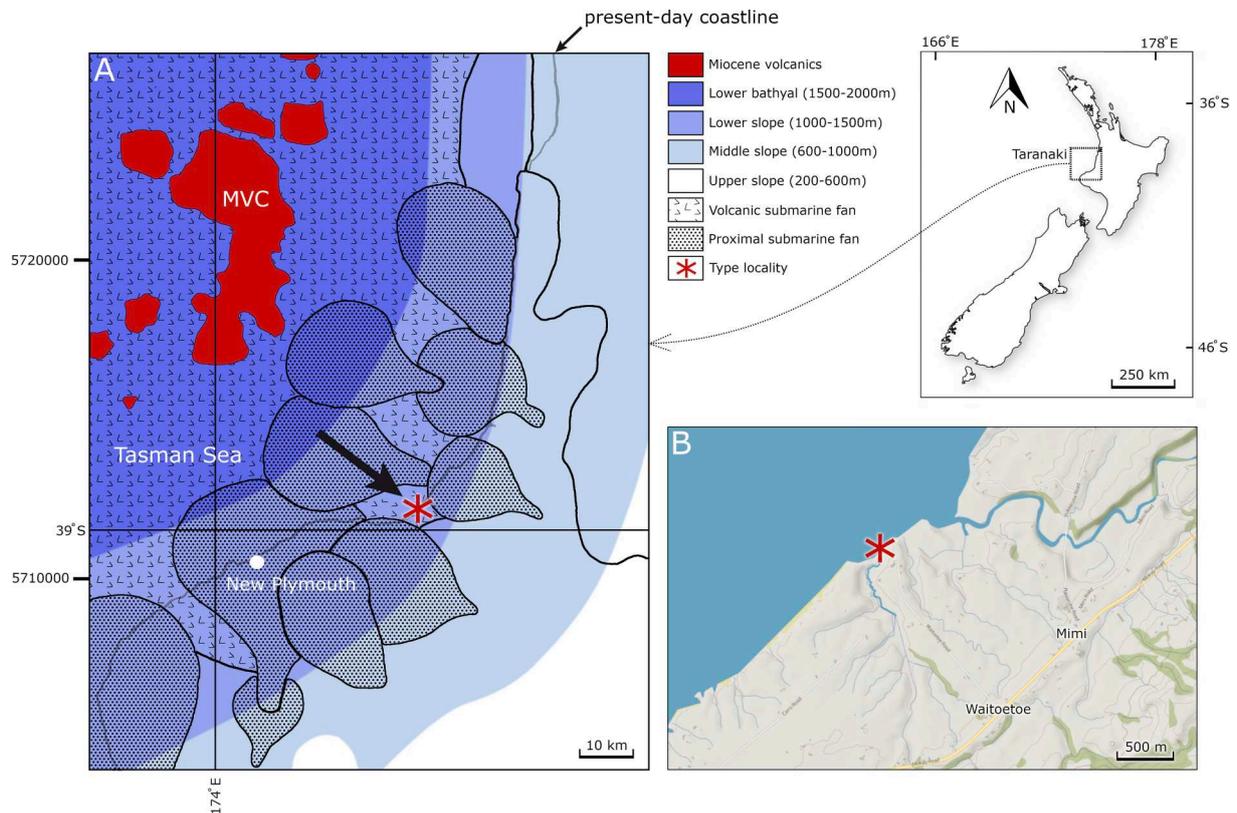


Figure 1. **A**, Early Tongaporutuan (late Miocene) palaeogeographical map (modified after Arnot and Bland 2016; Sagar et al. 2019) of the Taranaki Basin, showing the present-day coastline and the location of the northern Taranaki coastal section. **B**, Waitoetoe Beach, near Waitoetoe Campsite, just south of the mouth of the Mimi stream, Urenui, Taranaki (North Island, New Zealand). Contains data sourced from the LINZ Data Service (<https://data.linz.govt.nz/>) licensed for reuse under CC BY 4.0 (<https://creativecommons.org/licenses/by/4.0/>). The type location of *Pseudocarcinus karlraubenheimeri* n. sp. is indicated by a red asterisk, just south of tuff sample location U-C-27 of Maier et al. (2016).

Database (FRED) – <https://fred.org.nz/> (see Clowes et al. 2021). Crabs and other macrofossils were collected from boulders and concretions recovered from the foreshore.

The sedimentary rocks at the Waitoetoe Beach near the Mimi stream originate from the Urenui Formation, and are of late Miocene (early Tongaporutuan) age, approximately 8.8 myr (e.g. Maier et al. 2016).

Materials and methods

Specimens were prepared by the collector, Karl Raubenheimer, with pneumatic airscribes and grinders.

Systematic palaeontology

To denote the repositories of material described and referred to herein, the following institutional abbreviation is used: NMNZ: Museum of New Zealand Te Papa Tongarewa, Wellington, New Zealand. Section *Eubrachyura* de Saint Laurent (1980). Superfamily *Pseudocarcinoidea* Ng and Davie (2020). Family *Pseudocarcinidae* Ng and Davie (2020). Genus *Pseudocarcinus* H. Milne Edwards (1834).

Type species. *Cancer gigas* Lamarck (1818), by the subsequent designation of Miers (1886); gender masculine (ICZN Opinion 85, Direction 37).

Included species. *Pseudocarcinus gigas* (Lamarck 1818), as *Cancer gigas*, both fossil and extant, and *P. karlraubenheimeri* n. sp. (herein). Provisionally, also *P. sp.* (as *P. parvus* Jenkins 1972, name unavailable [ICZN 1999 article 8.1]; Oligocene, Australia), *P. chauvinii* de Berville (1856) (as *P. Chauvinii*, Eocene, France) and *P. pustulosus* Feldmann and Fordyce (1996) (early Miocene, New Zealand) are included.

Remarks. *Menippe mercenaria* (Say 1818) was listed as *Pseudocarcinus* by both H. Milne Edwards (1834, p. 409, as *P. ocellatus*) and Gibbes (1850, p. 176, as *P. mercenarius*), while *Menippe nodifrons* Stimpson 1859 was referred to as *Pseudocarcinus nodifrons* by H. Milne Edwards (1834, p. 408). Both species are currently considered to belong to *Menippe* De Haan, 1833–1850 (Ng et al. 2008).

Ever since its original description, *Pseudocarcinus* has been associated with members of *Menippe*, thus, an array of synonymies have merged extinct species of both genera. In addition, *Pseudocarcinus* has been the subject of different systematic placements at the familial or suprafamilial levels (see Ng and Davie

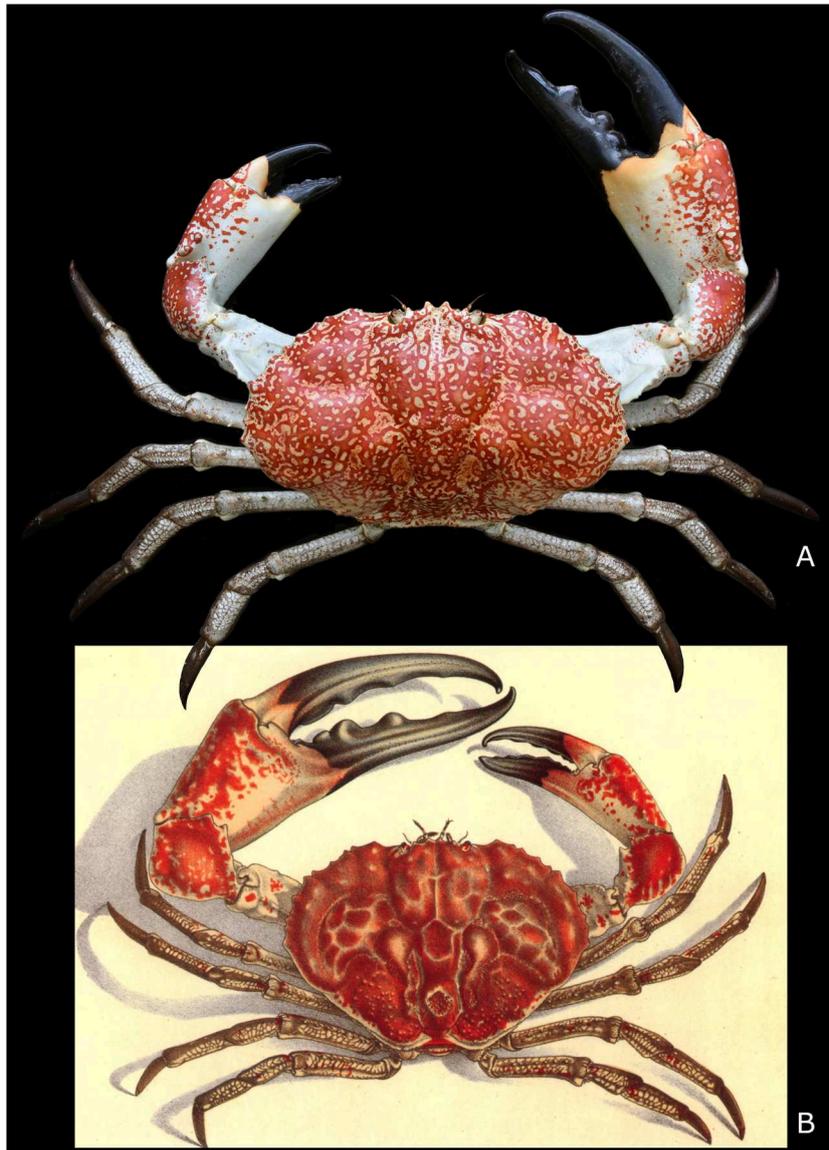


Figure 2. The extant ‘Southern Giant Crab’, *Pseudocarcinus gigas* (Lamarck 1818). **A**, dorsal view of male specimen, maximum carapace width 220 mm, maximum major claw length 270 mm (photograph by Ondřej Radosta). **B**, after McCoy 1889, originally drawn by John James Wild, scanned from the reference and kindly provided by P. Davie.

2020, p. 607, 608). Molecular works on the Eriphioidea (Lai et al. 2014) have questioned the placement of *Pseudocarcinus* within the Menippidae, a notion already hinted at in previous papers (e.g. Wetzer et al. 2003, Figure 3). Recently, Ng and Davie (2020) have provided evidence on morphological features to substantiate molecular data and differentiated *Pseudocarcinus* from the Menippidae by erecting a new family and superfamily for this genus.

From the fossil record, there are only few mentions of *Pseudocarcinus*. The sole exclusively fossil species assigned to *Pseudocarcinus* was described from the Oligocene of Australia in an unpublished PhD thesis (Jenkins 1972), but this name is unavailable under ICZN rules (article 8). The material of Jenkins (1972) should be re-examined and formally described; the claws that Jenkins assigned to his new species show lines of tubercles and short, stout fingers. Further study is needed to determine whether or

not this material is congeneric. Jenkins also recorded and illustrated a major right cheliped (pl. 20, fig. 6) of *Pseudocarcinus* cf. *P. gigas* from the upper lower or lower middle Miocene of Melbourne, as well as an isolated fixed finger (pl. 20, fig. 7) of *P. gigas* from Quaternary deposits of the Millicent area in South Australia. An isolated dactylus of a major right cheliped assigned to *Pseudocarcinus* sp. had earlier been described from the uppermost Miocene to Pliocene of Goldsborough, South Island, New Zealand (Glaessner 1960, p. 23). Until now, this cheliped dactylus constituted the sole New Zealand fossil record of the genus.

Feldmann and Fordyce (1996) described a single, large specimen of crab from the early Miocene Caversham Sandstone near Waikouaiti (Otago, South Island, New Zealand). These authors assigned this crab to the cancrid genus *Lobocarcinus* Reuss (1857) based on the lobose clusters of anterolateral spines,

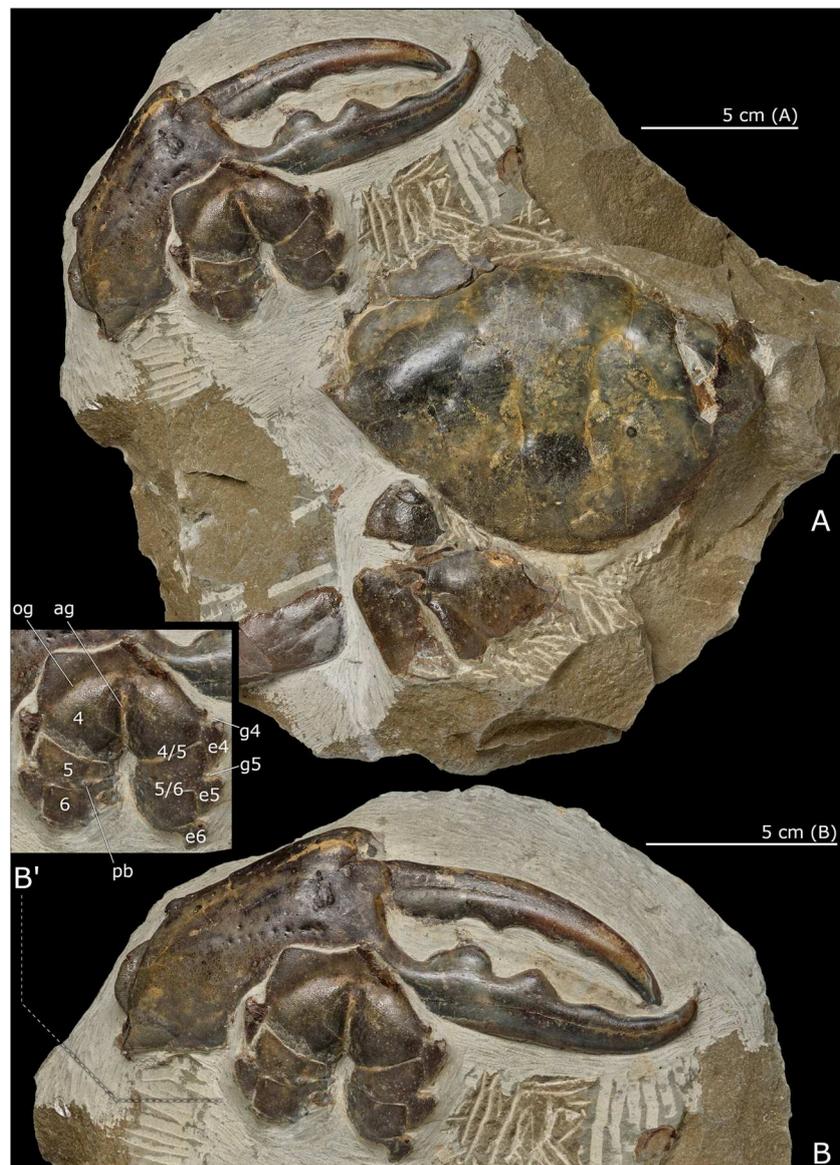


Figure 3. *Pseudocarcinus karlraubenheimeri* n. sp., **A**, holotype, NMNZ CR.027704, showing dorsal carapace, thoracic sternum and major right cheliped (male); **B**, detail of right major cheliped and thoracic sternum; **B'**, annotated detail of thoracic sternum, abbreviations: **4**, **5**, **6**, thoracic sternites 4, 5 and 6; **e4**, **e5**, **e6**, episternites 4, 5 and 6; **g4**, **g5**, gynglyme of thoracic sternites 4 and 5; **4/5**, **5/6**, thoracic sternal sutures 4/5 and 5/6; **ag**, axial groove; **og**, oblique groove; **pb**, press-button for pleonal holding mechanism. Photographs by Jean-Claude Stahl (NMNZ). Scale bars equal 50 mm.

presence of several posterolateral nodes, four-lobed front and strong development of carapace regions. *Lobocarcinus* is characterised by a carapace much wider than long, the posterolateral margin entirely armed with robust spines, and the anterolateral margin divided into clusters of spines by distinct notches. We assign *Lobocarcinus pustulosus* tentatively to *Pseudocarcinus* based on its carapace outline and ratio's, areolation of the dorsal carapace surface, granular posterior dorsal carapace surface, and similar orbitofrontal margin. Also, the conspicuous large size of *Lobocarcinus pustulosus* (maximum carapace width 119 mm) is similar to that of *P. karlraubenheimeri* n. sp. and of *P. gigas*. The sole specimen of *P. pustulosus* was collected from a unit for which a mid-outer shelf setting was concluded based on

foraminifera analysis (Feldmann and Fordyce 1996, p. 512).

Pseudocarcinus chauvinii de Berville 1856 (de Berville 1856, pp. 113–116, pl. 2, figs 1–9; as *P. Chauvinii*) from the Lutetian (Eocene) of the Département Oise (France) was subsequently re-assigned either to *Menippe* (see A. Milne-Edwards 1863, p. 299, pl. 12, fig. 1a–f) or *Peloeus* Eydoux and Souleyet 1842 (see Guinot 1968; Schweitzer 2005, p. 280, fig. 2.5.6; as *Pelaeus* [sic]). *Peloeus* is currently included in the eriphoid family Platyxanthidae Guinot (1977) (Ng et al. 2008, p. 66; Thoma et al. 2012). Casts of the type specimens of *Pseudocarcinus chauvinii* are in the collections of the Muséum national d'Histoire naturelle (carapace: MNHN.F.R03812, chelipeds: MNHN.F.A71898, A71899, abdomen:

MNHN.F.R03809; see <https://science.mnhn.fr/taxon/species/pseudocarcinus/chauvinii>, as well as Charbonnier and Garassino (2022). In *Pseudocarcinus chauvinii* the last anterolateral spine or epibranchial spine is markedly developed into a robust, outwardly directed spine; the anterolateral margin is arched and armed with approximately 3–4 faintly marked spiny lobes that give a spiniform, crenulate appearance to that margin.

The genotype *Peloeus armatus* Eydoux and Souleyet (1842) (see Thoma et al. 2012: fig. 9) has a conspicuously convex anterolateral margin with a subhorizontal anterior portion, in line with the orbito-frontal margin, as well as two distinct notches in the anterolateral margin subdividing it into three lobes with weakly crenulate margins (Thoma et al. 2012, p. 14). The thoracic sternum of *Peloeus armatus* shows sternite 4 only with a very posteriorly placed sternoabdominal cavity (see Thoma et al. 2012: fig. 10a), while in *Pseudocarcinus chauvinii* the sternoabdominal cavity extends along thoracic sternite 4 and nearly reaches sternite 3. For these reasons, *Pseudocarcinus chauvinii* cannot be included in *Peloeus*. The same morphology occurs with all other members included in the Eriphioidea, where the sternopleonal cavity only reaches the posterior third of sternite 4, thus precluding the inclusion of '*Peloeus*' in that superfamily (see Ng and Davie 2020, fig. 6B–F).

Instead, *Pseudocarcinus chauvinii* shows some morphological similarities to *Pseudocarcinus*, such as the anterolateral margins with spines grouped in clusters, and the front with four rounded spines with the frontal surface medially depressed. The thoracic sternum appears very similar overall; it is also relatively narrow, with the sternopleonal cavity almost reaching suture 3/4, sternite 3 with a medial longitudinal groove and similar concave suture 2/3 (compare Ng and Davie 2020, fig. 6A), and a similar groove pattern, with the exception of the oblique groove on sternite 4 towards episternite 4 (see Ng and Davie 2020: figs. 1c, 6a). There are also some clear differences with *Pseudocarcinus*, such as the longer posterolateral margins.

Pseudocarcinus chauvinii is incompletely preserved, and currently only a cast of the type specimen is known (see Charbonnier and Garassino 2022); this hampers a detailed morphological comparison with the diagnostic characters of a family based on an extant species. However, for reasons outlined above, we consider *P. chauvinii* to be better placed within the Pseudocarcinidae, rather than in the Platyxanthidae or any other eriphoid family. However, *P. chauvinii* differs from the type species, *P. gigas*, which lacks a strongly developed lateral (epibranchial) spine (see Ng and Davie 2020: fig. 1a). In addition, *P. gigas* has two distinct indentations in the anterolateral margin, grouping the anterolateral spines in well-

defined clusters. The posterolateral margins in *P. gigas* are also long, which results in the widest carapace width being seen at about mid-length (48% of maximum carapace length from the front). In contrast, *P. chauvinii* shows strongly developed lateral carapace spines, positioned approximately halfway along the carapace from the front, and moreover lacks anterolateral indentations. On the thoracic sternum, *P. gigas* shows a distinct, broad, oblique groove on sternite 4 towards episternite 4 (see Ng and Davie 2020: fig. 1c, 6a); this character is missing from *P. chauvinii*. For the time being, we leave '*Pseudocarcinus*' *chauvinii* provisionally in this genus until new material becomes available.

Pulalius dunhamorum Schweitzer et al. (2000), from the Eocene of Washington State (USA), has a pattern of grooves and sutures on sternites 3 and 4 (see Schweitzer 2005, fig. 3.1–2) that differs from that of the type species, *P. vulgaris* (Rathbun 1926), but is reminiscent of the pattern seen in *Pseudocarcinus*. Material of *Pulalius dunhamorum* should be re-examined and its morphology thoroughly compared with that of *Pseudocarcinus*.

Martinetta palmeri Blow and Manning (1997) (see Blow and Manning 1997, p. 173, pl. 1), from the middle Eocene of South Carolina, USA, was originally included in the Menippidae Ortmann (1893), and is currently assigned to the Zanthopsidae (Schweitzer et al. 2018, p. 17, fig. 12.2). The dorsal appearance of *M. palmeri* is reminiscent of *Pseudocarcinus chauvinii*, in showing slightly inflated gastric regions, a developed lateral (epibranchial) spine and distinct anterolateral spines; however, these are more numerous in *Martinetta*. *Martinetta palmeri* differs from *P. chauvinii* in lacking deep grooves on the anterior thoracic sternum, the lack of a complete groove between sternites 3 and 4 and the presence of a sterno-abdominal cavity that is positioned posteriorly on the thoracic sternite 4. The morphology of thoracic sternites 3 and 4 appears to be more closely similar to those of members of the Eriphioidea, thus, the familial placement of *Martinetta* should be revised (see also Ng and Davie 2020, fig. 6B–F). The fingers of the major claw of *M. palmeri* are shorter and more robust, and bear more teeth than those of *Pseudocarcinus*.

***Pseudocarcinus karlraubenheimeri* n. sp.**

Figures 3 and 4.

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Etymology. In honour of Karl Raubenheimer (New Plymouth, North Island, New Zealand), who collected and donated the holotype specimen described in the present study.

Material. The holotype is NMNZ CR.027704, a large nodule containing a large-sized male individual retaining the dorsal carapace, thoracic sternum and major right cheliped exposed. The paratype is



Figure 4. *Pseudocarcinus karlraubenheimeri* n. sp., **A**, paratype, NMNZ CR.027703, showing dorsal carapace, with both left (minor) and right (major) chelipeds; arrows indicate larger granules on posterior carapace surface; **B**, oblique view showing fingers of both chelipeds. Photographs by Jean-Claude Stahl (NMNZ). Scale bars equal 50 mm.

NMNZ CR.027703, a dorsal carapace with both left (minor) and right (major) claws preserved. Additionally, four specimens in the private collection of Karl Raubenheimer have been examined.

Type locality and level. The foreshore of Waitoetoe Beach, just south of the mouth of the stream; Urenui, Taranaki (North Island, New Zealand); locality registered in the New Zealand Fossil Record File, jointly managed by GNS Science and Geoscience Society of New Zealand, as Q19/f6523A. The type material was recovered from the Urenui Formation, early Tongaporutuan (late Miocene).

Diagnosis. Carapace transversely ovate, L/W ratio approximately 0.8; dorsal surface with granules on posterior half; regions weakly demarcated, gastric regions weakly inflated, branchiocardiac grooves distinct; anterolateral margin convex, with 11 robust blunt spines (excluding outer orbital corner), bundled

in clusters; posterolateral margin strongly converging, weakly convex; posterior carapace margin wide, nearly half of total carapace width, in a lower plane than carapace surface, weakly arched, broadly rimmed; orbito-frontal margin approximately one third maximum carapace width; orbits small, subcircular; front weakly projected beyond orbits, with four rounded spines, medial pair slightly more advanced and more closely spaced; intestinal region inflated, with two oblique grooves.

Adult male P1 unequal; major claw: merus massive, smooth; with outer distal spiniform tooth directed dorsally; carpus subpentagonal, with single, large triangular inner spine dorsally filling triangular space between propodus, carpus and carapace; major cheliped conspicuously enlarged, fingers gaping, longer than palm, with shallow groove, tips recurved, black; lower margin of fixed finger continuous with palm,

with massive molariform proximal tooth, slightly lower tooth halfway, two weak subdistal teeth, finger distally curved. Minor claw: about half size of major claw, fingers closing; fixed finger bent downwards, two proximal molariform teeth, three teeth decreasing in size, subequally divided; tips weakly curved, black. Female P1 subequal, major claw slightly larger than minor claw.

Thoracic sternum relatively narrow, widest at episternites 5; sternite 3 rhomboid in shape, subdivided into two inflated lobes by broad axial groove, separated from sternite 4 by distinct, deep, oblique groove; sternites 3 and 4 forming rather long subtrapezoidal plate; sternite 4 with broad axial and oblique lateral grooves, with convex lateral sides; episternite 4 prominent; sutures 4/5 and 5/6 curved, appearing complete, running into sternopleonal cavity; press-button on sternite 5 positioned near suture 5/6, just over edge of sternopleonal cavity; gynglymes 4 and 5 for pereopod 1 and 2 conspicuously large; male pleon broadly subtriangular; all somites and telson free, pleonal somite 6 longer than preceding somites, telson reaching sternite 4.

Remarks. The new species may be assigned to *Pseudocarcinus* on the basis of the following characters: a similar carapace outline, with long posterolateral margins, greatest carapace width anterior of mid-length; anterolateral margin with clusters of spines and posterior half of the carapace with large granules on the dorsal surface (see Figure 4A); thoracic sternites 3, 4 with wide axial groove; separated from each other by distinct, wide and deep sinuous groove; thoracic sternite 4 with prominent, complete, oblique grooves (compare Ng and Davie 2020: fig. 6); adult male major cheliped conspicuously enlarged, fingers longer than palm, gaping, with few molariform teeth.

Pseudocarcinus karlraubenheimeri n. sp. differs from the type species, *P. gigas*, in having a single, larger, triangular dorsal spine on the carpus of P1 (double spine on the carpus of *P. gigas*), a more projected front and less inflated gastric and epi-, meso- and metabranchial regions, as well as in lacking deep intestinal grooves. In addition, the anterolateral portion next to the outer orbital tooth does not recede.

The new species differs from *Pseudocarcinus* sp. (i.e. *P. parvus* sensu Jenkins 1972, name unavailable; Oligocene of Australia: see Jenkins 1972: pl. 19 figs. 1–7) by its significantly larger size; more subtle and blunt anterolateral lobes, and much less pronounced and shallower groove system.

Pseudocarcinus karlraubenheimeri n. sp. differs from *P. pustulosus*, in having less robust anterolateral spines, weaker inflated carapace regions and a shallower groove system, and less and more subtle granules on the posterior carapace surface (clearly rugose in *P. pustulosus*; compare Feldmann and Fordyce 1996: fig. 3).

Remarks

Palaeoenvironment

The extant 'Southern Giant Crab', *Pseudocarcinus gigas*, prefers muddy, bryozoan-rich substrates, between depths of 140–400 m, but typically occurs near the transition of outer continental shelf and upper bathyal environments. The species remains at this depth range to allow easy changes in depth and consequently preferred water temperature. This is of significance because *P. gigas*, as all brachyurans, has no other mechanism of metabolic temperature control (Levings 2008, p. 134), being dependent of the environment. On the basis of this depth regulation, the species has access to both warmer, shallower and food-rich waters and cooler, energy-saving deeper water (Levings 2008). Extant *P. gigas* prefers temperatures in the range of 10–15°C and does not typically seek shelter, because their very large size and heavy exoskeleton provide very good protection from predators. The species is a scavenging carnivore; food typically comprises gastropods, other crustaceans (notably paguroids; Levings 2008, pp. 31, 51), but also smaller crabs. Shells of prey items are crushed with its mighty major cheliped. Heeren and Mitchell (1997) studied the digestive tract and the morphology of the mouth parts, gastric mill and gastric contents of *P. gigas*, and concluded that all were consistent with a carnivorous lifestyle.

Strata assigned to the Urenui Formation at the type locality of *Pseudocarcinus karlraubenheimeri* n. sp. were deposited at upper bathyal water depths (200–600 m) on the upper to middle parts of a west-facing continental slope (see also Figure 1). The overlying inner to outer neritic water mass was typical of continental shelf environments or in a setting in close proximity to the continental shelf (King et al. 1993, 2007; Maier et al. 2016; Martin P. Crundwell, pers. comm., March 2022). These strata have been formed by terrigenous sediments deposited primarily via hemipelagic sedimentation and slope-channel fan systems, and are quite distinct from age-equivalent strata of the more outboard volcanoclastic Mohakatino Formation fan system. West of the Waitoetoe locality, the Urenui Formation interfingers with this volcanoclastic submarine fan succession, the latter being produced by ancient predominantly andesitic submarine volcanoes (Mohakatino Volcanic Centre) that erupted during the Middle to Late Miocene within this part of northern Taranaki Basin (see Giba et al. 2010; Shumaker and Graham 2014; Arnot and Bland 2016; Masalimova et al. 2016: fig. 1B; Shumaker et al. 2018; Sagar et al. 2019: fig. 1A). According to Shumaker et al. (2018, p. 2506): 'Composition and sedimentary structures indicate that most deposits in this area

are reworked volcanogenic material, rather than primary deposits from individual eruption events'. However, at the Waitoetoe locality, there is very little material from the Mohakatino Volcanic Centre within the Urenui Formation, other than a few thin airfall-derived ash layers (tephra, or tuff).

The Urenui Formation at the Waitoetoe Beach locality, as other nearby outcrops at the eastern margin of Taranaki Basin, contains large metre-scale pipe-like carbonate-cemented concretions that are interpreted to represent the near sub-surface 'plumbing systems' of then-active natural gas seeps (Nyman and Nelson 2011). It is likely that sea-floor gas seeps existed above these pipes, bringing CO₂ and/or methane to the sediment-water interface. Nelson et al. (2004: figs. 2, 3) and King et al. (2007: fig. 18b) studied and figured these pipes, and labelled them as 'paramoudra-like concretions'. Similar seeps, both active and ancient, in equivalent rocks along NZ's eastern coastline, are often surrounded by very diverse molluscan/crustacean faunas (Campbell et al. 2008; Kyle Bland, pers. comm. November 2023). This could explain the presence of Giant Crabs in Taranaki, feeding on abundant molluscs around active sea-floor seeps. Additionally, there are virtually no other locations along western New Zealand where Miocene-aged upper-slope rocks are exposed, probably explaining why *Pseudocarcinus karlsruhenheimeri* n. sp. has not yet been discovered elsewhere in New Zealand.

Gigantism amongst brachyurans and brachyuran claw size

Vermeij (2012, p. 776) studied the evolution of animal gigantism, noting 'broad advantages in competition and defence, varies in space and time according to the supply of (and demand for) resources, as well as the magnitude and effects of extinction'. Modern temperate seashores are characterised by large-sized eubrachiuran crabs, such as members of the Cancridae, predators of shell-bearing molluscs.

Gigantism of crabs and large claw sizes (both relative to body size, and absolute size), are often considered a coadaptation with molluscs: brachiuran crabs are important predators of shelled molluscs, and metabolic conditions are likely to be key determinants of crab claw size (Vermeij 1977). The crab's heavy exoskeleton and robust, thick-shelled claws, are significantly expensive with regard to resources for building and maintaining. Chelipeds of larger brachiurans usually are sexually and ontogenetically dimorphic. Predation on shell-bearing molluscs requires various morphological specialisations, in particular in chelipeds. Schweitzer and Feldmann (2010) recognised three kinds of adaptations in crab chelipeds for eating shelled prey; (1) heterochelous first

pereiopods; (2) molariform teeth on cheliped fingers and (3) a curved proximal tooth on the movable finger. *Pseudocarcinus gigas* may attain a body mass of 12 kg (Levings 2008: fig. 4.3) and has the largest chelipeds amongst decapods (Hale 1927; Heeren and Mitchell 1997); the largest male claw measured was an astonishing 470 mm (Levings 2008: fig. 6.6b). Schweitzer and Feldmann (2010, p. 177) noted that, 'Marked gape between fingers or the relationship between carapace width and claw size may suggest that the claw is used more for sexual display and less for shell crushing, despite marked heterochely'. For heterochely these authors stated (p. 175) that, 'Heterochely undoubtedly is not an adaptation solely for predation; thus, interpretation of a heterochelous fossil decapod taxon as a durophagous predator could be erroneous or overly simplistic'. Indeed, heterochely is a character state which in itself does not necessarily imply predation. A normal gaping of the major cheliped fingers could facilitate crushing thick-shelled objects such as bivalves and gastropods. *Pseudocarcinus* claws have a character set which makes it apparent that their morphology was adapted for mollusc crushing: their major claw is enlarged, thick-shelled, with opposing molariform teeth proximally and a moderate gape. Maximum sized (mature) male specimens have a greater gape and it is quite likely that there is a balance between functional predation morphology and mating display.

As far as the geological history of *Pseudocarcinus* is concerned, Jenkins (1972) concluded that the increase of carapace width amounted from 6 to 9 mm per million years, while ratios (CW/CL ratios; length of fixed finger/length of male major cheliped propodus ratio) remained relatively constant.

Giant claws occur in several brachiuran groups, at several moments in geological time. During the Middle and Late Cretaceous, both podotreme and eubrachiuran crabs developed large carapace sizes, with conspicuously large claws. Cenomanocarcinids appeared in the Albian and ranged up to the uppermost Maastrichtian (Van Bakel et al. 2012, 2019); these podotreme crabs may attain very large sizes (compare Guinot et al. 2008: fig. 6) and their claws may grow exceptionally large (see Jagt et al. 2014: pl. 5). Jagt et al. (2015, p. 136) stated that it may be assumed that *Cenomanocarcinus? heterodon* (Bosquet 1854) was an ambush predator. Brachiuran crabs are well known as predators of shelled molluscs (Vermeij 1977). Among eubrachiuran crabs, the mid-Cretaceous *Eogeryon elegius* Ossó 2021, exhibits very large major (right) claws with a shell-crushing dentition (see Ossó 2023: fig. 1). Of the Late Cretaceous (Campanian) *Dinocarcinus velauciensis* Van Bakel et al. (2023), only the exceptionally large claws are known, found in association with ornithopod dinosaur remains in continental deposits of southern

France (see Robin et al. 2019). Of the eubrachiuran *Styracocarcinus meridionalis* (Secretan 1961) from the upper Campanian of Morocco (see Ossó 2016), very large robust claw remains have also been discovered (Å. Ossó, personal collection); these require further research. In addition, the Late Cretaceous (Maastrichtian) eubrachiuran *Megaxantho zoque* Vega et al. (2001) has been characterised as one of the largest Mesozoic crabs known to date (Dietl and Vega 2008). The major right claw of *M. zoque* is very large ('measuring approximately 108 mm in length and approximately 57 mm in height', Dietl and Vega 2008, p. 290), and its morphology with a large, curved molariform tooth at the base of the dactylus, is indicative of a highly specialised shell-breaking mode of life.

In the Late Cretaceous and Palaeogene, benthic dwelling gastropods and bivalves had a significant radiation, and the broader use of them as prey seems to have led to subsequent advances in brachiuran claw engineering, and an increase of molluscivorous crabs. In the Eocene, giant crabs appear to belong mostly to the eubrachiuran clade, concomitant with the rapid decline of podotreme crabs. Massive crabs with thick cuticle and large major claws evolved, such as an Eocene (Bartonian) carpiliid from Barcelona, north-east Spain (Ferratges 2017: fig. 12A) with an exceptionally large major claw. Also, the Eocene *Menippe almerai* Vía 1941 (compare Vía Boada 1959: pls. 20, 21, 23.1-2) and *M. frescoensis* Rémy 1960 (see Rémy 1960: pl. 1, fig. 5) exhibit exceptionally large major claws. The male holotype specimen of *Martinetta palmeri* Blow and Manning 1997, from the Eocene Santee Limestone of South Carolina (USA), retains an incomplete major cheliped that exceeds 106 mm in length and 56 mm in height (Blow and Manning 1997, p. 177). Members of the genera *Harpactoxanthopsis* Vía Boada (1959), and *Palaeocarpilius* Milne-Edwards (1862), may reach very large sizes, as may their robust crushing claws (e.g. Beschin and De Angeli 2006; Vega et al. 2010). Several species of *Tumidocarcinus* Glaessner (1960), are known from the Eocene to Miocene of New Zealand and Australia; major claws reach up to 103 mm in height (Glaessner 1960, p. 28) and in excess of 180 mm in length (Fleming 1962: table 1; see also Feldmann 1998b: fig. 2).

In modern seas, crabs have larger absolute claw sizes in temperate regions than they do in tropical regions, although claws are smaller relative to body size in temperate seas (Vermeij 1977). The Miocene of New Zealand supported two species of giant crab with the largest crushing claws known; *Tumidocarcinus giganteus* and *Pseudocarcinus karlraubenheimeri* n. sp. Apparently, food sources, metabolic conditions and calcium-carbonate supply were favourable for these species. *Tumidocarcinus* became extinct by the end of the Miocene; *Pseudocarcinus* is currently known only from Australian waters.

Acknowledgements

We are grateful for Karl Raubenheimer and Kerr Sharpe-Young (New Plymouth, Taranaki, North Island, New Zealand) for generous donation of the material to science, and Shaun Murphy for assistance in the field and various kinds of information. Felix G. Marx (Museum of New Zealand, Te Papa Tongarewa) kindly provided collection registration numbers for the type material and photographs taken by Jean-Claude Stahl. Katherine Leigh Maier (National Institute of Water and Atmospheric Research, Wellington, New Zealand) and Martin P. Crundwell (Paleontology Department, GNS Science [Institute of Geological and Nuclear Sciences Limited], Lower Hutt, New Zealand) are thanked for items of literature and valuable information on the geology of the Waitoetoe Beach locality. Last, but not least, Ondřej Radosta (Czech Republic) kindly provided the photograph of Figure 2A, and Peter Davie (Queensland Museum, South Brisbane, Queensland, Australia) kindly provided Figure 2B. Peter Ng (National University of Singapore) provided info on *Pseudocarcinus gigas*. We thank the reviewers Carrie Schweitzer (Kent State University, Kent, Ohio, USA), Kyle Bland (GNS Science, Lower Hutt, New Zealand), and Peter Davie (Queensland Museum, South Brisbane, Queensland, Australia) for their constructive reviews and useful improvements. We thank Marianna Terezow (GNS Science, Lower Hutt, New Zealand) for her kind help with registering the type locality in FRED.

Disclosure statement

No potential conflict of interest was reported by the author(s).

Data availability statement

All data supporting the findings of this study are available within the paper and its references.

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