New Zealand Journal of Geology & Geophysics, 2008, Vol. 51: 43–58
0028–8306/08/5101–0043

Fossil isopod and decapod crustaceans from the Kowai Formation (Pliocene) near Makikihi, South Canterbury, New Zealand

RODNEY M. FELDMANN
Department of Geology
Kent State University
Kent, OH 44242 USA

CARRIE E. SCHWEITZER
Department of Geology
Kent State University Stark Campus
6000 Frank Ave NW
North Canton, OH 44720 USA

PHILLIP A. MAXWELL
Deceased

BRIAN M. KELLEY
Department of Geological and Environmental Sciences
Stanford University
Stanford, CA 94305 USA

Abstract Small concretions and specimens embedded in the matrix have yielded a new Pliocene crustacean fauna from the Kowai Formation near Makikihi, South Canterbury, New Zealand. The fauna is relatively robust, with five identifiable taxa. Three new species are named herein, including the isopod *Cirolana makikihi* and the decapods *Upogebia kowai* and *Austrohelice manneringi*. One new genus and species of decapod, *Kowaicarcinus maxwellae*, is also named. The fauna documents the second occurrences of fossil isopod and upogebiid from New Zealand. The fauna is indicative of a nearshore setting with some mixing with taxa from shallow, offshore, normal marine settings.

Keywords Crustacea; Decapoda; Isopoda; Brachyura, Cirolanidae; Thalassinidea; Upogebiidae; Goneplacoidea; Grapsidae; Pliocene; New Zealand; *Cirolana makikihi*; *Upogebia kowai*; *Austrohelice manneringi*; *Kowaicarcinus maxwellae*; new taxonomic names

INTRODUCTION

The Pliocene rocks and fossils along the Makikihi River, west from Makikihi, South Canterbury, have hardly been mentioned in the literature despite their being some of very few marine Pliocene rocks known from the east coast of the South Island south of Christchurch. The Makikihi exposures are far more accessible and more extensive than the other Pliocene occurrences discussed below. The Makikihi occurrence escaped notice until its discovery by J. D. Raeside in 1946 (Collins 1953). Since then there have been only brief published accounts of the locality (Field & Browne 1986; Forsyth 2001).

Occasional collecting by one of us (PAM) and Al Mannering, Christchurch, resulted in the collection of a well-preserved molluscan fauna along with other organisms including crustaceans. The notice of crustaceans prompted a more focused collecting effort by us in an attempt to increase the understanding of marine arthropods in New Zealand. Thus, the purpose of this work is to describe and illustrate isopod and decapod crustaceans from this locality. In so doing, four new species are described, including only the second fossil occurrence of isopods in New Zealand and the second occurrence of a representative of the Upogebiidae Borradaile, 1903. The assemblage represents a nearshore, shallow marine assemblage at the distal margin of the predominantly nonmarine Kowai Formation.

The fossil record of decapod crustaceans from New Zealand has become better known due to the efforts of several workers. Glaessner (1960) compiled a list of known fossil decapods from New Zealand and described the evolution of the Order Decapoda. This work was the first compilation of data on decapods in New Zealand and was based primarily upon museum collections. Subsequently, one of us (RMF) began fieldwork focused on collection of decapod crustaceans that resulted in several descriptive papers. Feldmann & Keyes (1992) collected and catalogued data describing species-level taxa and localities in Cenozoic and Mesozoic rocks, and Feldmann & McLay (1993) summarised the geological history of New Zealand brachyuran decapods.

LITHOLOGY AND SEDIMENTOLOGY

The following comments on lithology and sedimentology are based on information supplied by Brad Field (GNS) (summarised in Field & Browne 1986), as well as on personal observations of one of us (PAM). About 50 m of gently dipping, barely consolidated to cemented conglomerate, sand, and sandstone with locally developed foreset bedding are exposed in high bluffs on the north bank of the Makikihi River, c. 4 km upstream from Makikihi. The fossiliferous layer is exposed along the base of the bluff, at 171°06′08.2″E and 44°36′50.9″S. Rapid lateral changes in lithology are evident but are difficult to study in detail because of the discontinuous nature of the outcrops. Conglomerate clasts, overwhelmingly of indurated sandstone (greywacke) derived from Paleozoic Torlesse rocks, range from pebbles to cobbles, and are typically clast-supported and imbricated. Macrofossils are chiefly molluscs, but bryozoans, barnacles, shark teeth, and rare cetaceans also occur in the conglomerate beds and in interbedded sandstone units.

Nearly all of the decapods discussed in this paper were collected from a thin, well-cemented sandstone bed at the foot of a prominent bluff and close to the base of the exposed section. The unit is not planar but curves upward at the downstream (eastern) end of the exposure. Decapods occur in small, randomly oriented, pale grey-weathering

G07024; Online publication date 29 February 2008
Received 17 September 2007; accepted 7 January 2008

concretions, associated with scattered greywacke pebbles and anomiid bivalves. The sandstone is overlain by c. 2 m of graded, massive, sandy conglomerate with matrix-supported clasts and very rare macrofossils, which in turn is succeeded sharply by fossiliferous, irregularly cemented, interbedded conglomerate and sandstone with a fine, sandy coquina at the base and exhibiting some minor cross-bedding. Large burrows originating at or a short distance above the contact penetrate deep into the upper part of the conglomerate. The succeeding beds consist of well-stratified alternating conglomerate and sandstone or siltstone.

AGE AND CORRELATION

Macrofossils are locally common at Makikihi, particularly in the sandstone/conglomerate unit overlying the graded conglomerate, but are of low diversity, typically difficult to collect (except for the oysters), and often poorly preserved. According to Collins (1953), the original collection of fossils contained 12 species of molluscs and crustaceans, three of which were alleged to indicate a Pliocene rather than a Pleistocene age. Collins concluded (1953, p. 130), "the best correlation is with the Waitotaran stage (Lower Pliocene), and hence with the Kowhai [sic], Greta, and Motunau formations of North Canterbury." The Waitotaran is no longer recognised in the standard scheme of New Zealand Cenozoic stages, its former substages, the Waipipian and Mangapanian, having been elevated to stage rank (see Beu 2001 for a summary of Wanganui Series stages); furthermore, the Waipipian and Mangapanian are now correlated with the late Pliocene.

Gair (1959) proposed the name Cannington Gravels for "weathered greywacke gravels, silts and clays" overlying either marine sandstone (Southburn Sand) or lignite (White Rock River Coal Measures) of early Miocene age in the Pareora district, c. 14 km north of Makikihi. He noted their similarity to the "greywacke gravels" at Makikihi, suggested they are of similar age, and correlated them with the Kowai Gravels, which had been proposed by Speight (1919) for similar conglomerate-dominated beds in the Waipara district in North Canterbury. Gair (1967) later included the Makikihi beds in Cannington Gravels, but Field & Browne (1986) synonymised Cannington Gravels with the Kowai Formation, which they interpreted as a non-marine/shallow marine unit with a wide distribution in Canterbury. The Kowai Formation in South Canterbury is predominantly non-marine, but marine beds occur at various horizons throughout the unit in North Canterbury, and the associated molluscan assemblages indicate an age range of Opoitian–Nukumaruan (early–late Pliocene) (Browne & Field 1985; Andrews et al. 1987). The molluscan assemblage from the well-bedded conglomerate/sandstone unit overlying the graded conglomerate is of low diversity, and is dominated by the still extant *Ostrea chilensis* Philippi in Küster & Kobelt, 1844, and *Anomia trigonopsis* Hutton, 1877 (Table 1). However, the presence of *Crassostrea ingens* (Zittel, 1864), *Xenostrobus huttoni* (Suter, 1914), and *Stiracolpus uttleyi* (Marwick, 1957) indicate an early Nukumaruan age for this unit (A. G. Beu pers. comm.). The Nukumaruan Stage is currently regarded as latest Pliocene, extending from 2.4 to 1.63 Ma (Beu et al. 2004). Unfortunately, the decapod bed itself has not been dated, and it could be substantially older. The sharp contact between the conglomerate/sandstone and the graded conglomerate, and the presence of prominent burrows below the contact, is evidence for a depositional hiatus between the two units, but there is currently no way of knowing just how much time is represented by the break. The decapod bed is probably late Pliocene, but in the absence of other evidence it is not possible to be more precise.

Table 1 Mollusca from Makikihi (identified by A. G. Beu, P. A. Maxwell).

Bivalvia
Ostrea chilensis Philippi in Küster and Kobelt, 1844
Crassostrea ingens (Zittel, 1864)
Anomia trigonopsis Hutton, 1877
Xenostrobus huttoni (Suter, 1914)
Tawera Marwick, 1927 sp.
Panopea Menard, 1807 sp.

Gastropoda
Trochus (*Coelotrochus*) *tiaratus* Quoy & Gaimard, 1834
Sigapatella Lesson, 1830 sp.
Stiracolpus uttleyi (Marwick, 1957)

There is little direct evidence for the age of the Kowai Formation in eastern South Canterbury, despite the wide occurrence of fine-grained lithologies that might be expected to yield pollen. Mildenhall (2001) had only modest success in recovering microfloras from the Kowai Formation in the Mackenzie Basin, c. 100 km northwest of the Pareora/Makikihi area: only 38 samples out of 107 contained palynomorphs, and of these no more than 22 had sufficient pollen for statistical studies. The dated assemblages range in age from Waipipian (late Pliocene) to early Castlecliffian (early Pleistocene).

Gair (1961) reported marine molluscs from the Kowai Formation underlying the Timaru Basalt in a drillhole sunk near Timaru; these were dated as early Nukumaruan (i.e., broadly coeval with the most fossiliferous unit at Makikihi) and it was assumed on the basis of this date that the basalt erupted close to the Pliocene/Pleistocene boundary (Matthews & Curtis 1966). On the basis of revised decay rates, the basalt has a K-Ar whole-rock age of 2.52 ± 0.74 Ma (Forsyth 2001), which is not inconsistent with such a stratigraphic position; the Timaru Basalt is not known south of the Pareora River.

Forsyth (2001) mentioned reports of shells having been found in drillholes sunk at Pareora, and one of the authors (PAM) has been told of shells that were noticed in artesian drillholes near Waimate. More recently, a large, well-preserved cetacean vertebra (now at the South Canterbury Museum) was recovered from a depth of c. 100 m in a drillhole sunk near the junction of State Highway 1 with State Highway 82, c. 7.5 km northeast of Waimate (R. E. Fordyce pers. comm.). Marine beds are probably widespread in the eastern (distal) part of the Kowai Formation, but despite its considerable areal extent underlying the low hills close to the coast, from the Pareora River south almost to the Waitaki River, there are relatively few surface exposures of the unit. The Kowai Formation in South Canterbury probably spans most of the Pliocene, but a substantially greater age is possible for the lower part of the unit (e.g., at Elephant Hill Stream where it succeeds the early Miocene Southburn Sand with little or no unconformity). The Makikihi occurrence is evidently near the top of the unit.

Marine Pliocene macrofossils are also recorded from offshore North Otago. Badly worn specimens of the late Miocene to early Pliocene gastropod *Struthiolaria* (*Callusaria*) *obesa* Hutton, 1885, are sometimes found washed up on the beaches between Cape Wanbrow and Kakanui, and in 1966 a local fisherman trawled blocks of fine sandstone containing this species from near the mouth of Awamoa Creek.

The associated molluscan fauna indicates an Opoitian (early Pliocene) age (Fordyce et al. 1985; Beu & Maxwell 1990). This unit may also be the source of cetacean bones cast up on Cape Wanbrow (R. E. Fordyce pers. comm.). Although the sandstone may represent a relatively distal marine facies within the Kowai Formation, it is more likely to have come from a distinct unit so far unrecorded on land.

DEPOSITIONAL ENVIRONMENT

The abundance of *Ostrea chilensis*, the presence of prominent imbricated conglomerates with foreset bedding, and the rapid lateral changes in lithology are consistent with rapid deposition and erosion in a very shallow water, high-energy environment close to shore for most of the Makikihi sequence. Clast orientation and foreset bedding in the conglomerates indicate a northwest-flowing current; small-scale foreset bedding in the sands show a bimodal distribution in current direction, one to the northwest and the other to the east and southeast (B. D. Field pers. comm.). The conglomerate clasts were almost certainly derived from the rising Hunters Hills a few kilometres to the west, so the presence of foreset bedding indicating deposition in the opposite direction is evidence for strong shoreward currents (Field & Browne 1986).

The graded conglomerate may have accumulated in a deeper water environment than the overlying units; certainly far enough from its original depositional site for the conglomerate to move downslope into quieter waters. The grading is evidence that it moved as a slurry rather than en masse, but with minor disruption to the decapod bed which presumably was already lithified. An allochthonous origin for the decapod-bearing nodules themselves is indicated by their random orientation within the sandstone bed. The unconformity at the top of the conglomerate suggests that its emplacement was either followed by a period of non-deposition at this site, or that any sediments that were deposited prior to the existing well-bedded conglomerate/sandstone were removed by subsequent erosion. Paleontological and sedimentological evidence point to a very shallow water depositional environment for the beds above the unconformity, suggesting the resumption of sedimentation at this site resulted from shallowing, possibly associated with a fall in sealevel. An up-section increase in the frequency of fine-grained units, however, may indicate subsequent deepening.

SYSTEMATIC PALEONTOLOGY

Class MALACOSTRACA Latreille, 1802

Order ISOPODA Latreille, 1817

Suborder CYMOTHOIDA Wägele, 1989

Superfamily CIROLANOIDEA Dana, 1852

Family **CIROLANIDAE** Dana, 1852

Genus ***Cirolana*** Leach, 1818

TYPE SPECIES: *Cirolana cranchii* Leach, 1818.

INCLUDED FOSSIL SPECIES: *Cirolana enigma* Wieder & Feldmann, 1992; *C. makikihi* new species.

DIAGNOSIS: “Cephalon lacking projecting rostrum. Frontal lamina distinct, but not projecting prominently. Antenna longer than antennule. Pleon consisting of five free pleonites plus pleotelson (pleonite 1 often obscured by pereonite VII). Lateral margins of pleonite 5 overlapped by those of pleonite 4. Pleopods 1 and 2 similar, not operculiform. Inner apex of uropod peduncle produced.” (Kensley 1978, p. 63).

DISCUSSION: The diagnosis of Kensley (1978) is quoted directly because it strongly emphasises the characters of the dorsum of the organisms. It is extremely rare to find the mouthparts and appendages of isopods preserved; these are important features in the classification of extant forms. In fact, the posterior portion of isopods including the last three pereonites and the pleon are commonly the only parts of isopods that are preserved, owing to the effects of biphasic molting (George 1972). During that process the posterior part of the exoskeleton is cast off as a single unit before molting of the anterior part of the exoskeleton. This latter unit often breaks apart and is less likely to be preserved in recognisable form.

The primary specimen that forms the basis for the description of this new species consists of the pleon and only a single pereonite. Another specimen consists of just three partial pereonites. Whether this is indicative of the molting pattern in *Cirolana* or whether the absence of two additional pereonites is a result of preservational bias is problematic.

Cirolana makikihi n. sp. Fig. 1A–C

DIAGNOSIS: Cirolanid with 5 pleonites of equal length and small, rounded-triangular pleotelson.

DESCRIPTION: Size typical for genus, consisting of 3 pereonites, 5 pleonites, and pleotelson; total length of pleon and pleotelson 30.5 mm, maximum width of pleon 20.7 mm, tapering posteriorly.

Pereonites smoothly arcuate anteriorly, axial length 6.7 mm on holotype, 4.5 mm on paratype; tergal surface smooth with very tiny, broadly spaced pores, posterior border slightly raised and rolled to overlap first pleonite; pleura smooth with broadly spaced pores, inflated, cordate outline with termination directed posterolaterally.

Five pleonites of equal axial length, 4.6 mm, decreasing in width posteriorly. First pleonite 20.6 mm wide, pleura c. 3.5 mm wide and 2.9 mm long, quadrate, directed laterally. Second pleonite 20.5 mm wide, similar in form to first pleonite. Pleonites 3–5 similar in form but becoming progressively narrower posteriorly; 17.4, 13.7, and 11.5 mm, respectively; pleura of pleonites 3–5 narrow, separated from terga by narrow longitudinal ridge, downturned. Surface of all pleonites apparently smooth. Sutures between pleonites very slightly convex anteriorly.

Pleotelson small, triangular, 7.4 mm wide proximally and 6.2 mm long. Anterior margin moderately convex forward; lateral margins nearly straight; terminus slightly rounded. Surface smooth, borders rounded, and with 2 shallow depressions, one positioned on either side of longitudinal axis near tip of pleotelson. Uropods not visible.

ETYMOLOGY: The trivial name alludes to the Makikihi River which flows at the base of the exposure of the Kowai Formation from which the specimen was collected.

TYPES: The holotype, CM1998.171.41, consisting of part and counterpart of 1 pereonite, 5 pleonites, and the pleotelson, and the paratype, CM1998.171.42, consisting of parts of 3 pereonites, are deposited in the Canterbury Museum, Christchurch, New Zealand.

TYPE LOCALITY: The specimens were collected on the north bank of the Makikihi River, c. 4 km upstream from Makikihi, South Canterbury, New Zealand, at 171°06′08.2″E and 44°36′50.9″S.

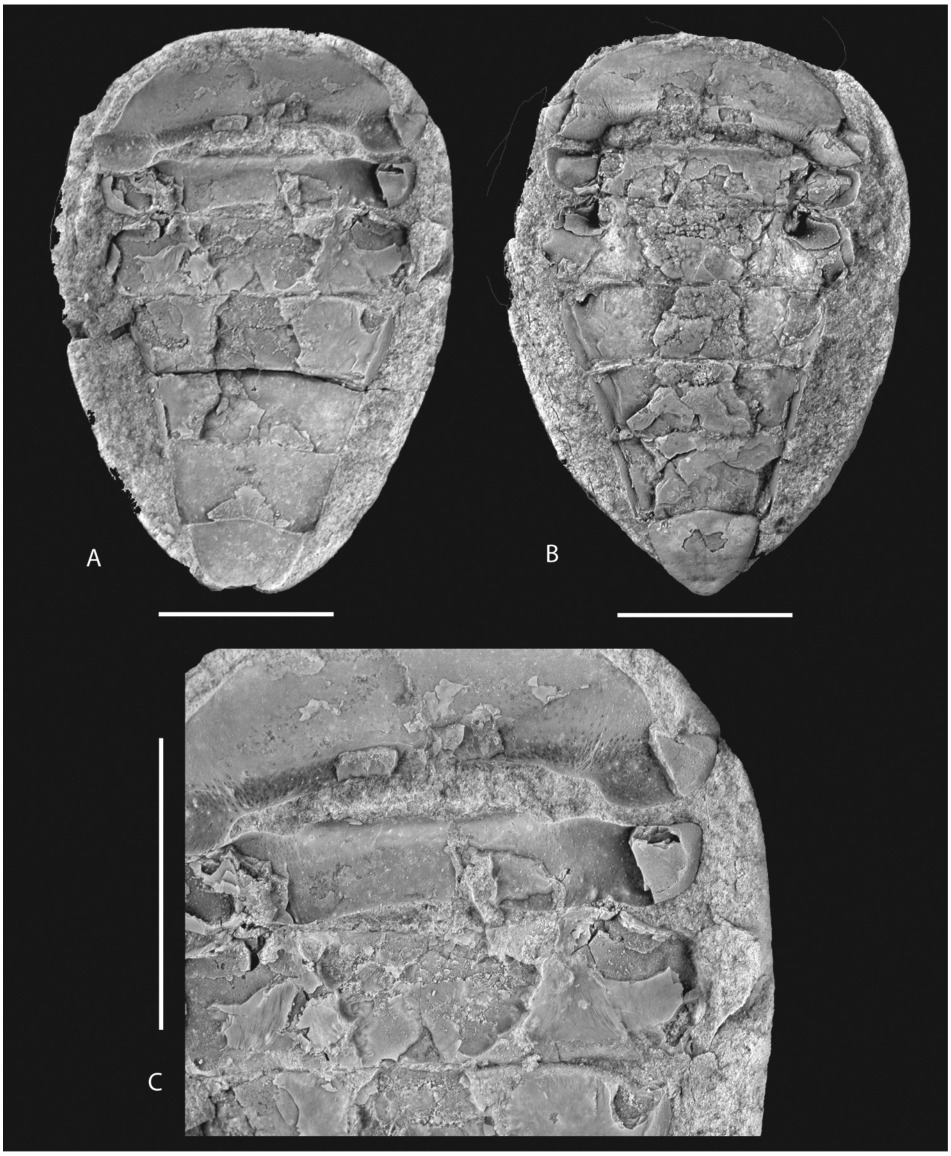

Fig. 1 *Cirolana makikihi* n. sp. **A–C**, CM1998.171.41, holotype, counterpart (A) and part (B). Close-up of counterpart (C), showing pereonites and small triangular pleura (epimeres). Scale bars = 1 cm.

DISCUSSION: Recognition of the specimens referred to the Isopoda is based upon the observation that the pleonites bear distinct pleura, or epimeres. Identification of fossil isopods is plagued by several problems. In addition to the difficulties arising from the observation that features of the venter are rarely preserved, the dorsal aspect of some genera is variable and the variable morphology can overlap that of different genera. Additionally, the condition of biphasic molting (George 1972) often results in only partial preservation of the dorsal surface. In the present instance, placement of *Cirolana makikihi* within the Flabellifera is certain because the morphology of the preserved parts conforms closely to the diagnosis of the suborder (Hessler 1969) and is similar to many of the described members of the subfamily known from the modern and fossil record. However, within the Flabellifera, two families—the Aegidae White, 1850, and Cirolanidae—each embrace genera that are extremely difficult to distinguish based upon the morphology of the terminal pereonites and the pleon. Specifically, *Aega* Leach, 1815, and *Cirolana* are similar in number of pleonites, development of pleurae, and shape of the pleotelson. Both genera are represented by a large number of species in modern seas (Schotte et al. 1995) but only one reference to *Cirolana* has been made in the fossil record (Wieder & Feldmann 1992). The Makikihi fossils were referred to *Cirolana* because the morphology of the pleotelson closely resembled that of several species within that genus, including *C. hirtipes* H. Milne Edwards, 1840 and *C. natalensis* Barnard, 1940. Furthermore, examination of bathymetric ranges of the two genera indicate the *Aega* spp. are found at depths below 80 m whereas *Cirolana* is found in shallow water from the intertidal to c. 120 m (Kensley 1978; Schotte et al. 1995). Although we recognised that ecological preference is not a basis for systematic placement, it is reasonable to consider bathymetry in the absence of other evidence.

Identification of *Cirolana makikihi* represents only the second record of isopods in the fossil record of New Zealand. The first notice was that of *Palaega kakatahi* Feldmann & Rust, 2006, from the Pliocene of the North Island. The paucity of fossil isopods throughout the world is remarkable because they are known to inhabit a range of environments from terrestrial to shallow and deep marine. Furthermore, they often occur in very large numbers. It is likely that their scarcity is a reflection of their low preservation potential. The exoskeleton of isopods is not calcified to any degree and the molted remains are extremely fragile. Thus, the discovery is remarkable.

Order DECAPODA Latreille, 1802

Infraorder THALASSINIDEA Latreille, 1831

Superfamily CALLIANASSOIDEA Dana, 1852

Family **UPOGEBIIDAE** Borradaile, 1903

Genus ***Upogebia*** Leach, 1814

TYPE SPECIES: *Cancer stellatus* Montagu, 1808 (ICZN Opinion 434), by original designation.

INCLUDED FOSSIL SPECIES: *Upogebia barti* Fraaije, van Bakel, Jagt, & Coole, 2006, late Oligocene, Washington state, USA; *U. boehmi* Glaessner, 1930, Late Cretaceous, Poland; *U.? clypeata* (Carter, 1898), as *Gebia*, Bathonian, England; *U.? dura* (Moericke, 1897), as *Gebia*, Tithonian, Czech Republic; *U. eocenica* Rathbun, 1926, Eocene, Washington state, USA; *U. gamma* (Rathbun, 1935), as *Callianassa*, Eocene, Alabama, USA; *U. kowai* new species, Pliocene, New Zealand; *U. lambrechtsi* Fraaije, van Bakel, Jagt, & Coole, 2006, early Eocene, Belgium; *U. midwayensis* Rathbun, 1935, Eocene, Alabama, USA; *U. mizunamiensis* Karasawa, 1989, Miocene, Japan; *U. perarolensis* De Angeli & Messina, 1992, Oligocene, Italy; *U. rhacheochir* Stenzel 1945, Late Cretaceous, Texas, USA; *U. scabra* Müller, 1974, Miocene, Hungary; *U. striata* Karsawa & Kishimoto, 1996, middle Miocene, Japan; *U. tanegashimensis* Karasawa & Inoue, 1992, middle Miocene, Japan; *Upogebia* sp. cf. *U. imperfecta* Sakai, 1982, Pleistocene, Japan; *Upogebia* sp. Karasawa, 1989, early Miocene, Japan; *U.* sp. Feldman & Keyes, 1992, late Eocene to early Oligocene and early Miocene, New Zealand; *U.* sp. Kato & Koizumi, 1992, Pleistocene, Japan; *U.* sp. Müller, 1993, middle Miocene, Spain; *U.* sp. Kato, 1996, early Miocene, Japan.

DIAGNOSIS: Carapace with flattened gastric region and projecting rostrum. Dorsal spines prominent, often arrayed in rows or other distinct patterns. Setal pits often prominent in anterior part of dorsal surface anterior to cervical groove and set in advance of spines or rugae. Median dorsal furrow often indistinct. Gastric surface bordered laterally by distinct furrow which diverges posteriorly and lateral crests, each bearing about 12 spines. Lateral ridges become less prominent posteriorly. Cervical groove prominent, often with spinose lateral shoulder. Linea thalassinica present anteriorly and often absent posteriorly (modified from Williams 1993, p. 13, to emphasise diagnostic carapace characters).

DISCUSSION: The diagnosis emphasises the aspects of carapace morphology likely to be visible on fossils. Those characters of the pereiopods and terminal segments of the abdomen used by Williams (1993) to define the genus are unlikely to be seen on fossils. Variations in the development of spines, rugae, grooves, and lineae are significant points of distinction between species (Williams 1993, p. 72) and, therefore, their description is important.

Upogebia is a wide-ranging species in modern seas; Williams (1993) stated that there were 125 species within the Upogebiidae (Williams 1993, p. 1), nearly all of which were referable to *Upogebia*. Sakai (2006) considered the extant Upogebiidae to be composed of 11 genera and 157 species. In the fossil record, 14 species have been named based upon body fossils, two others have been tentatively assigned to the genus, and seven records of *U.* sp. have been cited. In all likelihood, the species list of the genus will continue to grow as collecting continues. This statement is supported by the occurrence of the ichnogenus *Psilonichnus* Fürsich, 1981, which has been widely attributed to the activity of *Upogebia* (Bromley & Frey 1974; Frey et al. 1984; Nesbitt & Campbell 2002). As often seems to be the case, burrowing traces are rarely accompanied by the preserved tracemaker, so the association of trace and tracemaker remains circumstantial.

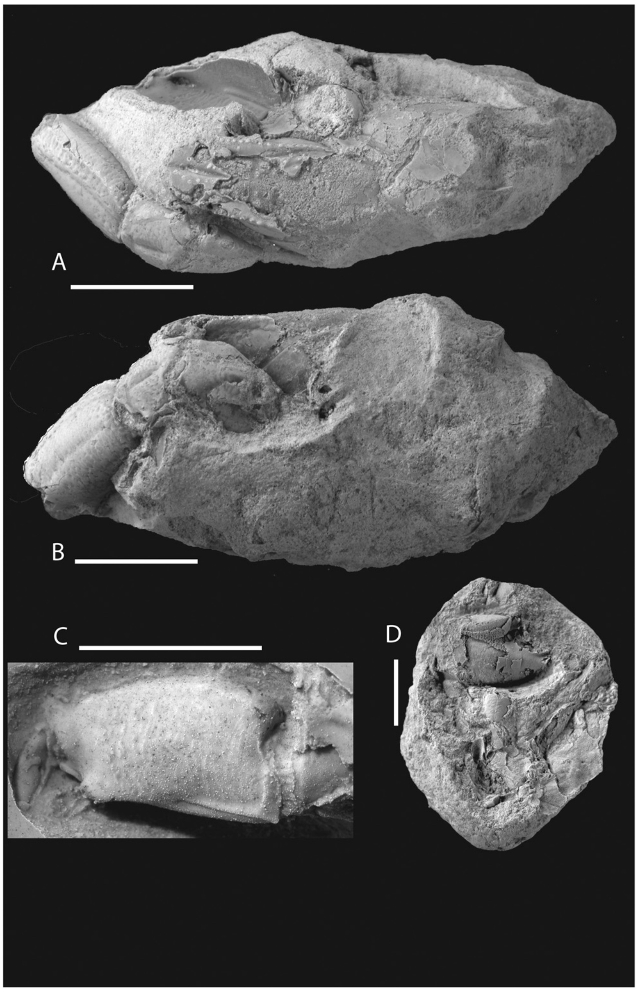

Fig. 2 Thalassinidea. **A–C**, *Upogebia kowai* n. sp., CM1998.171.1, holotype, dorsal carapace view (A), lateral view of carapace and cheliped (B), and silicone cast of chela (C). **D**, Callianassoidea indeterminate, CM1998.171.43, major chela and other carapace and appendage fragments. Scale bars = 1 cm.

Upogebia kowai **n. sp.** Fig. 2A,B

DIAGNOSIS: Typical *Upogebia* with prominent median dorsal sulcus on dorsal surface and distinct lateral furrow bordered by 2 rows of spinose crests. First pereiopod ovoid in outline, slightly longer than high, lacking stridulating structures on inner surface.

DESCRIPTION: Carapace generally quadrate in cross-section; flattened dorsally, broadening to 7 mm at position of cervical groove, tapering uniformly anteriorly to broadly triangular rostrum; posterior part of carapace badly fractured.

Rostrum slightly broader than long, weakly downturned termination, sulcate axially, rimmed laterally by 2–3 blunt spines. Surface of rostrum between rims densely pitted except in axial sulcus.

Dorsal carapace surface, where preserved, bordered by distinct acute crest bearing about 15 blunt spines. A distinct furrow lies parallel to crest defining its inner margin. Sulcus extends from rostrum at least to cervical groove.

Median dorsal furrow deeply impressed in dorsal surface a continuation of rostral sulcus, extending posteriorly at least one-quarter distance from rostrum to cervical groove; sulcus surface smooth, lacking setal pits. Remainder of carapace surface with blunt spines, where preserved; setal pits closely spaced anteriorly and apparently absent posteriorly.

Antero-lateral flanks of carapace strongly concave below rim, bearing field of weakly elevated swellings at about half-length between front of carapace and cervical groove; otherwise flanks are smooth.

Cervical groove broad, deeply impressed, straight on flanks, approaching dorsal surface at c. 35° angle, crossing dorsal surface in concave forward arc.

Remainder of carapace and abdomen fragmentary.

First pereiopods large, strong. Left pereiopod 1 with short merus, about as high as long, narrow proximally and broadening to about midlength and uniformly high to distal margin. Carpus triangular with longitudinal sulcus at midheight and an array of distally directed spines near lower termination. Propodus robust, elongate-ovoid in lateral view, hand 7.5 mm high, 11.3 mm long, bluntly spined keel on upper surface with 2 longitudinal, parallel rows of setal pits on upper half of outer surface and a third longitudinal row of setal pits in shallow depression in lower half. Upper margin more convex than lower one. Fixed finger stout at base, directed downward and distally at c. 45° angle. Surface with subtle pattern of very low, broad, anastomosing ridges with general trend transverse to long axis.

Propodus of right cheliped similar to left, 7.3 mm high, 12.4 mm long, with well-developed sharp, longitudinal ridge extending from midlength of hand to proximal end along lower part of inner surface. Dactylus stout, tapering distally, axis nearly at right angles to axis of propodus. Inner surface of hand with moderately strong anastomosing ridges.

ETYMOLOGY: The trivial name refers to the Kowai Formation, the unit from which the specimens were collected.

TYPES: The holotype, CM1998.171.1, consisting of the anterior part of the cephalothorax, and right and left chelae; paratypes, CM1998.171.2 consisting of fragments of the cephalothorax and appendages, and CM1998.171.40, consisting of a right cheliped, are deposited in the Canterbury Museum, Christchurch, New Zealand.

TYPE LOCALITY: The specimens were collected on the north bank of the Makikihi River, c. 4 km upstream from Makikihi, South Canterbury, New Zealand, at 171°06′08.2″E and 44°36′50.9″S.

DISCUSSION: The specimens assigned to *Upogebia* herein conform closely to the generic diagnosis of Williams (1993) and placement is certain. Although the specimens are incomplete, enough of the carapace is preserved to recognise that the conformation of the rostrum, prominent development of setal pits on the anterior part of the carapace, and development of spinose lateral crests and furrows on the dorsal margin of the carapace all confirm the placement. The presence of a sulcate axial region is a variable character within the genus and serves to distinguish the new species from several others within the genus.

Comparison of *Upogebia kowai* with other fossil representatives of the genus demonstrates that it is different. The recognition of *U? gamma* as a member of the genus is questionable. It was originally referred to *Callianassa* and was subsequently referred to *Upogebia* by Stenzel (1945); however, the conformation of the cheliped bears strong resemblance to *Callianassa* claws and is strikingly dissimilar to the chelipeds of *U. kowai*. *Upogebia eocenica* has a more granular dorsal carapace surface than does the new species and it also bears well-developed stridulating ridges on the 1st pereiopod, a feature noted to be unusual in the genus (Rathbun 1926, p. 125). The dorsal surface of the carapace of *U. mizunamiensis* does not narrow uniformly from the cervical groove to the front, the pereiopods are not ovoid in outline, and the 1st pereiopods bear distinctive stridulating ridges on the inner surfaces similar to those of *U. eocenica*. The part of the dorsal surface of *U. perarolensis* anterior to the cervical groove is finely granular overall, bearing only a single spinose ridge; the 1st pereiopods are extremely long and slender. Although *U. scabra* is not well illustrated, the outline of the dorsal carapace surface is vase-shaped and does not narrow uniformly as in *U. kowai*. *Upogebia striata* is represented only by a 1st pereiopod that bears stridulating ridges on the inner surface and is long, slender, and not ovoid; thus, it cannot be confused with *U. kowai*. The form of the propodus of *U. tanegashimensis* bears two rows of nodes on the outer surface and is not ovoid in outline so that it is different from that of the new species. It is not possible to make comparisons between the new species and *U. midwayensis* and *U. rhacheochir* because comparable parts of the anatomy are not preserved.

The only other fossil record of the genus in New Zealand was that of *Upogebia* sp. from the early Miocene Waitemata Group on Waiheke Island, Auckland. The sole specimen, AU11631, is deposited in the collections of Auckland University and, although reported by Feldmann & Keyes (1992), has never been described. The specimen consists of fragments of abdomen and appendages.

CALLIANASSOIDEA family, genus, and species indeterminate Fig. 2D

DESCRIPTION: Outer surface of right propodus well exposed; other appendages and possibly carapace badly fragmented.

Propodus stout; manus c. 12 mm long, 10 mm high; fixed finger broken, more than 5 mm long. Outer surface of manus strongly inflated, lacking spines, but with deep sulcate region extending from approximately the upper proximal corner and broadening and deepening arc to upper distal corner of manus. Upper surface of manus a broad, smooth, inflated, weakly convex surface extending the length of manus. Proximal margin of propodus not exposed. Lower surface of propodus including fixed finger smoothly curved. Tip and occlusal surface of finger broken. Surface of propodus smooth except sulcate region which bears distally directed setal pits.

REFERRED SPECIMEN: The sole specimen, CM1998.171.43, is deposited in the Canterbury Museum, Christchurch, New Zealand.

COLLECTING LOCALITY: The specimen was collected on the north bank of the Makikihi River, c. 4 km upstream from Makikihi, South Canterbury, New Zealand, at 171°06′08.2″E and 44°36′50.9″S.

DISCUSSION: The specimen referred to the Callianassoidea is enigmatic. The morphology of the propodus bears little resemblance to other decapods in our experience. The overall outline is most reminiscent of some pagurids, the hermit crabs.

The lower surface of the hand is smoothly convex, much in the manner of many pagurids and some callianassids. The deep, setose sulcus is not reminiscent of either group. Finally, the extremely broad, smooth, convex upper surface is not known to us from either group. The one aspect of the specimen that suggests relationships to the Callianassoidea rather than to the pagurids is that the remainder of the enclosing concretion contains a jumble of small fragments of appendages and possibly the cephalothorax. This manner of preservation is commonly seen in the Callianassoidea, whereas the pagurids are almost invariably preserved as single chelipeds or as appendages within snail shells. Because this evidence is circumstantial and because the claw morphology differs so significantly from that of other callianassoids, it seems prudent to illustrate the specimen and to leave it in open nomenclature for the time being.

Infraorder BRACHYURA Latreille, 1802
Section HETEROTREMATA Guinot, 1977
Superfamily GONEPLACOIDEA MacLeay, 1838
Family **GONEPLACIDAE** MacLeay, 1838

DIAGNOSIS: See Karasawa & Schweitzer (2006).

DISCUSSION: Karasawa & Schweitzer (2006) recently re-evaluated the Xanthoidea *sensu lato* and the Goneplacoidea. They elevated the subfamilies of the Goneplacidae *sensu lato* to family status and the Goneplacidae to superfamily status; we follow their classification herein. *Kowaicarcinus* new genus is placed within the Goneplacidae *sensu stricto* (see Karasawa & Schweitzer 2006) based upon its possession of a straight front, three anterolateral spines, entire orbital margins, a relatively broad fronto-orbital width to carapace width ratio (70%), and all male abdominal somites free and apparently covering sternite 8. This combination of characters is unique to the family among those brachyurans with a xanthoid or goneplacoid carapace morphology (Davie 2002; Karasawa & Kato 2003; Karasawa & Schweitzer 2006).

Other members of the Goneplacidae are previously known from New Zealand. Fossil occurrences of *Carcinoplax* H. Milne Edwards, 1852, have been reported from Eocene through Pleistocene rocks; *Goneplax* Leach, 1814, has been reported from Miocene rocks; and *Ommatocarcinus* White, 1852, has been noted from Miocene through Pleistocene rocks (Feldmann & Keyes 1992; Karasawa & Kato 2003). Thus, the family is well known from the area.

The new taxon described below bears superficial similarity to some members of the Grapsidae *sensu lato* MacLeay, 1838, and the freshwater crab family Parathelphusidae Alcock, 1910. *Hemigrapsus crenulatus* (H. Milne Edwards, 1837), a member of the Grapsidae *sensu lato*, is similar to the new genus and species described below, at least in terms of the dorsal carapace morphology (Rathbun 1918, pl. 68; McLay 1988, p. 287). The dorsal carapace of *H. crenulatus* is rounded and bears three anterolateral spines including the outer-orbital spine; the front is straight and relatively wide; and the orbits are entire and forward facing. These are all characteristics of the new taxon described below. However, the new taxon is characterised by male and female sterna that are unlike those of the Grapsidae. Grapsids possess sterna that are broad from sternites 4–8 and that narrow considerably at the position of sternite 3. The sternum of *Kowaicarcinus* is rounded as in many goneplacids. The sternum of *Kowaicarcinus* possesses a marked notch between sternites 3 and 4, which clearly separates these two sternites (Fig. 3I–K). These two sternites are also clearly distinct from one another on *Kowaicarcinus*, as seen in many goneplacids. In the grapsids, sternites 3 and 4 are fused into a single unit and are not distinct from one another, and there is usually no notch or a very reduced one between sternites 3 and 4 (e.g., Rathbun 1918, pl. 68). Thus, the specimens referred to *Kowaicarcinus* cannot be referred to a grapsid genus.

Kowaicarcinus also bears some superficial similarities to some species of freshwater and semiterrestrial crabs, such as *Austrothelphusa* Bott, 1969, especially in terms of the carapace shape; straight, rimmed front; forward-directed, simple orbits; and relatively poorly defined carapace regions. However, the sternum of *Kowaicarcinus* is different from that of *Austrothelphusa* and other freshwater crabs. In *Austrothelphusa* and other freshwater and semiterrestrial crabs known from Australia, such as *Cardisoma* Latreille, 1828, of the Gecarcinidae MacLeay, 1838, sternite 3 is fused to sternite 4 such that a suture or other line is not evident and is much reduced, and there is no notch or a very small lateral notch between those two sternites (Short 1994). In *Kowaicarcinus*, sternites 3 and 4 are distinct from one another, sternite 3 is pronounced, and there is a large notch in the lateral margin between sternites 3 and 4. In the freshwater crabs, sternites 2 and 3 are not markedly separated, whereas in *Kowaicarcinus*, there is a clear, complete suture between those two sternites (Fig. 3K). In the freshwater crabs, sternites 4–6 have anterior and posterior margins that are parallel, and the sternites are directed laterally. In *Kowaicarcinus*, sternites 4 and 5 are directed anterolaterally, sternite 6 is directed laterally, and sternite 7 is directed posterolaterally (Fig. 3I–K). Thus, *Kowaicarcinus* cannot be accommodated within any of the freshwater crab families that occur in Oceania. To date, there is only one occurrence of a strictly freshwater crab in New Zealand (Towers & McLay 1995), although seven are known from neighbouring Australia (Davie 2002).

Genus ***Kowaicarcinus*** n. gen.

TYPE SPECIES: *Kowaicarcinus maxwellae*, by monotypy.

DIAGNOSIS: As for species.

DESCRIPTION: As for species.

ETYMOLOGY: The generic name is a combination of Kowai, the name of the formation from which the specimens were collected, and "carcinus," meaning crab, a common stem used within the Infraorder Brachyura.

DISCUSSION: *Kowaicarcinus* n. gen. bears numerous similarities with the extinct genera *Amydrocarcinus* Schweitzer et al., 2002, and *Magyarcarcinus* Schweitzer & Karasawa, 2004; and the extant *Carcinoplax* H. Milne Edwards, 1852, which is also known from fossil occurrences in New Zealand. However, there are sufficient differences with each that justify naming a new genus to accommodate the new material. *Kowaicarcinus* is similar to the extant goneplacid *Carcinoplax*. *Carcinoplax* is a variable genus, but always possesses small, attenuated, needle-like anterolateral spines and a rectangular or ovate carapace. Such small anterolateral spines are not seen in the new genus, which possesses three anterolateral lobes, nor is the carapace rectangular in the new genus. Thus, *Carcinoplax* was excluded. *Kowaicarcinus* is easily excluded from the other goneplacid genera known from the fossil record of New Zealand, *Goneplax* and *Ommatocarcinus*, because those two genera have extremely long orbits that occupy almost the entire frontal margin of the carapace. That feature is not present in *Kowaicarcinus*.

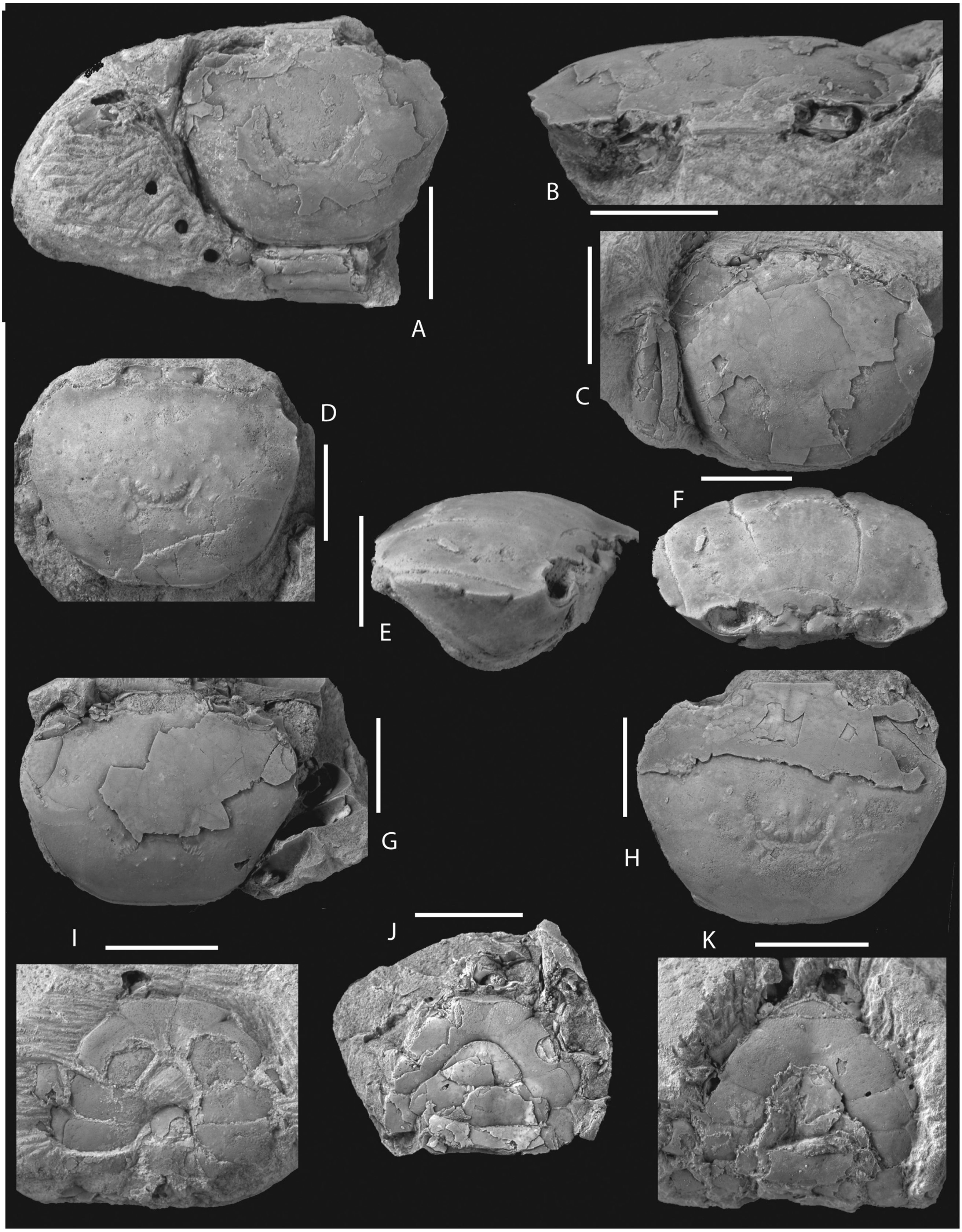

Fig. 3 **A–K** *Kowaicarcinus maxwellae* n. sp. **A, B** CM1998.171.31, paratype, dorsal carapace and portion of immature female abdomen (A) and anterior view showing orbits (B). **C**, CM1998.171.28, paratype, dorsal carapace and posterior appendage. **D**, CM1998.171.26, dorsal carapace with well-preserved front. **E, F** CM1998.171.20, paratype, oblique lateral view showing anterolateral spines and orbit (E) and deflexed anterior view showing orbital rims and front (F). **G**, CM1998.171.17, paratype, dorsal carapace with portions of appendages. **H**, CM1998.171.16, holotype, dorsal carapace with very well preserved front, orbits, and anterolateral margins. **I**, CM1998.171.18, paratype, male sternum and abdomen. **J**, CM1998.171.24, paratype, mature female sternum and abdomen. **K**, CM1998.171.27, paratype, sternum with preserved sternites 1 and 2. Scale bars = 1 cm.

Kowaicarcinus is most similar to *Amydrocarcinus* and *Magyarcarcinus*. *Amydrocarcinus* is similar to *Kowaicarcinus* in possessing an ovate outline; deep, forward-directed orbits with entire margins; and a relatively smooth unornamented carapace. However, *Kowaicarcinus* has three anterolateral lobes, which *Amydrocarcinus* lacks. *Magyarcarcinus* is more square than *Kowaicarcinus* and possesses more prominently rimmed, shallower orbits. *Kowaicarcinus*, *Amydrocarcinus*, and *Magyarcarcinus* share a characteristic long sternite 4 that is oriented anterolaterally, and sternite 3 fused with sternite 4 axially and separated laterally by a notch. All three taxa show some indication of preserved eyes and eyestalks (Fig. 3B) (Schweitzer & Karasawa 2004, fig. 1.1,1.4) and even antennal structures in *Magyarcarcinus* (Schweitzer & Karasawa 2004, fig. 1.4). This is also true of the goneplacoid family Euryplacidae Stimpson, 1871, in which many extinct taxa have preserved eyestalks (Karasawa & Schweitzer 2006). Preserved eyestalks are unusual and do not occur in all brachyurans. Thus, this feature seems to be diagnostic for some goneplacoids and may indicate a life habit in which the eye required additional protection via calcification.

Amydrocarcinus is known only from Eocene rocks of the Pacific coast of Mexico (Schweitzer et al. 2002; Schweitzer & Karasawa 2004), and fossil occurrences of *Carcinoplax* are known only from the Pacific, ranging in age from Miocene to Pleistocene (Karasawa & Kato 2003) except *C. barnardi* Capart, 1951, from the eastern Atlantic (H. Karasawa pers. comm.). *Magyarcarcinus* is known from the Eocene of southern and central Europe, in what would have been the Tethys Seaway (Schweitzer & Karasawa 2004). Thus, the Pliocene occurrence of *Kowaicarcinus* in New Zealand fits within the framework of a Tethyan distribution for the family westward into the Pacific or eastward through the Central American Seaway to Pacific coastal Mexico and then dispersing throughout the Pacific Ocean. Other extinct or fossil members of the Goneplacidae also display Pacific distributions (Karasawa & Schweitzer 2006).

Kowaicarcinus maxwellae n. sp. Fig. 3A–K

DIAGNOSIS: Carapace hexagonal to transversely ovate, length c. 80% maximum width, widest about half the distance or a little less posteriorly; moderately vaulted longitudinally, weakly vaulted transversely, dorsal carapace regions poorly defined. Front straight or nearly straight, without median notch, with finely beaded rim, with ridge parallel to frontal margin, c. 35% maximum carapace width. Orbits rimmed, set posteriorly from frontal margin, ovoid, deep, directed forward, no evidence of fissures or notches, outer-orbital angle produced into small, blunt spine; fronto-orbital width c. 70% maximum carapace width. Anterolateral margin convex, very weakly tri-lobed or entire; posterolateral margin straight or weakly convex; posterolateral re-entrant well developed, rimmed; posterior margin straight or weakly convex, rimmed.

DESCRIPTION: As for diagnosis. Carapace hexagonal to transversely ovate, length c. 80% maximum width, widest about half the distance or a little less posteriorly; moderately vaulted longitudinally, weakly vaulted transversely, dorsal carapace regions poorly defined. Front straight or nearly straight, without median notch, margin with finely beaded rim, with ridge on upper surface parallel to frontal margin, upper surface axially sulcate; frontal width c. 35% maximum carapace width. Orbits rimmed, set posteriorly from frontal margin, ovoid, deep, directed forward, no evidence of fissures or notches, outer-orbital angle produced into small, blunt spine; fronto-orbital width c. 70% maximum carapace width. Anterolateral margin convex, very weakly tri-lobed or entire; posterolateral margin straight or weakly convex; posterolateral re-entrant marked, rimmed; posterior margin straight or weakly convex, rimmed.

Anterolateral margin convex, weakly scalloped by 3 broad but subtle anterolateral lobes, each moderately curved forward, margins of each beaded; anterolateral margin length c. 37% maximum carapace length. Posterolateral margin entire, overall length c. 57% maximum carapace length, nearly straight for c. 41% its length posteriorly, weakly convex for the remainder; posterolateral re-entrant well developed, rimmed. Posterior margin straight or very weakly convex, rimmed, c. 36% maximum carapace width.

Carapace surface finely granular throughout. Regions poorly defined in general. Epigastric regions weakly inflated. Mesogastric region moderately expressed, slightly elevated above remainder of carapace, as wide as cardiac region, bounded by weak cervical groove and bearing strong posterior gastric muscle scars on mold of interior. Cardiac region weakly expressed on internal mold, widest at midlength, posterior medial region contains cluster of 5 nodes in a convex-forward arch, single nodes near lateral margins at midlength, 2 additional nodes near midline of anterior half of the region. Epibranchial regions arcuate on internal mold, branchial regions otherwise undefined. Other regions not well defined.

Abdomen of mature female broad, with convex lateral margins, widening to midpoint of somite 5, then narrowing toward telson; somite 1 approximately equal in width to posterior margin; all somites free; somites gently vaulted longitudinally, with straight anterior and posterior margins and rounded at lateral margins, suture between somites 6 and telson moderately concave forward; telson triangular with rounded apices; somites 2–5 approximately equal in length; somite 1 approximately half as long as others; somite 6 longer than others and approximately equal in length to telson. Abdomen of immature female similar to mature female but less broad and with straighter lateral margins.

Abdomen of male with concave lateral margins, somites 2 and 3 very broad; somites 4–6 narrowing; telson missing; all somites appear to have been free.

Male sternum ovate; sternites 1–2 apparently fused with no evidence of suture or line, separated from sternite 3 by continuous suture; sternites 3 and 4 fused axially and separated by small notch laterally; sternite 4 oriented at high angle, longer than other sternites; sternites 5 directed anterolaterally, with episternal projection; sternite 6 directed laterally, appearing to have had an episternal projection; sternite 7 directed posterolaterally, apparently somewhat longer than sternites 5 and 6; sternite 8 not evident. Female sternum not as well exposed but appearing to have been similar.

Merus of cheliped triangular in cross-section; ischium of third walking leg appears most massive of the 4 walking legs; ischia of all walking legs appears oval in cross-section, apparently rather stout.

MEASUREMENTS: Measurements (in mm) taken on *Kowaicarcinus maxwellae* may be found in Table 2.

ETYMOLOGY: The trivial name honors Sue Maxwell, who assisted PAM in all aspects of fieldwork and who made the publication of this work possible.

TYPES: The holotype, CM1998.171.16, and 23 paratypes, CM1998.171.17–CM1998.171.39, are deposited in the Canterbury Museum, Christchurch, New Zealand.

TYPE LOCALITY: The specimens were collected on the north bank of the Makikihi River, c. 4 km upstream from Makikihi, South Canterbury, New Zealand, at 171°06′08.2″E and 44°36′50.9″S.

DISCUSSION: *Kowaicarcinus maxwellae* n. sp. is well represented by numerous specimens, representative of males (Fig. 3I), immature females (Fig. 3A), and mature females (Fig. 3J). Thus, members of both genders apparently lived in the same area, as they were preserved together. Occurrences of the related *Amydrocarcinus*, in specimens for which gender has been determinable, have all been males (Schweitzer et al. 2007). It is possible that the reasons are attributable to mode of preservation. In the case of *Amydrocarcinus*, the specimens appear to have been preserved in place as corpses along with other decapod taxa. The specimens of *Kowaicarcinus maxwelli* were preserved in concretions among gravel and other clastic fragments; thus, it is possible that the specimens were carried in from various areas. This seems unlikely, however. More likely is that the two taxa had different life modes or reproductive strategies.

Section THORACOTREMATA Guinot, 1977

Superfamily GRAPSOIDEA MacLeay, 1838

Family **GRAPSIDAE** MacLeay, 1838

Subfamily **CYCLOGRAPSINAE** H. Milne Edwards, 1853

DIAGNOSIS: The subfamily has been recently diagnosed by Karasawa & Kato (2001) and Davie (2002).

DISCUSSION: Karasawa & Kato (2001) were the first authors in recent times to use the subfamily Cyclograpsinae, originally designated as a tribe by H. Milne Edwards. They noted in their cladistic analysis of the Grapsidae, using adult morphology, that a small group of genera traditionally assigned to the Sesarminae Dana, 1851, in fact formed a morphologically consistent group which they assigned to the Cyclograpsinae. These genera included *Cyclograpsus* H. Milne Edwards, 1837; *Helice* de Haan, 1835; *Metaplax* H. Milne Edwards, 1852; and the extinct *Miosesarma* Karasawa, 1989.

Independently and without reference to the work of Karasawa & Kato (2001), Davie (2002) also resurrected the Cyclograpsinae for a group of grapsid genera that had previously been assigned to the Sesarminae and that displayed some superficial morphological similarities to the Varuninae H. Milne Edwards, 1853. Davie's interpretation of the subfamily was similar to that of Karasawa & Kato (2001), including the same three extant taxa plus four others. Davie (2002) did not treat extinct taxa. Poore (2004) maintained the same usage of the subfamily as Davie (2002).

Schubart et al. (2006) performed a phylogenetic analysis of the grapsoid crabs using mitochondrial DNA and suggested that *Helice* and *Cyclograpsus* belonged to the Varunidae. They did not refer to the previous works of Karasawa & Kato (2001) or Davie (2002); thus, they did not include the Cyclograpsinae at all. They suggested that the Grapsoidea MacLeay, 1838, as currently understood (in which subfamilies are elevated to family status, as in Martin & Davis (2001)), was polyphyletic, as was the Ocypodoidea Rafinesque, 1815, and that superfamily designations should not be used for those groups. Sakai et al. (2006) provided an extensive review of the recent works on the Grapsidae and referred the genera discussed in their paper to the Cyclograpsinae, although they did not discuss the composition of the subfamily as a whole.

Because the works of Karasawa & Kato (2001), Davie (2002), and Poore (2004) are based on adult morphology, and because Davie (2002) accounted for such phenomena as homoplasy, convergence, and environmental adaptations, we opt to retain the use of the Cyclograpsinae for this group of grapsid crabs. Karasawa & Kato (2001), because they included fossil taxa in their analysis, accounted for the evolutionary variation and history of the family. The most recent work on the group by Sakai et al. (2006) includes the Cyclograpsinae, and in it, they evaluated and revised the species from Australia and New Zealand. These works, therefore, address grapsid crabs inhabiting areas geographically near to the fossil collecting localities; thus, we feel that the classification of Karasawa & Kato (2001), Davie (2002), and Sakai et al. (2006) at this time best reflects the phylogeny of the animals.

None of the above described works particularly agrees on the composition of the subfamily. Genera that appear to be widely held to belong to the subfamily include those treated by Karasawa & Kato (2001), listed above; those listed by Davie (2002); and the new genera named by Sakai et al. (2006). However, this has by no means been tested, as far as is known, and represents a composite list from the literature.

Grapsid crabs are not common in the fossil record. Karasawa & Kato (2001) summarised the occurrences known up until that time, noting that the vast majority of the fossils were recovered from Miocene or younger rocks. However, there are a few Eocene occurrences from southern Europe as well (Karasawa & Kato 2001; De Angeli & Garassino 2006), indicating that that may be the area of origin for the family.

Miograpsus Fleming, 1981, from Miocene rocks of the North Island, is the only other grapsid crab known from the fossil record of New Zealand. Thus, the family was already known from the area; however, it has been placed within a different subfamily, the Varuninae (Karasawa & Kato 2001).

Genus ***Austrohelice*** **Sakai,** Türkay, and Yang, 2006

TYPE SPECIES: *Helice crassa* Dana, 1851, by original designation.

OTHER SPECIES: *Austrohelice manneringi* n. sp.

DIAGNOSIS: As in Sakai et al. (2006, p. 53).

DISCUSSION: The diagnosis provided by Sakai et al. (2006) contains few characters that are recognisable in fossils. The markedly sinuous orbital margin and sinuous narrow ridges on the branchial regions of the dorsal carapace seem to be unique to the genus; other genera possess such ridges but they are straighter and shorter, such as in *Pseudohelice* Sakai et al., 2006. The new specimens possess the sinuous orbits and the narrow ridges on the dorsal carapace; thus, we herein refer them to *Austrohelice*.

The new fossils are similar to *Miosesarma* Karasawa, 1989, from Miocene rocks of Japan; however, that genus possesses a large, triangular outer orbital spine, which the new specimens lack. In addition, the carapace regions of *Miosesarma* are better developed than in the new specimens, and the orbital margins are less sinuous in *Miosesarma* than in the new specimens. *Miograpsus* is not much wider than long and has spines extending almost the entire length of the lateral margins, neither of which typifies the new specimens. *Miograpsus* also appears to lack the narrow ridge on the branchial region which is so distinctive on the new specimens.

Austrohelice manneringi n. sp. Fig. 4A–F

DIAGNOSIS: Front bilobate, projecting well in advance of orbits, occupying about one-third maximum carapace width; orbits very wide, fronto-orbital width equal to maximum carapace width; eyestalk arising from base of front, long, extending almost to outer-orbital spine; mesobranchial region broadly inflated, with narrow oblique ridge extending from lateral margin toward axis about two-thirds the distance axially.

DESCRIPTION: Carapace wider than long, length c. 62% maximum width at position of outer-orbital spine, about one-quarter the distance posteriorly on carapace; flattened transversely, weakly vaulted longitudinally; carapace regions moderately defined; carapace dorsoventrally compressed and tabular overall in shape.

Front bilobate, axially broadly concave, projecting well in advance of orbits, occupying about one-third maximum carapace width. Orbits very wide, fronto-orbital width equal to maximum carapace width; upper orbital margin sinuous, extending obliquely posteriorly from base of front, terminating in small, triangular outer orbital spine; eyestalk arising from base of front, long, appearing to have lain horizontally in orbital groove when retracted, extending almost to outer orbital spine.

Anterolateral and posterolateral margins confluent, anterolateral portion with 3 spines including outer orbital spine; spines decreasing in size posteriorly; posterior re-entrant large, rimmed; posterior margin straight, rimmed.

Frontal region axially sulcate; epigastric regions broadly inflated. Protogastric regions wider than long, weakly inflated; mesogastric region with long anterior process, widened posteriorly, marked on posterior margin by deep cervical groove; urogastric region poorly developed; cardiac region ovate, well-marked by branchio-cardiac groove; intestinal region depressed below level of cardiac region. Hepatic regions short, wide. Epibranchial regions short, wide, extending in weak concave-forward arc from last anterolateral spine to mesogastric region; mesobranchial region broadly inflated, with narrow oblique ridge extending from lateral margin toward axis about two-thirds the distance axially; metabranchial region short, depressed below level of mesobranchial region.

Chelipeds heterochelous, appearing to be short. Other appendages relatively short.

Female abdomen broad, somites wide, short.

MEASUREMENTS: Measurements (in mm) taken on the dorsal carapace of *Austrohelice manneringi* n. sp. are given in Table 3.

ETYMOLOGY: The trivial name honours Al Mannering, South Island, New Zealand, a dedicated amateur who assisted with fieldwork and collection of specimens.

TYPES: The holotype, CM1998.171.3, and 12 paratypes, CM1998.171.4–CM1998.171.14, are deposited in the Canterbury Museum, Christchurch, New Zealand.

TYPE LOCALITY: The specimens were collected on the north bank of the Makikihi River, c. 4 km upstream from Makikihi, South Canterbury, New Zealand, at 171°06′08.2″E and 44°36′50.9″S.

DISCUSSION: The new species differs from the type and sole extant species, *Austrohelice crassa*, in possessing a more projected frontal area and longer eyestalks. In other regards, however, the two species are similar as might be expected for species inhabiting the same general geographic area, albeit separated by several million years. This suggests an ancestor-descendent relationship.

Although several specimens are referable to *Austrohelice manneringi* n. sp., none are particularly complete. None retains the sternum and only one retains broad somites of a female abdomen. However, many of the specimens retain well-preserved eyestalks. This feature was apparently well-calcified, and the orbits were deep. This indicates that the eyes required protection, as might be expected for an animal living in shallow water or intertidal areas.

DISCUSSION

The Pliocene record of decapods in New Zealand is not particularly robust. Feldmann & Keyes (1992) listed seven genera of brachyurans and one genus of anomuran from localities in the southern areas of the North Island and along the east coast of the South Island in North Canterbury and

Table 2 Measurements (in millimetres) taken on the dorsal carapace of *Kowaicarcinus maxwellae* n. sp. W = maximum carapace width; L = maximum carapace length; FOW = fronto-orbital width; FW = frontal width; L to Max W = length to position of maximum carapace width.

Specimen number	W	L	FOW	FW	L to Max W
CM1998.171.16 (Holotype)	30.6	24.5	21.3	10.5	10.8
CM1998.171.28	25.4	20.1	18.3	9.1	10.5
CM1998.171.31	23.6	19.4	15.4	8.2	11.6
CM1998.171.17	31.6	24.9	22.4	11.2	11.4

Table 3 Measurements (in millimetres) taken on the dorsal carapace of *Austrohelice manneringi* n. sp. W = maximum carapace width; L = maximum carapace length; FOW = fronto-orbital width; FW = frontal width; L to Max W = length to position of maximum carapace width.

Specimen number	W	L	FOW	FW	L To Max W
CM1998.171.3 (Holotype)	25.0	15.1	25.0	–	4.3
CM1998.171.6	>22.5	16.5	–	7.9	–
CM1998.171.13	>19.0	15.2	–	6.5	–
CM1998.171.14	23.2	14.5	–	–	–
CM 1998.171.7	26.8	17.1	–	9.0	–

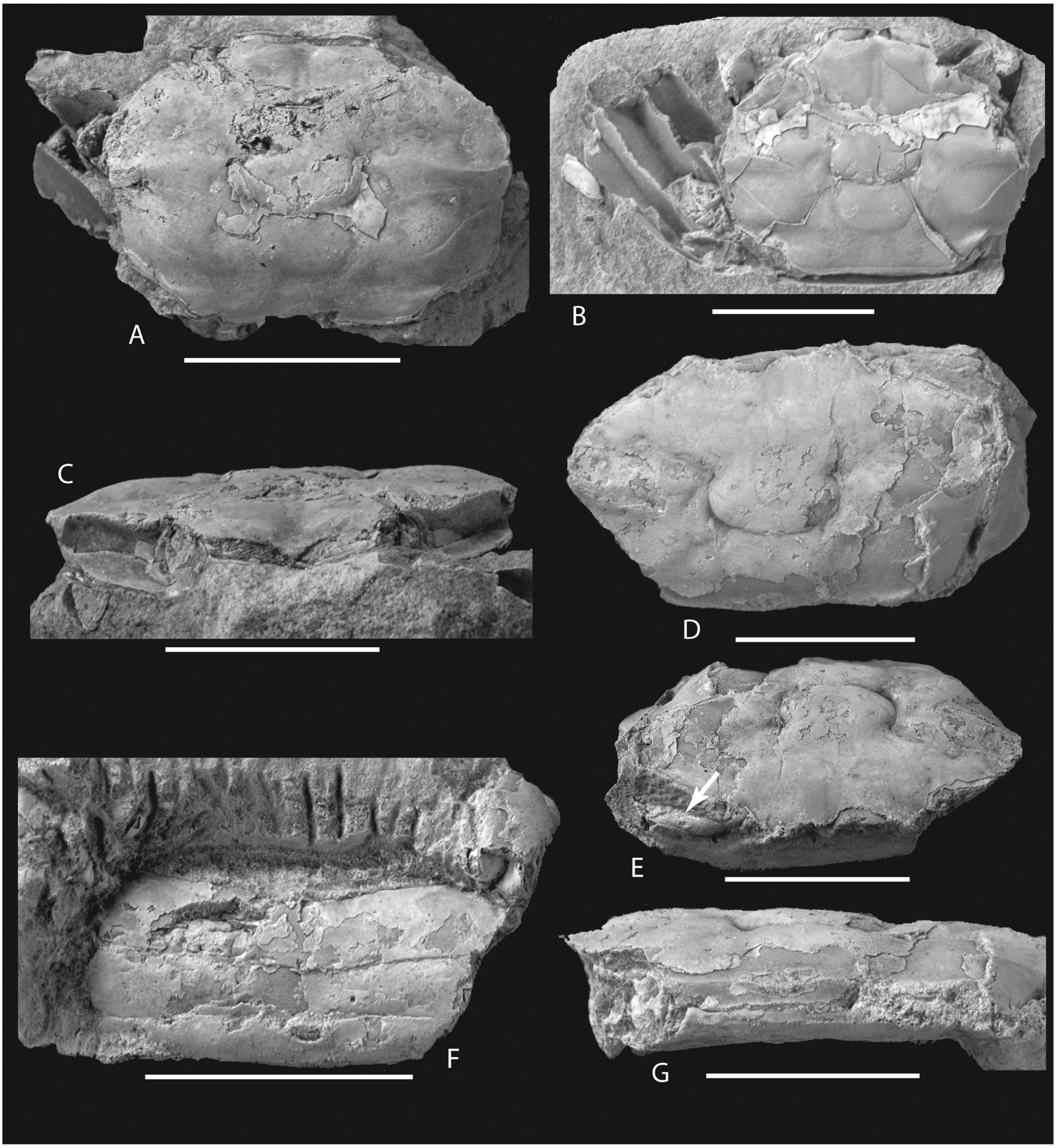

Fig. 4 **A–F** *Austrohelice manneringi* n. sp. **A, C** CM1998.171.3, holotype, dorsal carapace view (A) and anterior view showing broad orbits and front (C). **B**, CM1998.171.13, paratype, dorsal carapace and appendage elements. **D–F**, CM1998.171.6, paratype, dorsal carapace with preserved eyestalk (D), front view showing detail of eyestalk (arrow) (E), female abdomen (F), and posterior view of female abdomen (G). Scale bars = 1 cm.

Marlborough. In addition to the decapods, Feldmann & Rust (2006) recently added the first record of an isopod fossil from New Zealand. Caution should be exercised when examining the stratigraphic list of decapod localities recorded by Feldmann & Keyes (1992, p. 66) as several Miocene localities are erroneously recorded as Pliocene in age. In contrast to the Pliocene, 11 genera of decapods are recorded from the Pleistocene and 18 genera are noted from the Miocene. The Miocene record has been increased to 19 with the naming of *Tongapapaka* Feldmann et al., 2006, from North Canterbury. Thus, the addition of four new generic records and one new isopod record for the Pliocene of New Zealand is particularly significant.

The presence of the Kowai fauna within concretions and the matrix of conglomeratic sandstone is remarkable. All indications are that the environment of deposition was a relatively high energy, nearshore environment, as discussed above. However, the preservation of the arthropods is remarkable in that many of the specimens are fully articulated or, if the appendages are missing, complete carapaces and abdomina. Cuticle is present in nearly pristine condition unless where broken away during exposure or preparation. Preparation of the material is made difficult because the interiors of the carapaces are generally not filled with matrix, so that exposure of the surface of the specimen frequently results in breaking through to the interior. This delicate manner of preservation in such a high energy environment seems anomalous; however, it can be explained by very rapid entrainment of specimens that have recently died and are completely or nearly completely articulated. In the event that the remains were not subsequently reworked and lithification occurred rapidly, the delicate remains could be preserved. The conditions of rapid burial and lithification probably did not occur over broad areas of the depositional site but, rather, may have been confined to localised swales on the seafloor. This interpretation is supported by the observation that the exposure of decapod-bearing rock was very small and lenticular.

The occurrence of a member of the Goneplacoidea, which are generally found in at least 15 m of water and deeper (i.e., Rathbun 1918; Sakai 1976), in association with members of the Upogebiidae and Grapsidae, is somewhat enigmatic. Upogebiids and grapsids are certainly most frequent inhabitants of intertidal, estuarine, mangrove, or other very nearshore environments, with specific reports of these types of environments for these families for Australia and New Zealand (McLay 1988; Davie 2002; Poore 2004) as well as Japan (Sakai 1976) and the Americas (Rathbun 1918). We note that the coast of New Zealand was certainly an active one during the Pliocene, exhibiting a narrow continental shelf as well as frequent tectonic activity, as now, so it is possible that nearshore inhabitants were mixed with somewhat deeper water, offshore crabs. Indeed, such faunal mixing within the Decapoda has previously been reported for active margins on the Pacific Slope of North America (Feldmann et al. 1991; Schweitzer & Feldmann 1999). There are also some reports of extant goneplacoid crabs inhabiting relatively shallow water (8–10 m; Rathbun 1918), so they are not exclusively limited to deep, offshore environments.

ACKNOWLEDGMENTS

We thank Brad Field (GNS Science) for information on the sedimentology of the Kowai Formation at Makikihi; Alan Beu (GNS Science) for his assessment of the age indicated by the molluscs; and Ewan Fordyce (Otago University) for information on Pliocene cetacean occurrences in South Canterbury and North Otago. Al Mannering (Christchurch) discovered the specimen of *Crassostrea ingens* that helped establish the age and joined us in collection of specimens. J. Maxwell assisted in the field. R. Lemaitre and K. Reed, United States National Museum of Natural History, Smithsonian Institution, Washington DC, USA; M. Türkay, Forschungsinstitut Senckenberg, Frankfurt, Germany; and S. Donovan and C. Fransen, Nationaal Natuurhistorisch Museum, Leiden, the Netherlands, each provided access to the collections at their respective institutions. Fieldwork for Feldmann, Schweitzer, and Kelley was supported by NSF Grant OPP-9909184 to Feldmann and K. L. Bice. Examination of freshwater crabs and other comparative material at the United States National Museum, Smithsonian Institution, Washington DC; the biological collections at the Senckenberg Museum in Frankfurt, Germany; and the biological collections at Leiden, the Netherlands, was funded by NSF Grant EF-0531670 to Feldmann and Schweitzer. H. Karasawa, Mizunami Fossil Museum, Japan, and C. McLay, University of Canterbury, Christchurch, New Zealand, provided constructive reviews that improved the paper.

Phillip Maxwell

Personal note from Rod Feldmann

It is also appropriate to acknowledge the many years of association, collaboration, and friendship that I shared with our co-author, the late Phil Maxwell. Phil and his wife Sue have hosted me as well as several Kent State students since their days in Wellington. Together we worked in the field several times and, on every occasion, I was truly impressed by Phil's vast knowledge of New Zealand geology and paleontology. He unselfishly made his decapod specimens available to me and arranged for their deposit in the appropriate museum upon completion of the work. Whether collaborating on a publication or reviewing work of my own, he kept me honest, made certain that what I wrote was geologically sound, and unravelled the mysteries of the English and later Metric grid systems. On a more personal note, Phil was one of the kindest, gentlest, and most generous people I have ever had the pleasure of knowing. I miss him.

REFERENCES

Alcock AW 1910. On the classification of the Potamonidae (Thelphusidae). Records of the Indian Museum 5(4): 253–261.

Andrews PB, Field BD, Browne GH, McLennan JM 1987. Lithostratigraphic nomenclature for the Upper Cretaceous and Tertiary sequence of central Canterbury, New Zealand. New Zealand Geological Survey Record 24: 1–40.

Barnard KH 1940. Contributions to the crustacean fauna of South Africa. 12. Further additions to the Tanaidacea, Isopoda, and Amphipoda together with keys for the identification of the hitherto recorded marine and freshwater species. Annals of the South African Museum 32: 381–543.

Beu AG 2001. Local stages to be used for the Wanganui Series (Pliocene–Pleistocene), and their means of definition. New Zealand Journal of Geology and Geophysics 44: 113–125.

Beu AG, Maxwell PA 1990. Cenozoic Mollusca of New Zealand. New Zealand Geological Survey Paleontological Bulletin 58: 1–518.

Beu AG, Alloway BV, Cooper RA, Crundwell MP, Kamp PJJ, Mildenhall DC, Naish TR, Scott GH, Wilson GS 2004. Chapter 13 Pliocene, Pleistocene, Holocene (Wanganui Series) In: Cooper RA ed. The New Zealand geological timescale. Lower Hutt, Institute of Geological & Nuclear Sciences Monograph 22: 1–284.

Borradaile LA 1903. On the classification of the Thalassinidea. Annals and Magazine of Natural History Series 7, 12: 534–551, 638.

Bott R 1969. Flusskrabben aus Asien und ihre Klassifikation (Crustacea: Decapoda). Senckenbergiana Biologica 50(5/6): 359–366.

Bromley RG, Frey RW 1974. Redescription of the trace fossil *Gyrolithes* and taxonomic evaluation of *Thalassinoides*, *Ophiomorpha* and *Spongeliomorpha*. Geological Society of Denmark Bulletin 23: 311–335.

Browne GH, Field BD 1985. The lithostratigraphy of Late Cretaceous to Early Pleistocene rocks of northern Canterbury, New Zealand. New Zealand Geological Survey Record 6.

Capart A 1951. Crustacés Décapodes, Brachyures. In: Expedition Océanographique Belge, Eaux côtiéres Afriques Atlantiques Sud (1948–1949), 3(1): 11–205, pl. 1–3.

Carter J 1898. Contribution to the palaeontology of the decapod Crustacea of England. Quarterly Journal of the Geological Society of London 54: 15–44, pl. 1, 2.

Collins BW 1953. Discovery of Pliocene marine fossils in South Canterbury. Proceedings of the 7th Pacific Science Congress 2: 130.

Dana JD 1851. Conspectus crustaceorum quae in orbis terrarium circumnavigatione Carolo Wilkes e classe Republicae Foederatae duce lexit et descripsit. Proceedings of the Academy of Natural Sciences of Philadelphia 5: 247–254, 267–272.

Dana JD 1852. Macroura. Conspectus Crustaceorum & Conspectus of the Crustacea of the Exploring Expedition under Capt. C. Wilkes, U.S.N. Proceedings of the Academy of Natural Sciences of Philadelphia 6: 10–28.

Davie PJF 2002. Crustacea: Malacostraca: Eucarida (Part 2): Decapoda–Anomura, Brachyura. In: Wells A, Houston WWK ed. Zoological catalogue of Australia. Vol. 19.3B. Melbourne, Australia, CSIRO Publishing. xiv 641 p.

De Angeli A, Garassino A 2006. Catalog and bibliography of the fossil Stomatopoda and Decapoda from Italy. Memorie della Società Italiana di Scienze Naturali e del Museo Civico di Storia Naturale di Milano 35. 95 p.

De Angeli A, Messina V 1992. *Upogebia perarolensis* nuova specie di crostaceo del Terziario del Veneto (Italia). Lavori, Società di Scienze Naturali 17: 183–191.

Feldmann RM, Keyes IW 1992. Systematic and stratigraphic review with catalogue and locality index of the Mesozoic and Cenozoic decapod Crustacea of New Zealand. New Zealand Geological Survey Record 45: 1–73.

Feldmann RM, McLay CL 1993. Geological history of brachyuran decapods from New Zealand. Journal of Crustacean Biology 13: 443–455.

Feldmann RM, Rust S 2006. *Palaega kakatahi* n. sp.: the first record of a marine fossil isopod from the Pliocene of New Zealand. New Zealand Journal of Geology and Geophysics 49: 411–415.

Feldmann RM, Tucker AB, Berglund RE 1991. Paleobathymetry of decapod crustaceans, Washington. National Geographic Research and Exploration 7: 352–363.

Feldmann RM, Schweitzer CE, McLaughlin D 2006. Additions to the records for decapod Crustacea from Motunau and Glenafric Beaches, North Canterbury, New Zealand. New Zealand Journal of Geology and Geophysics 49: 417–427.

Field BD, Browne GH 1986. Lithostratigraphy of Cretaceous and Tertiary rocks, southern Canterbury, New Zealand. New Zealand Geological Survey Record 14: 1–55.

Fleming CA 1981. A new grapsid crab from the upper Miocene of New Zealand. Journal of the Royal Society of New Zealand 11: 103–108.

Fordyce RE, Hornibrook NdeB, Maxwell PA 1985. Field trip guide to Cenozoic geology of North Otago and South Canterbury, Hornibrook Symposium, Christchurch. Geological Society of New Zealand Miscellaneous Publication 33B.

Forsyth PJ comp. 2001. Geology of the Waitaki area. Institute of Geological & Nuclear Sciences 1:250 000 Ggeological Map 19. 1 sheet + 64 p. New Zealand, Institute of Geological & Nuclear Sciences Ltd.

Fraaije RHB, van Bakel BWM, Jagt JWM, Coole Y 2006. Two new Paleogene species of mud shrimp (Crustacea, Decapoda, Upogebiidae) from Europe and North America. Bulletin of the Mizunami Fossil Museum 33: 77–85.

Frey RW, Curran HA, Pemberton SG 1984. Tracemaking activities of crabs and their environmental significance: the ichnogenus *Psilonichnus*. Journal of Paleontology 58: 333–350.

Fürsich FT 1981. Invertebrate trace fossils from the Upper Jurassic of Portugal. Communiçoes Serviços Geologicos de Portugal 67: 53–168.

Gair HS 1959. The Tertiary geology of the Pareora District, South Canterbury. New Zealand Journal of Geology and Geophysics 2: 265–296.

Gair HS 1961. Drillhole evidence of the Pliocene-Pleistocene boundary at Timaru, South Canterbury. New Zealand Journal of Geology and Geophysics 4: 89–97.

Gair HS 1967. Sheet 20—Mt Cook. Geological map of New Zealand 1:250 000. Wellington, New Zealand, Department of Scientific and Industrial Research.

George RY 1972. Biphasic moulting in isopod Crustacea and the finding of an unusual mode of moulting in the Antarctic genus *Glyptonotus*. Journal of Natural History 6: 651–656.

Glaessner MF 1930. Neue Krebsreste aus der Kreide. Jahrbuch der preussischen Geologischen Landesanstalt 1: 1–7.

Glaessner MF 1960. The fossil decapod Crustacea of New Zealand and the evolution of the Order Decapoda. New Zealand Geological Survey Paleontological Bulletin 31: 1–79.

Guinot D 1977. Propositions pour une nouvelle classification des Crustacés Décapodes Brachyoures. Comptes Rendus de l'Académie des Sciences, Paris, Série D285: 1049–1052.

Haan W de 1833–50. Crustacea. In: de Siebold PF, Fauna Japonica sive description animalium, quae in Itinere per Japoniam, Jussu et auspiciis superiorum, qui Summum in India Batava Imperium tenent, suscepto, annis 1823–1830 collegit, notis, observationibus et adumbrationibus illustravit. J. Müller, Lugduni-Batavorum (=Leiden). Pp. 1–244, pl. 1–55, A–Q, 1–2.

Hessler RR 1969. Peracarida. In: Moore RC ed. Treatise on invertebrate paleontology, part R, Arthropoda 4. Lawrence, Kansas, Geological Society of America and University of Kansas Press. R360–R393.

Hutton FW 1877. Descriptions of some new Tertiary Mollusca from Canterbury. Transactions of the New Zealand Institute 9: 593–598.

Hutton FW 1885. Descriptions of new Tertiary shells. Transactions of the New Zealand Institute 17: 313–332.

Karasawa H 1989. Decapod crustaceans from the Miocene Mizunami Group, central Japan, Part 1. Superfamily Thalassinoidea, Leucosioidea and Grapsidoidea. Bulletin of the Mizunami Fossil Museum 16: 1–28.

Karasawa H, Inoue K 1992. Decapod crustaceans from the Miocene Kukinaga Group, Tanegashima Island, Kyushu, Japan. Tertiary Research 14: 73–96.

Karasawa H, Kato H 2001. The systematic status of the genus *Miosesarma* Karasawa, 1989 with a phylogenetic analysis within the family Grapsidae and a review of fossil records (Crustacea: Decapoda: Brachyura). Paleontological Research 5(4): 259–275.

Karasawa H, Kato H 2003. The family Goneplacidae MacLeay, 1838 (Crustacea: Decapoda: Brachyura): systematics, phylogeny, and fossil records. Paleontological Research 7(2): 129–151.

Karasawa H, Kishimoto S 1996. Two new species of decapod crustaceans from the middle Miocene Katsuta Group, Japan. Bulletin of the Mizunami Fossil Museum 23: 35–37.

Karasawa H, Schweitzer CE 2006. A new classification of the Xanthoidea *sensu lato* (Crustacea: Decapoda: Brachyura) based on phylogenetic analysis and traditional systematics and evaluation of all fossil Xanthoidea *sensu lato*. Contributions to Zoology 75: 23–73.

Kato H 1996. Miocene decapod crustacean from the Chichibu Basin, Central Japan. Transactions and Proceedings of the Palaeontological Society of Japan, new series 183: 500–521.

Kato H, Koizumi A 1992. Decapod fossils from the Pleistocene Shimosueyoshi Formation in the northern part of Yokohama City. Bulletin of the Kanagawa Prefectural Museum (Natural Sciences) 21: 45–53 (in Japanese with English abstract).

Kensley, B 1978. Guide to the marine isopods of southern Africa. Cape Town, Trustees of the South African Museum.

Küster HC, Kobelt W 1844. Systematisches Conchylien-Cabinet von Martini und Chemnitz, Fortgesetzt von Hofrath Dr. G. H. Schubert and Professor Dr. J. A. Wagner. Neu herausgegeben und vervolltstandigt von Dr. H. C. Küster. Nürnberg, Bauer, and Raspe. Vol. 2, abth. 2–3. 372 p.

Latreille PA 1802–03. Histoire naturelle, générale et particulière, des crustacés et des insectes: Vol. 3. Paris, F. Dufart. 468 p.

Latreille PA 1817. Nouveau dictionnaire d'histoire naturelle, appliquée aux arts à l'agriculture, à l'economie rurale et domestique, à la médecine, etc. 10: 1–404.

Latreille PA 1828. Encyclopédie Méthodique. Histoire Naturelle. Entomologie, ou Histoire naturelle des Crustacés, des Arachnides et des Insectes. Serville et Guérin, Le Peletier de St.-Fargeau. Vol. 10(2). Pp. 345–852.

Latreille PA 1831. Cours d'entomologie, ou de l'histoire naturelle des Crustacés, des Arachnides, des Myriapodes et des Insectes, etc. Annales I. Atlas. Paris, Roret. 26 p.

Leach WE 1814. Crustaceology. In: Brewster D, The Edinburgh Encylopaedia 7: 383–437.

Leach WE 1815. A tabular view of the external characters of four classes of animals, which Linnée arranged under Insecta, with the distribution of the genera composing three of these classes into orders, and description of several new genera and species. Transactions of the Linnaean Society of London 11: 306–400.

Leach WE 1818. Dictionnaire des Sciences Naturelles. Paris & Strasbourg.

Lesson RP 1830. Mollusques. Chapter 11 in: Duperry MLI, Voyage autour la monde sur la Coquille pendant 1822–25 par MLI Duperry. Zoologie 2(1). Paris, Arthus Bertrand. Pp. 239–448, 16 pl.

McLay CL 1988. Brachyura and crab-like Anomura of New Zealand. Leigh Laboratory Bulletin 22. University of Auckland, New Zealand.

MacLeay WS 1838. On the brachyurous decapod Crustacea brought from the Cape by Dr. Smith. In: Smith A ed. Illustrations of the Annulosa of South Africa; consisting chiefly of figures and descriptions of the objects of natural history collected during an expedition into the interior of South Africa, in the years 1834, 1835, and 1836; fitted out by "The Cape of Good Hope Association for Exploring Central Africa." London, Smith, Elder, and Co. Pp. 53–71, 2 pl.

Martin JW, Davis GE 2001. An updated classification of the Recent Crustacea. Natural History Museum of Los Angeles County Science Series 39: 124 p.

Marwick J 1927 The Veneridae of New Zealand. Transactions of the New Zealand Institute 57: 567–635.

Marwick J 1957. New Zealand genera of Turritellidae, and the species of *Stiracolpus*. New Zealand Geological Survey Paleontological Bulletin 27. 54 p.

Matthews WH, Curtis GH 1966. Date of the Plio-Pleistocene boundary in New Zealand. Nature 212: 979–980.

Menard de la Groye FJB 1807. Mémoire sur un nouveau genre de coquille de la famille des Solénides. Annales du Muséum d'Histiore Naturelle de Paris 9 (50–51): 131–139.

Mildenhall DC 2001. Pollen analysis of Pliocene-Pleistocene Kowai Formation (Kurow Group), Mackenzie Basin, South Canterbury, New Zealand. New Zealand Journal of Geology and Geophysics 44: 97–104.

Milne Edwards H 1834–40. Histoire naturelle des Crustacés, comprenant l'anatomie, la physiologie et la classification de ces animaux 1(1834): i-xxxv + 1–468; 2(1837): 1–532; 3 (1840): 1–638, Atlas, 1–32. Paris.

Milne Edwards H 1852. De la famille des ocypodides (Ocypodidae). Second Mémoire. Observations sur les affinités zoologiques et la classification naturelle des crustacés. Annales des Sciences Naturelles, Zoologie, Série 3 18: 109–166.

Milne Edwards H 1853. Mémoires sur la famille des Ocypodiens, suite. Annales des Sciences Naturelles, Zoologie, Série 3 20: 163–228, pl. 6–11.

Moericke W 1897. Die Crustaceen der Stramberger Schichten. Palaeontographica. Supplement II: 43–72, pl. 6.

Montagu G 1808. Description of several marine animals found on the south coast of Devonshire. Transactions of the Linnaean Society of London 9: 81–114.

Müller P 1974. Decapoda (Crustacea) fauna a Budapesti Miocénből (2), 104: 275–287.

Müller P 1993. Neogene decapod crustaceans from Catalonia. Scripta Musei Geologici Seminari Barcinonensis 255: 1–39.

Nesbitt EA, Campbell KA 2002. A new *Psilonichnus* ichnospecies attributed to mud-shrimp *Upogebia* in estuarine settings. Journal of Paleontology 76: 892–901.

Poore GCB 2004. Marine decapod Crustacea of southern Australia. Collingwood, Australia, CSIRO Publishing.

Quoy JCR, Gaimard P 1832–35. Voyage de découverts de *l'Astrolabe*, execute par ordre du Roi pendant les années 1826–1827–1828–1829, sous le commandement de M. J. Dumont d'Urville. Mollusques. Zoologie, Tome 2, 686 p., Tome 3, 954 p., Atlas Zoologique, 200 pl.

Rafinesque CS 1815. Analyse de la nature ou tableau de l'univers et de corps organizes. Palermo, Italy, L'Imprimérie de Jean Barravecchia. 224 p.

Rathbun MJ 1918. The grapsoid crabs of America. United States National Museum Bulletin 97: 613 p.

Rathbun MJ 1926. The fossil stalk-eyed Crustacea of the Pacific slope of North America. United States National Museum Bulletin 138: 1–155.

Rathbun MJ 1935.Fossil Crustacea of the Atlantic and Gulf Coastal Plain. Geological Society of America Special Papers 2: 1–160.

Sakai T 1976. Crabs of Japan and the adjacent seas. Vol. 1, 2. Tokyo, Kodansha Ltd. 773 p., 251 pl.

Sakai K 1982. Revision of Upogebiidae (Decapoda, Thalassinidea) in the Indo-West Pacific region. Researches on Crustacea, The Carcinological Society of Japan, special number 1: 1–106, pl. A–G.

Sakai K 2006. Upogebiidae of the world (Decapoda, Thalassinidea). Brill Academic. 185 p.

Sakai K, Türkay M, Yang S-L 2006. Revision of the *Helice*/*Chasmagnathus* complex (Crustacea: Decapoda: Brachyura). Abhandlungen der Senckenbergischen Naturforschenden Gesellschaft 565: 1–76.

Schotte MBF, Kensley BF, Shilling S 1995 onwards. World list of marine, freshwater and terrestrial Crustacea Isopoda. National Museum of Natural History Smithsonian Institution. Washington, DC. http://www.nmnh.si.edu/iz/isopod/ (accessed 7 July 2007).

Schubart CD, Cannicci S, Vannini M, Fratini S 2006. Molecular phylogeny of grapsoid crabs (Decapoda, Brachyura) and allies based on two mitochondrial genes and a proposal for refraining from current superfamily classification. Journal of Zoological Systematics and Evolutionary Research 44: 193–199.

Schweitzer CE, Feldmann RM 1999. Fossil decapod crustaceans from the late Oligocene to early Miocene Pysht Formation and the late Eocene Quimper Sandstone, Olympic Peninsula, Washington. Annals of Carnegie Museum 68: 215–273.

Schweitzer CE, Karasawa H 2004. Revision of *Amydrocarcinus* and *Palaeograpsus* (Decapoda: Brachyura: Xanthoidea) with definition of three new genera. Paleontological Research 8: 71–86.

Schweitzer CE, Feldmann RM, Gonzáles-Barba G, Vega FJ 2002. New crabs from the Eocene and Oligocene of Baja California Sur, Mexico and an assessment of the evolutionary and paleobiogeographic implications of Mexican fossil decapods. Paleontological Society Memoir 59: 1–43.

Schweitzer CE, Feldmann RM, Gonzáles-Barba G, Ćosović V 2007. Decapod crustaceans (Brachyura) from the Eocene Tepetate Formation, Baja California Sur, Mexico. Annals of Carnegie Museum 76: 1–14.

Short JW 1994. A new species of freshwater crab (Sundathelphusidae) from Cape York Peninsula. Memoirs of the Queensland Museum 35: 235–240.

Speight R 1919. The older gravels of North Canterbury. Transactions of the New Zealand Institute 51: 269–281.

Stenzel HB 1945. Decapod crustaceans from the Cretaceous of Texas. University of Texas, Contributions to Geology 4401: 401–476, pl. 34–45.

Stimpson W 1871. Preliminary report on the Crustacea dredged in the Gulf Stream in the Straits of Florida, by L. F. Pourtales, Assist. U. S. Coast Survey. Bulletin of the Museum of Comparative Zoology at Harvard College 2: 109–160.

Suter H 1914. Revision of the Tertiary Mollusca of New Zealand, based on type material. Part I. New Zealand Geological Survey Paleontological Bulletin 2. 64 p.

Towers DJ, McLay CL 1995. Rare hymenosomatid, *Amarinus lacustris* (Chilton, 1882) found in Mangere River, Northland (Brachyura, Hymenosomatidae). New Zealand Natural Sciences 22: 91–93.

Wägele J-W 1989. Evolution und phylogenetisches System der Isopoda. Stand der Forschung und neue Erkenntnisse. Zoologica (Stuttgart) 140: 1–262.

White A 1850. Description of two new species of Crustacea in the British Museum. Proceedings of the Zoological Society London 18: 95–97, pl. 15–16.

White A 1852. Descriptions of some new species of Annulosa. In: Macgillivray J, Narrative of the voyage of the H.M.S. *Rattlesnake* during the years 1846–1850, 2. Pp. 387–395.

Wieder RW, Feldmann RM 1992. Mesozoic and Cenozoic fossil isopods of North America. Journal of Paleontology 66: 958–972.

Williams AB 1993. Mud shrimps, Upogebiidae, from the Western Atlantic (Crustacea: Decapoda: Thalassinidea). Smithsonian Contributions to Zoology 544: 1–77.

Zittel KA 1864. II. Fossile Mollusken und Echinodermen aus Neu-Seeland. Nebst beiträgen von den Herren Bergrath Franz Ritter V. Hauer und Professor Eduard Suess. In: Hochstetter F von, Hörnes M, Ritter von Hauer F ed. Paläontologie von Neu-Seeland. Beitrage zur Kenntniss der Fossilien Flora und Fauna der Provinzen Auckland und Nelson. Reise der Österreichischen Fregatte Novara um die Erde, Geologischer Theil 1(2): 15–68.