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New species of Miocene spider crabs from New Zealand, and a partial cladistic analysis of the genus *Leptomithrax* Miers, 1876 (Brachyura: Majidae)

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Abstract Two new species of *Leptomithrax*, *L. elongatus* n. sp. and *L. garthi* n. sp., are described from North Canterbury deposits of Miocene age. Associated fossils suggest that these crabs lived in a cool temperate, shallow shelf environment. They bring to six the number of fossil *Leptomithrax* species known from New Zealand, which still has five Recent representatives of this genus. In addition, nearby Australia has two fossil and six Recent species. In total there are now eight fossil (all restricted to Australasia) and 15 Recent species of *Leptomithrax* from the western Pacific. The relationships of the eight fossil Australasian species and eight Recent species from Australasia and Japan were investigated by applying cladistic methods to a set of carapace characters describing shape and ornamentation. Using this analysis we tested Jenkin's hypothesis about the phylogenetic relationships of the Australasian *Leptomithrax* species. Our cladistic analysis of a set of carapace characters describing shape and ornamentation recognises five major groupings within *Leptomithrax*: the "*L. elegans*" and the "*L. griffini*" are known only from the fossil record; and the "*L. longimanus*", "*L. tuberculatus*", and "*L. longipes*" clades are known from both fossil and Recent records. The primary branching events resulting in these clades occurred around the time of the Eocene–Oligocene boundary.

Keywords Crustacea; Decapoda; Brachyura; Majidae; Miocene; new species; cladistic analysis; New Zealand

INTRODUCTION

With their relatively fragile exoskeletons, brachyurans are rare as fossils and, with few exceptions, most preserved species are known only from a few specimens. Majid or "spider crabs" have a more or less pyriform to subquadrate carapace which is divided into regions and which bears a well-developed rostrum and lateral spines. The spider crabs tend to bear hooked setae. The common name derives from their relatively long, slender legs, which are rarely preserved. Their fossil record extends from the Eocene to the Recent, with some chelipeds from the Late Cretaceous which may have belonged to majids (Glaessner 1969). However, their origins remain obscure. The female genital aperture is sternal, but the male aperture is coxal. Thus, the majids are included within the Heterotremata Guinot, 1977.

The spider crab genus *Leptomithrax* Miers, 1876, includes eight fossil and 15 extant species distributed in both hemispheres in the western Pacific (Table 1). *Leptomithrax* belongs to the subfamily Majinae, which contains 86 species, 10% occurring only in the Indian Ocean, 30% in the Indo-West Pacific, but 60% are known only from the West Pacific (Griffin & Tranter 1986).

The type species of the genus, *Leptomithrax longimanus* Miers, 1876, is endemic to New Zealand. Glaessner (1960) described three fossil species of *Leptomithrax*: *L. atavus* (upper Miocene), *L. irirangi* (lower Pliocene), and *L. uruti* (upper Miocene). Feldmann & Maxwell (1990) added a fourth species, *L. griffini* (late Eocene). The other fossil majids known from New Zealand include *Actinotocarcinus chidgeyi* Jenkins and *A. mclauchlani* Feldmann (late mid Miocene), *Notomithrax allani* Feldmann & Maxwell, *Micromithrax? miniscutus* Feldmann & Wilson, as well as *Jacquinotia edwardsi* (Jacquinot) (from late Pliocene and early Pleistocene) which survives today (Fleming 1975; Beu et al. 1977).

The purpose of this work is to describe two new species from middle to late Miocene rocks of North Canterbury, South Island (Fig. 1), which brings to six the number of *Leptomithrax* fossil species known from New Zealand and eight from Australasia. *Leptomithrax* is a prominent and longstanding constituent of the majid fauna of New Zealand. The earliest known occurrence of the genus, in the Eocene, is in New Zealand, and five of 21 described extant species of New Zealand majids are referred to the genus (see Griffin 1966; Griffin & Tranter 1986). As a result, it is possible to examine the existing evolutionary relationships of the genus by application of cladistic techniques.

Leptomithrax has received little attention, other than taxonomic consideration, except for the study by Hand (1975) on the use of anemones by *L. longipes* Thomson, 1902, as a defence against predators, such as *Octopus maorum* Hutton. Hand noted that four species of anemones belonging to different genera are planted by large male crabs on their carapace and/or legs. *Leptomithrax longipes* also lodge pieces of algae, sponges, and hydroids in the hooked setae on its body, as does *L. australis* (Jacquinot, 1853). Despite these precautions, *Leptomithrax* species are still consumed by various fish predators (McLay 1988). Roper (1979) investigated some aspects of *L. longipes* sex ratio

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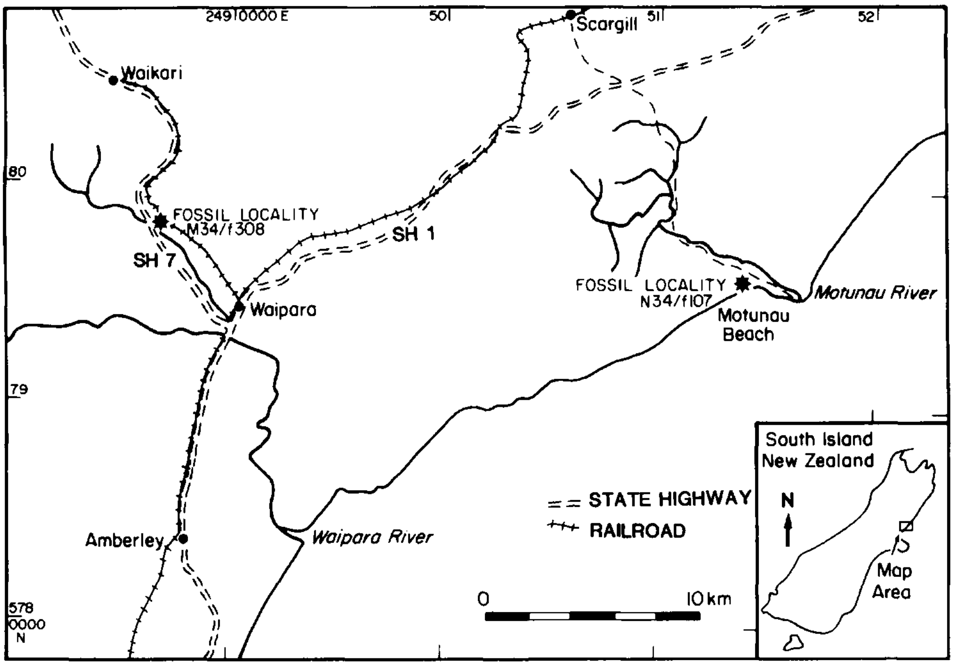

Fig. 1 The localities from which specimens of new species of *Leptomithrax* were collected.

variation between shallow and deeper waters, which may be explained by seasonal migrations and the impact of a feminising bacterium isolated from crabs of indeterminate sex.

Jenkins (1985) examined the phylogenetic relationships between five fossil and 11 living Australasian species of *Leptomithrax* (Fig. 2). He largely retained the five informal groups recognised by Griffin (1966): the *L. longimanus* Miers, 1876 group, *L. tuberculatus* (Whitelegge, 1900) group, *L. gaimardii* (H. Milne Edwards, 1834) group, *L. longipes* (Thomson, 1902) group, and the *L. richardsoni* Dell, 1960 group. Griffin had rejected the three subgenera proposed by Bennett (1964). Griffin's *L. richardsoni* group is no longer relevant because Griffin & Tranter (1986) transferred this species to *Teratomaia* Griffin & Tranter. Additionally, the *L. tuberculatus* group no longer contains *L. parvispinosus* (Ward, 1933), which Griffin & Tranter transferred to *Tumulosternum* McCulloch. Jenkins included

Table 1 List of extant and fossil species of the genus *Leptomithrax* Miers, 1876, their distribution, and ratio of carapace length (CL) to carapace width (CW).

Species	CL/CW	Distribution
Recent		
L. australis (Jacquinot, 1853)	1.03	New Zealand
L. garricki Griffin, 1966	1.13	New Zealand
L. longimanus Miers, 1876	1.07	New Zealand
L. longipes (Thomson, 1902)	1.15	New Zealand
L. tuberculatus mortenseni Bennett, 1964	1.20	New Zealand
L. depressus Richer de Forges, 1993	1.20	Australia
L. gaimardii (H. Milne Edwards, 1834)	1.15	Australia
L. globifer Rathbun, 1918	1.27	Australia
L. sternocostulatus (H. Milne Edwards, 1851)	1.28	Australia
L. tuberculatus (Whitelegge, 1900)	1.24	Australia
L. waitei (Whitelegge, 1900)	1.08	Australia
L. bifidus Ortmann, 1893	1.26	Japan
L. edwardsi (De Haan, 1839)	1.13	Japan
L. kiiensis Sakai, 1969	1.22	Japan
L. sinensis Rathbun, 1916	1.26	China
Fossil		
L. atavus Glaessner, 1960	1.08	New Zealand
L. elongatus sp. nov.	1.36	New Zealand
L. garthi sp. nov.	1.11	New Zealand
L. griffini Feldman & Maxwell, 1990	1.13	New Zealand
L. irirangi Glaessner, 1960	1.08	New Zealand
L. uruti Glaessner, 1960	1.19	New Zealand
L. elegans Jenkins, 1985	1.30	Australia
L. martensis Jenkins, 1985	1.31	Australia

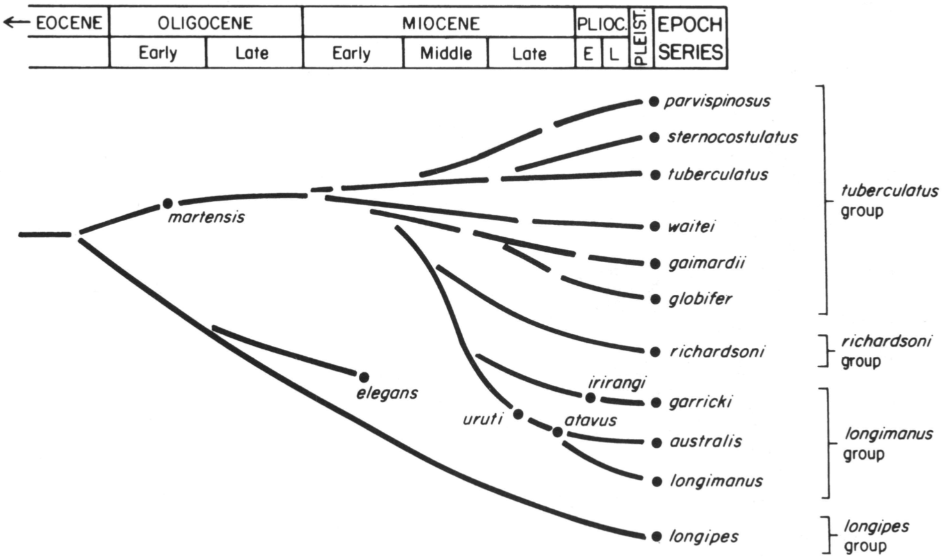

Fig. 2 Phylogenetic relationships between species of *Leptomithrax* as suggested by Jenkins (1985).

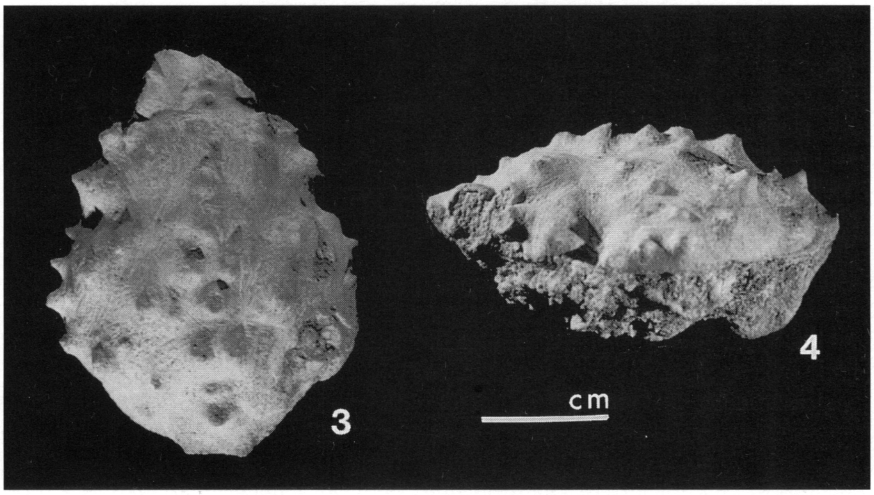

Fig. 3, 4 Carapace of the holotype of *Leptomithrax elongatus* n. sp.: 3, dorsal view; 4, left lateral view.

the species of the *L. gaimardii* group in the *L. tuberculatus* group, thus recognising four groupings. Thus, with the removal of *L. richardsoni*, only three groups are left. Jenkins (1985) postulated that *L. martensis* Jenkins, 1985 was ancestral to the *L. tuberculatus* group, that Glaessner's (1960) three species (*L. irirangi*, *L. atavus*, and *L. uruti*) gave rise to the *L. longimanus* group, and that *L. elegans* Jenkins, 1985 was an early offshoot of the line which gave rise to *L. longipes*. It is these taxonomic changes, coupled with the description of two new species, that prompt the cladistic analysis which follows.

Family **MAJIDAE** Samouelle, 1819
Subfamily **MAJINAE** Samouelle, 1819
Genus ***Leptomithrax*** Miers, 1876

Leptomithrax elongatus n. sp. Fig. 3–5

DESCRIPTION: Carapace pyriform, much longer than wide, ratio 1.36:1, tuberculate. Dorsal surface strongly convex transversely, moderately convex longitudinally, sloping downward more gradually at anterior end, regions well defined. Rostral spines broken but probably well developed; bases of spines quite broad; sulcate rostral axis broadens anteriorly, and divergent ridges on frontal region project into rostral spines; ridges converge posteriorly and terminate as 2 spines directed toward prominent, axial mesogastric spine. Supraorbital eave swollen, with pustulose rim. Orbital spines broken but intercalated spine stout, directed anterolaterally, and well separated basally from orbital spines. Hepatic spine short, broad based and acute, separated from branchial spines by broad, deep lateral termination of transversely directed cervical groove. Anterior-most 3 branchial spines along lateral margin and on a lower level than hepatic spine; posterior-most 2 branchial spines curve away from carapace margin and extend adaxially around posterior margin of swollen mesobranchial region, terminating close to cardiac region. Five branchial spines becoming progressively larger posteriorly; first 3 approximately equidistant, last 2 more widely separated. Posterolateral corner with well-developed, smoothly convex rim. Posterior carapace margin with blunt tubercle on either side of mid-line.

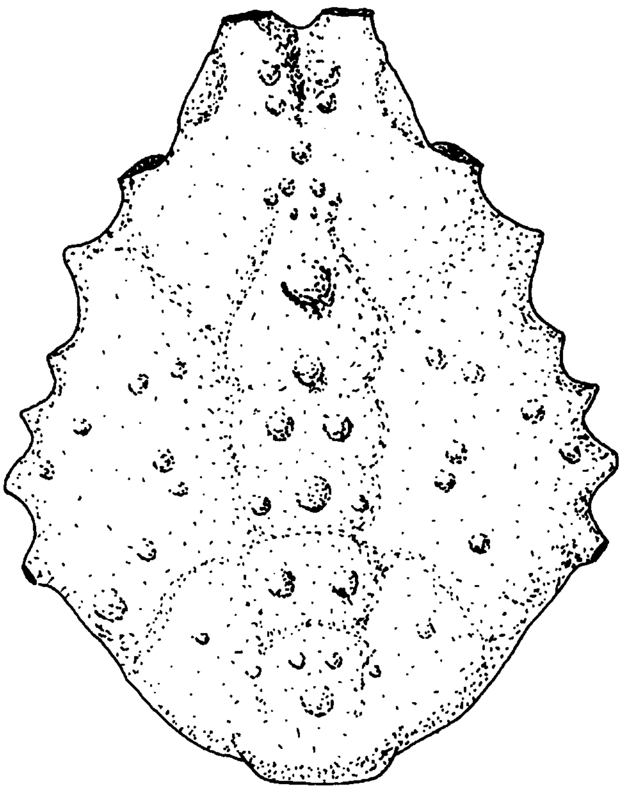

Fig. 5 Line drawing of the carapace of *Leptomithrax elongatus* n. sp.

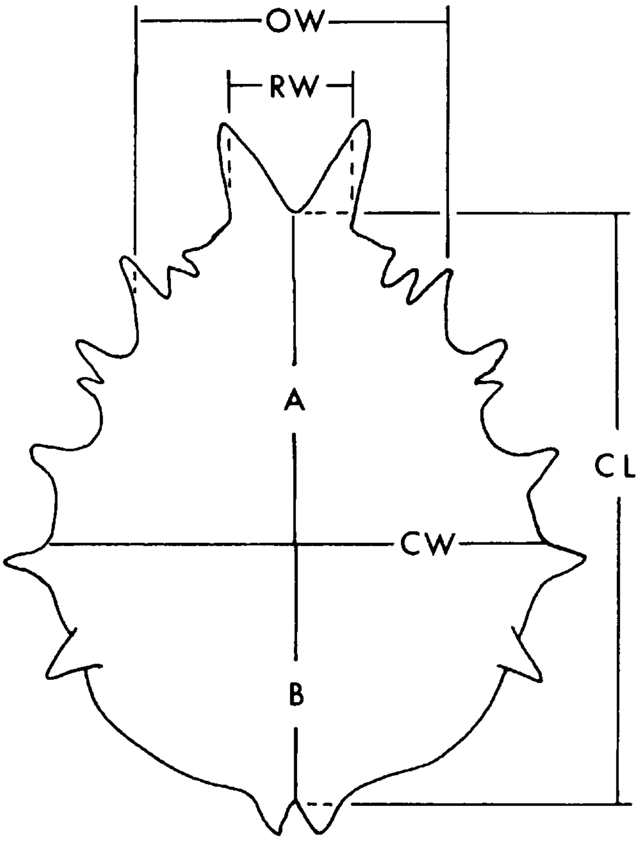

Fig. 6 Outline of a generalised carapace of *Leptomithrax* spp., showing the position of measurements taken.

Protogastric region weakly swollen, with 1 centrally placed spine and another smaller spine close by posteriorly. Mesogastric region with 2 axial spines decreasing in size posteriorly and clusters of small pustules between spines. Metagastric region diamond-shaped with 2 prominent tubercles, posterior largest. Urogastric region defined by broad, shallow branchiocardiac groove; 3 spines form posteriorly directed triangle, posterior-most axial spine largest. Cardiac region with a pair of strong tubercles. Intestinal region poorly defined, with 2 axial spines, posterior one largest. No hepatic spines. Mesobranchial area has 2 anterior, subequal spines as well as 5 or 6 smaller scattered pustules, metabranchial area has 2 spines.

Ventral surface of carapace, appendages, and abdomen not preserved.

MEASUREMENTS: The following measurements do not include any spines. Carapace width (CW) = 23.6 mm, carapace length (CL) = 31.0 mm, rostrum width (RW) = 5.8 mm, orbital width (OW) = 15.8 mm, distance from front to a line connecting the widest part of carapace = 16.5 mm. The positions at which these measurements were taken are illustrated in Fig. 6.

ETYMOLOGY: The species name alludes to the elongate shape of the carapace.

TYPE: The holotype, zfc376, is deposited in the Canterbury Museum, Christchurch, New Zealand.

LOCALITY AND STRATIGRAPHIC POSITION: The single specimen of *Leptomithrax elongatus* n. sp. was collected from a railway cutting exposure (grid reference, M34/863986; N.Z. Fossil Record File No. M34/f308) of the c. 1 m thick *Hinnites* shellbed situated at the base of the uppermost Mount Brown (E) limestone of Thomson (1920). The "E" or Glenmark limestone forms the most easterly of three prominent limestone escarpments transecting the Weka Pass district. The specimen was collected from the exposure on the southwestern wall of the cutting (Fig. 1).

The precise stratigraphic position and the paleontologic and the lithologic character of the *Hinnites* shellbed has been well documented by Wilson (1964, fig. 16, pp. 50, 54). It is a bivalve/gastropod-dominated assemblage although terebratulid and rhynchonellid brachiopods, flabellid corals, echinoid, and barnacle fragments are common. Overall, the fauna suggests a realtively clear water, shallow shelf environment with a substrate consisting largely of unconsolidated, comminuted skeletal carbonate debris. The *Hinnites* shellbed is assigned to the Waiauan Stage (middle Miocene), based on the presence of the benthic foraminiferan *Loxostomum truncatum* Finlay.

REMARKS: This species can be distinguished from all other New Zealand species by the very elongate carapace shape which greatly exceeds the ratio of carapace length to width found in any other New Zealand form, fossil or Recent. In this character it resembles the Australian fossils *L. elegans* and *L. martensis*. Recent species with elongate carapaces

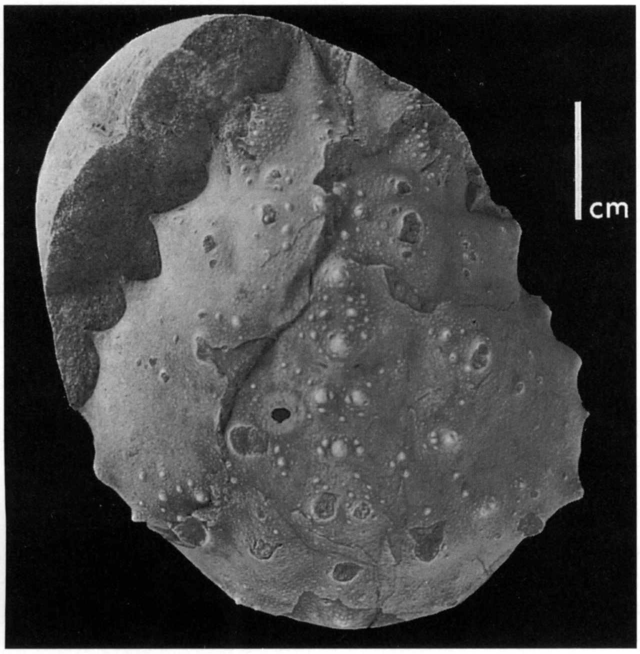

Fig. 7 Dorsal view of the carapace of the holotype of *Leptomithrax garthi* n. sp.

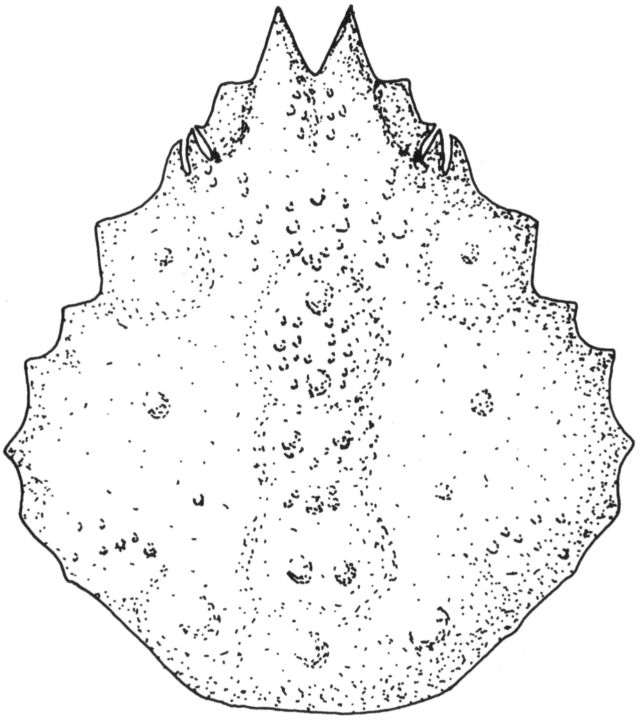

Fig. 8 Line drawing of the carapace of *Leptomithrax garthi* n. sp.

are found in Australia (*L. sternocostulatus*, *L. globifer*), Japan (*L. bifidus*), and China (*L. sinensis*). The carapace shape of *L. elongatus* also differs from the other species in being more broad-fronted and having its widest region of the carapace closest to the front. Also, its carapace tends to be less densely ornamented than many of the other species. The specific differences between *L. elongatus* and *L. garthi* n. sp. are discussed below.

Leptomithrax garthi **n. sp.** Fig. 7, 8

DESCRIPTION: Carapace pyriform, longer than wide, ratio 1.11:1, tuberculate. Dorsal surface strongly convex transversely, moderately convex longitudinally, sloping downward more gradually at anterior end, regions well defined. Rostral spines short, stout, base of spines c. 80% of spine length, tapering to forward-directed sharp terminations; sulcate rostral axis broadens anteriorly, and ridges on frontal region project into rostral spines, diverging anteriorly; ridges converge posteriorly, carrying 3 or 4 tiny pustules, and terminate near prominent, axial metagastric spine. Supraorbital eave swollen, with pustulose rim. Intercalated spine stout, pustulose, extends anterolaterally and nearly contacts posterolateral corner of eave. Postorbital spine curving anteriorly, broad at base, tip directed toward tip of intercalated spine. Thus, the supraorbital eave, intercalated and postorbital spines are closely approximated. Hepatic spine short, broad based and acute, separated from branchial spines by broad, deep lateral termination of transversely directed cervical groove. Anterior-most 3 branchial spines along lateral margin and on a lower level than hepatic spine; posterior-most 2 branchial spines curve away from carapace margin and extend adaxially around posterior margin of swollen mesobranchial region, terminating close to cardiac region. Five branchial spines progressively decrease in size posteriorly; first 3 approximately equidistant, last 2 more widely separated. Posterolateral corner with well-developed, smoothly convex rim. Posterior carapace margin with a single blunt spine.

Protogastric region weakly swollen, with 1 centrally placed spine. Mesogastric region with 2 axial spines decreasing in size posteriorly and clusters of small pustules between spines. Metagastric region with 2 prominent tubercles, posterior-most largest. Urogastric region defined by broad, shallow branchiocardiac groove; 3 spines form posteriorly directed triangle, posterior-most axial spine largest. Cardiac region with pair of strong tubercles. Intestinal region poorly defined, with 1 axial spine. Single hepatic spine. Branchial area with anteromedially directed line of 3 or 4 spines, a single large mesobranchial spine near mid-line, and 4 or 5 smaller scattered pustules, and 2 or 3 metabranchial spines, anterior-most largest. Field of 2 or 3 small tubercles situated anterior to last pair of large marginal branchial spines.

Ventral surface of carapace, appendages, and abdomen not preserved.

MEASUREMENTS: The following measurements do not include any spines. CW = 41.7 mm, CL = 45.5 mm, RW = 9.3 mm, OW = 21.8 mm, distance from front to a line connecting the widest part of carapace = 30.6 mm. Positions at which the measurements were taken are illustrated in Fig. 6.

ETYMOLOGY: The species name honours the late J. S. Garth, Allan Hancock Foundation, Los Angeles, for his substantial contribution to the study of Pacific majids.

TYPES: The type specimen, zfc347, consisting of part (a) and counterpart (b), has been deposited in the Canterbury Museum, Christchurch, New Zealand.

LOCALITY AND STRATIGRAPHIC POSITION: The single specimen of *Leptomithrax garthi* n. sp., contained within a concretion, was collected from the mouth of the Motunau River at Motunau (grid ref. N34/147958; N.Z. Fossil Record File No. N34/f107), interpreted to have been derived from the Greta Siltstone horizon in cliffs. This rock unit has a mid–late Miocene, Waiauan–Tongaporutuan, age. Thus, this fossil may be coeval with, or come from a slightly younger stratum than, the Weka Pass fossil. Associated biota includes a bivalve and gastropod assemblage, isolated bones of marine mammals, sharks and bony fish, and other decapods, including the crabs *Trichopelturion greggi* Dell, *Actinotocarcinus chidgeyi* Jenkins, *A. mclauchlani*, *Cancer novaezelandae* (Jacquinot & Lucas), and *Tumidocarcinus giganteus*. One species of lobster, *Metanephrops motunauensis* Jenkins, is also reported from this locality. In addition, a claw, possibly from a hermit crab, has been found.

REMARKS: Although *Leptomithrax garthi* is similar to *L. elongatus*, described above, it can be distinguished by the characteristics listed in Table 2. The most notable of these are the smaller CL/CW ratio, the closer approximation of supraorbital eave and postorbital spine to the intercalated spine, the gradual decrease in size of marginal branchial spines posteriorly, and the absence of any spine on the posterior margin of the carapace. This latter character state is shared with only one other New Zealand fossil species, *L. griffini*. The closely approximated orbital spines are found only in *L. longipes*. With respect to CL/CW, *L. garthi* is similar to other fossil species of this genus described by Glaessner (1960) and the Recent species from New Zealand. Most of the living and fossil species from Australia, Japan, and China have higher CL/CW ratios. The two new species, along with *L. uruti* and *L. irirangi*, have five or six marginal branchial spines, a larger number than any of the other species under consideration.

PALEOECOLOGY

A good indication of the likely environment in which the two new species of *Leptomithrax* lived is given by studies of the marine benthos off the Otago Peninsula, southeastern New Zealand (Probert & Batham 1979; Probert & Wilson 1984; Schembri 1988; Taylor et al. 1989). On the continental shelf of this area, there is a rich diversity of polychaetes, Bryozoa, Mollusca, Echinodermata, hermit crabs (Anomura), and crabs (Brachyura). Of particular interest are the tube-dwelling hermit crabs and their bryozoan hosts, because *L. elongatus* was collected in association with related organisms. Taylor et al. (1989) found over 60 species of Bryozoa growing on shelters occupied by six species of hermit crabs; *Paguristes barbatus* Heller, *Pagurus* n. sp. B Schembri & McLay, *Australeremus cooki* (Filhol), *A. stewarti* (Filhol), *A. laurentae* (McLaughlin & Gunn), and *Lophopagurus thompsoni* (Filhol). Thirteen of these species form tube-like shelters, of which the most common are *Disporella gordoni* Taylor et al., *Osthimosia monilifera* Taylor et al., *O. socialis* Taylor et al., *Heteropora parapelliculata* Taylor et al., and *Crepidacantha zelanica* Canu & Bassler. Some of these genera and species are found among the hermit crab shelters preserved in similar sediments as *L. elongatus*, but other fossil shelters were made by very different bryozoans. These bryozoan shelters, found in great abundance in the fossil strata, no doubt contained the ancestors of the modern species found today, although none has been collected. Clearly, this symbiotic association between hermit crabs and bryozoans is a longstanding one, and the presence of these fossil shelters provides an important insight into the nature of the benthic community in which *L. elongatus* lived.

Leptomithrax garthi is not known to be associated with the hermit crabs utilising bryozoans as shelters. It does, however, occur with a rather diverse assemblage of decapods, including an undescribed hermit crab and several majids. The majids recorded to be living off the Otago Peninsula by Probert & Batham (1979) include *Leptomithrax longipes*, *Thacanophrys filholi* (A. Milne Edwards), and *Eurynolambrus australis* H. Milne Edwards & Lucas, but the distribution records of Griffin (1966) suggest that seven additional species occur in this fauna: *L. australis*, *L. longimanus*, *Jacquinotia edwardsi*, *Trichoplatus huttoni* A. Milne Edwards, *Notomithrax minor* (Filhol), *N. peronii* (H. Milne Edwards), and *N. ursus* (Herbst). Of these, spider crabs (*J. edwardsi*) are known from early Pleistocene deposits near Napier. Thus, there are at least 10 majid species known from the Recent fauna, three of which belong to the genus *Leptomithrax*.

Our PAUP analysis (see below) suggests that the two new Miocene species are most closely related to *L. longimanus*, which occasionally occurs in shallow water

Table 2 Comparison of differences between *Leptomithrax elongatus* and *L. garthi*. (CL = carapace length, CW= carapace width, OW= orbital width.)

Character	*L. elongatus*	*L. garthi*
Ratio CL/CW	1.32	1.11
Position of widest part of carapace	Close to mid-point of CL	Well behind mid-point of CL
Ratio OW/CW	0.65	0.51
Intercalated spine	Separated by a gap on both sides	Closely approximated on both sides
Marginal branchial spines	Increase in size posteriorly	Decrease in size posteriorly
Rostral ridges	Two prominent spines	Three or four tiny pustules
Anteromedially directed line of spines in branchial area	Absent	Present
Number of mesobranchial spines	7	5–6
Number of spines on posterior carapace margin	2	1
Number of intestinal spines	2	1
Number of metagastric spines	2	3
Number of hepatic spines	0	1
Number of metabranchial spines	2	3

but is much more common offshore on muddy or sandy bottoms, associated with polychaetes, molluscs, sponges, and bryozoans to a depth of 200 m, and occasionally to 550 m (McLay 1988). *Leptomithrax longimanus* does not clothe itself with algae or anemones, unlike some of the other species of *Leptomithrax*, but its carapace sometimes carries serpulid worms and sponges. The modern species of *Leptomithrax* are benthic predators and scavengers whose major enemies are small sharks (*Mustelus lenticulatus* Phillipps) and fish such as red cod (*Pseudophycis bachus* Bloch & Schneider). These species all grow to a much larger size (max. CL c. 100 mm) than that of the two new fossil species, and so the specimens reported here may represent species with a smaller maximum size or are small immature individuals. If the former, predator/prey relationships may have been different. These comparisons suggest that *L. elongatus* and *L. garthi* were members of a cool temperate, mid to outer continental shelf fauna, rich in other decapod Crustacea.

RELATIONSHIPS OF THE SPECIES OF *LEPTOMITHRAX*

General

Phylogenetic relationships amongst the eight known fossil species of *Leptomithrax* and the five Recent New Zealand species of this genus were explored using PAUP version 2.4. In addition, *L. depressus* Richer de Forges, 1993, from the Gascoyne Seamount, Tasman Sea, and *L. kiiensis* Sakai, 1969, and *L. edwardsi* (DeHaan, 1839), from Japan, were included. New Zealand shares with Australia *L. tuberculatus* (Whitelegge, 1900) in the form of the subspecies *L. tuberculatus mortenseni* Bennett, 1964. Insufficient data were available to allow inclusion of the remaining six *Leptomithrax* spp. The data matrix consists of 20 characters which describe the overall shape of the carapace and its ornamentation for the 16 species in question. Multiple equally parsimonious trees were searched for, using global branch swapping (i.e. options GLOBAL and MULPARS) with all characters unordered.

Characters used

The characters selected for analysis are confined to those of the carapace because attached crab limbs are rarely preserved. Four characters were used to describe carapace shape (Table 3), one for the orbit, 14 for the number of spines in different areas, and one character for the arrangement of spines. The definitions of carapace regions used are those of Griffin (1966, fig. 1). The coding of each character is shown in Table 3. For the most part, each character state is equivalent except that at the extremes it was sometimes necessary to create larger categories to avoid having unused character states.

(1) Carapace length and width were measured exclusive of spines and their ratio was used as an overall index of shape. All species have carapace lengths which exceeded the width, and five character states were recognised with very elongate carapaces having a high code value.

(2) The position of the widest part of the carapace (exclusive of spines) was measured along the median axis and seven states were used. This character added more precision to the shape character with a code of high value designating a shape where maximum width was toward the posterior end.

(3) and *(4)* Two measures, rostral and orbital widths, expressed as a proportion of the maximum carapace width, were used. Four and five states, respectively, were recognised, with high code values indicating a more narrow fronted carapace.

(5) The only orbital character used described the proximity of the supraorbital eave, intercalated spine, and postorbital spine. Four states were used: no gap separating the intercalated spine from either the eave or postorbital spine (usually associated with exclusion of the intercalated spine from the orbital margin), a gap

Table 3 Coding of *Leptomithrax* carapace characters used in PAUP analysis.

	Code						
Character	0	1	2	3	4	5	6
1. Ratio of carapace length to width	1–1.05	1.06–1.10	1.11–1.15	1.16–1.20	>1.20		
2. Position of widest part of carapace	1.11–1.20	1.21–1.30	1.31–1.40	1.41–1.50	1.51–1.60	1.61–1.70	>1.70
3. Ratio of orbital width to carapace width		>0.65	0.65–0.61	0.60–0.56	0.55–0.51	0.50–0.45	
4. Ratio of rostral width to carapace width	0.30–0.26	0.25–0.20	0.19–0.15	0.14–0.10			
5. Intercalated spine	closed	0 + 1	1 + 0	open			
6. No. hepatic marginal spines	1	2					
7. No. branchial marginal spines	4	5	6				
8. No. protogastric spines	1	2	3	4	5–7	>7	
9. No. medial mesogastric spines	2	3	4	5			
10. No. submedial mesogastric spines	0	2	4				
11. No. metagastric spines	0	1	2	3	5	6	
12. No. urogastric spines	1	2	3				
13. No. cardiac spines	0	1	2	4	6		
14. No. intestinal spines	0	1	2	3	5	8	
15. No. spines on posterior border	0	1	2				
16. No. hepatic spines	0	1	4	6	8		
17. No. epibranchial spines	0	1	2	4	5	6	9
18. No. mesobranchial spines	1–6	7–11	12–15	16–21	22–27		
19. No. metabranchial spines	0	1–2	3–4	5–6	7–8	>8	
20. Dorsal surface spine type	blunt	acute					

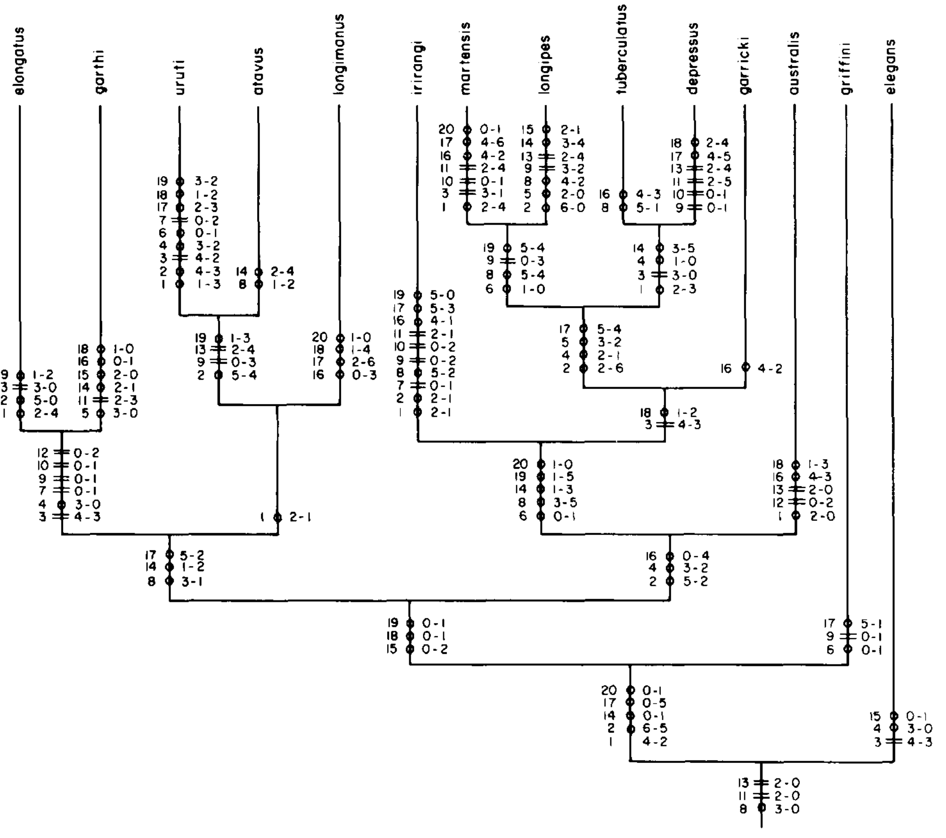

Fig. 10 PAUP tree showing the phylogenetic relationships between the Australasian species of *Leptomithrax* using the hypothetical ancestor as the outgroup. Symbols and legends as described in Fig. 9.

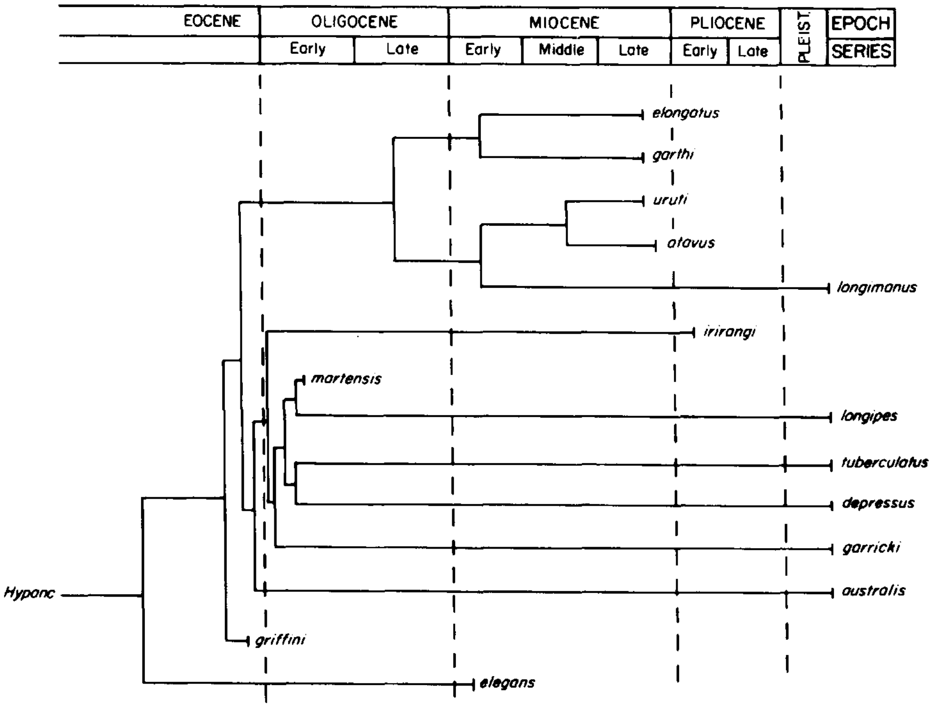

Fig. 11 PAUP tree of Australasian species of *Leptomithrax* fitted to time lines based upon occurrences of known fossils.

fossil group, and likewise in the extant group, can be estimated by the average number of character differences resulting from pairwise comparison of the species, and by the average deviation of each character in these pairwise comparisons (Table 5). The first question concerns variation within each group and determines whether or not the fossil species are more different from each other than are the extant species. The mean number of character differences between fossil species (13.96) is larger than the mean number of differences between Recent species (12.0); however, the average deviation of each character is not significant, 24.25 and 22.8, respectively ($P > 0.05$) (Table 6). This result is

Fig. 12 PAUP tree showing the phylogenetic relationships between the Australasian and Japanese species of *Leptomithrax* using a hypothetical ancestor as the outgroup. Symbols and legends as described in Fig. 9.

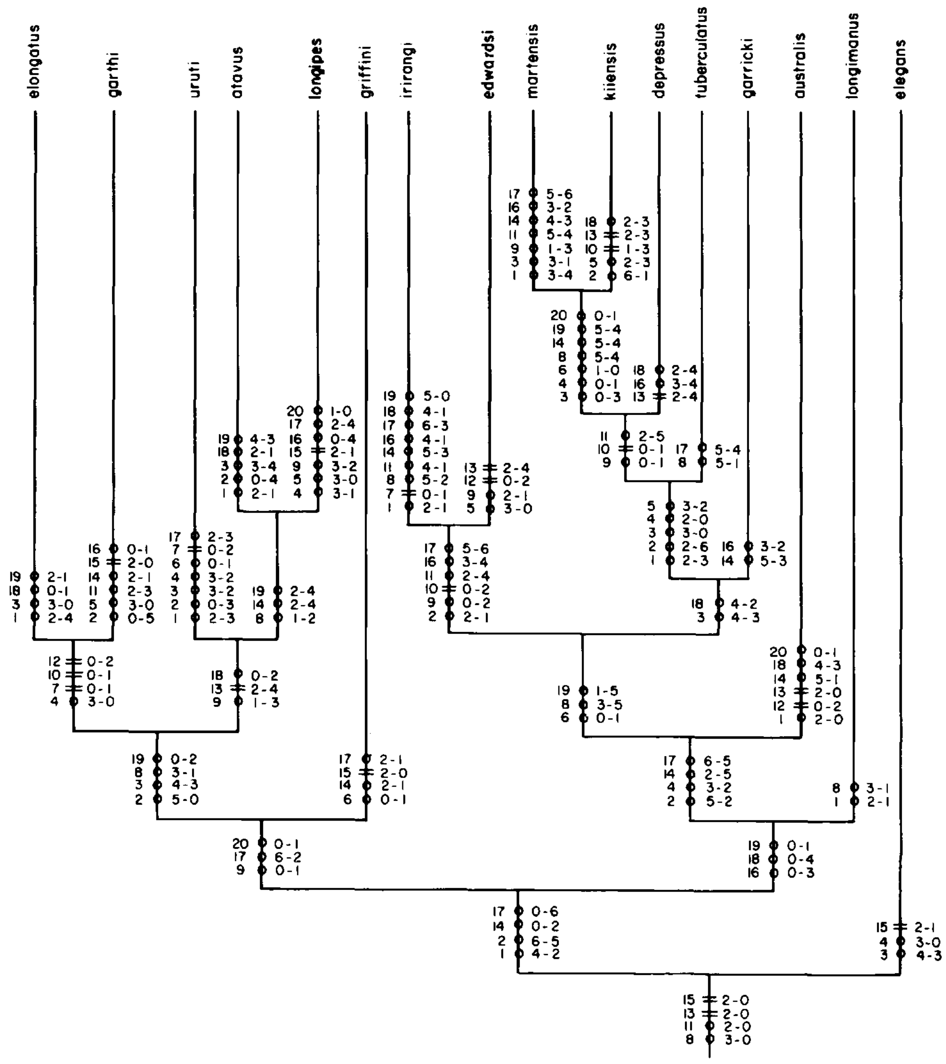

Table 5 Comparison of character differences between *Leptomithrax* spp. The subdiagonal section shows the number of character differences (max. = 20) and the supradiagonal section shows the sum of the absolute differences between character scores (max. = 71).

Species	1	2	3	4	5	6	7	8	9	10	11	12	13	14
1. *L. elongatus* (F)	0	20	20	22	27	27	30	24	28	31	30	31	28	39
2. *L. garthi* (F)	11	0	26	28	27	19	30	23	30	29	29	33	30	38
3. *L. uruti* (F)	13	17	0	16	15	23	26	28	28	25	25	23	26	35
4. *L. irirangi* (F)	15	17	14	0	19	21	32	28	24	23	25	21	31	41
5. *L. atavus* (F)	12	17	11	13	0	18	27	27	27	22	22	24	29	36
6. *L. griffini* (F)	14	12	13	14	11	0	33	13	25	22	34	26	33	42
7. *L. martensis* (F)	14	16	15	16	14	17	0	30	32	27	27	21	20	19
8. *L. elegans* (F)	13	15	15	15	13	10	14	0	30	25	35	29	28	39
9. *L. australis* (R)	13	16	14	16	12	12	16	13	0	15	29	19	32	39
10. *L. longimanus* (R)	12	16	13	13	10	11	14	11	10	0	28	20	23	32
11. *L. longipes* (R)	17	16	15	16	12	15	14	12	16	14	0	20	23	28
12. *L. garricki* (R)	16	17	12	15	14	12	13	11	11	11	12	0	19	24
13. *L. tuberculatus* (R)	14	17	12	15	15	14	13	12	14	10	13	9	0	15
14. *L. depressus* (R)	15	17	15	16	16	15	14	15	17	15	15	12	8	0