NEW ZEALAND
DEPARTMENT OF SCIENTIFIC AND INDUSTRIAL RESEARCH

NEW ZEALAND GEOLOGICAL SURVEY
(R. W. WILLETT, Director)

Paleontological Bulletin 31

The Fossil Decapod Crustacea of New Zealand and the Evolution of the Order Decapoda

by

MARTIN F. GLAESSNER
University of Adelaide, South Australia

DECEMBER

1960

PRICE: Paper cover, 16s. 6d.
Quarter bound, 20s.

N.Z. geol. Surv. paleont. Bull. 31

R. E. OWEN, GOVERNMENT PRINTER, WELLINGTON, NEW ZEALAND—1960

Contents

	PAGE
ABSTRACT	5
INTRODUCTION	5
PART 1. THE FOSSIL DECAPOD CRUSTACEA OF NEW ZEALAND	7
Systematic list of New Zealand fossil decapod Crustacea	7
Descriptions	8
Paleo-ecological observations	32
Stratigraphic distribution and faunal relations	32
PART 2. EVOLUTION AND TAXONOMY OF THE DECAPOD CRUSTACEA	36
Evolution of the carapace	36
The carapace and the internal skeleton	36
Morphology and evolution of the carapace furrows	39
Origin of carapace furrows	42
The reduction of the abdomen	44
Evolutionary trends in the Brachyura	45
Outline of the classification of decapod Crustacea	47
REFERENCES	50
APPENDIX 1: Catalogue of Specimens	52
APPENDIX 2: Localities of New Zealand Fossil Decapoda	55
APPENDIX 3: Stratigraphic Distribution of Decapod Collections	59
INDEX	60

TEXT FIGURES

FIGURE		PAGE
1 a, b	*Mecochirus marwicki*, carapace and abdomen, restored	9
2	*Callianassa awakina*, palms of right and left chelae	11
3	*Jasus flemingi*, pleura of abdominal segments	14
4	*Laeviranina perarmata*, restoration of carapace	15
5	*Lyreidus elegans*, restoration of carapace	17
6	*Leptomithrax atavus*, restoration of carapace	18
7	*Leptomithrax uruti*, restoration of carapace	19
8	*Leptomithrax irirangi*, restoration of carapace	20
9	*Portunites granulifer*, restoration of carapace	21
10	*Tumidocarcinus tumidus*, anterior portion of carapace	26
11	*Tumidocarcinus giganteus*, anterior portion of carapace	26
12	Carapace shape in *Goneplax rhomboides*, *Ommatocarcinus arenicola*, *O. corioensis*, and *O. macgillivrayi*	29
13	*Galene proavita*, restoration of carapace	30
14	*Hemiplax major*, partial restoration	31
15 a, b	Relations of carapace and internal skeleton in *Homarus vulgaris*	37
16	Relations of carapace and internal skeleton in *Dromia*	37
17	*Astacus fluviatilis*, transverse section of cephalothorax	37

FIGURE PAGE
18 Evolution of carapace in Nephropsidea 40
19 Evolution of carapace in Glypheocarida, Anomocarida, Palinura, and Brachyura 41
20 Position of carapace furrows in relation to segmentation in Malacostraca . 43
21 a, b, c Reduction of abdomen in decapod Crustacea 44
22 Genetic relations and stratigraphic distribution of the most important families of Brachyura 47
23 Geographic distribution of fossil decapod Crustacea (North Island) . . 54
24 Geographic distribution of fossil decapod Crustacea (South Island) . . 56

TABLE

TABLE 1 Stratigraphic distribution of New Zealand Tertiary decapod Crustacea . . 34

PLATES

PLATES 1–7 . . . . . At end.

The Fossil Decapod Crustacea of New Zealand and the Evolution of the Order Decapoda

ABSTRACT

In the first part of this work 30 species of fossil decapod Crustacea from New Zealand are recognised. Twenty-two of these are named, 16 are new, and one is placed in a new genus. Four species are from the Mesozoic, the others are from the Cainozoic deposits, from which only one species had been described previously. Most of the species are Brachyura. Although only few representatives of the many decapod Crustacea that must have existed in the past are known, they indicate the presence of ancestors of some living species among the late Oligocene to Miocene assemblages. Some species of this age are common to Australia and New Zealand. Earlier Tertiary faunas are similar to those known from other areas but not to the well known Tethyan warm-water faunas. The late Tertiary assemblages gradually approach the composition of the living fauna.

The second part outlines the foundations for the classification and morphological terminology used in the descriptive part. The evolution and morphological significance of the carapace, and particularly the carapace furrows on which the classification of the fossil decapod Crustacea largely depends, are discussed, and the reduction of the abdomen in various phyletic lines is reviewed. The evolution of the Brachyura is outlined on the basis of paleontological evidence. The resulting classification of the decapod Crustacea is listed, mostly to family level, with stratigraphic ranges.

INTRODUCTION

ONLY one species of fossil decapod Crustacea was known, prior to this study, from the Tertiary of New Zealand, which has produced rich and well known faunas of Foraminifera, Mollusca, and other marine invertebrates and vertebrates. The present monographic study was undertaken on the suggestion of Dr C. A. Fleming, Chief Paleontologist of the New Zealand Geological Survey, who with much care brought together a large number of crustacean remains from various collections, mainly those in the possession of the Geological Survey. The study of this material proved rewarding in that about 25 additional species were recognised. It was found necessary to describe 16 of them as new, and also to establish one new genus. Several species have definable stratigraphic ranges which may prove to be of value for correlation, others establish links with Australia, America, and Europe, and others again are close enough to living species from New Zealand to determine their status as endemic forms.

The material, however, represents only a first approach to our knowledge of the fossil decapod Crustacea of New Zealand. Its composition shows many obvious gaps in our knowledge, when compared with that from other regions. There are two or three Mesozoic Macrura but no Mesozoic Brachyura; there is only one Tertiary macrurous crustacean, a palinurid, but no Homaridae, which must have existed and which are common fossils elsewhere. These are obvious "collection failures" and one may hope that interest in this group will be sufficiently stimulated to lead to further discoveries soon. The student of Recent faunas will be struck by the absence of the common living group, the "Natantia". This is, however, not entirely due to "collection failure" but partly to difficulties of preservation, to facies conditions, and also to the late appearance of the Caridea in the evolution of the Crustacea Decapoda.

The New Zealand material, consisting largely of Tertiary crabs, has added little to our knowledge of major evolutionary trends and their taxonomic expression, but it will be better understood if the background of decapod evolution and taxonomy is presented. The evolution of this group has

Manuscript received for publication 11 August 1959.

become largely clarified by paleontological studies in the last 30 years. The description of two Mesozoic Macrura from New Zealand establishes the well known genera to which they belong as world wide. The significance of their morphology and the meaning of the terms in which it is described, as well as their place in the system, can only be seen clearly against a background of a review of decapod evolution. A system based on the real historical record of available fossils, rather than on hypothetical relationships of living genera and species only, was first established by the author and other paleontologists many years ago. It differs considerably from current purely zoological classifications, and for this reason it was considered necessary to present it here again, in outline and with modifications brought about by more recent work. It is supported by a new interpretation of the evolution of those morphological features of the decapod skeleton that are most clearly observable in fossils and that can be claimed to reflect the course of the evolution of this group. Most of the invertebrates were well established at the beginning of Paleozoic time; others did not develop hard skeletons and left no fossil remains. The decapod Crustacea are one of the few major groups of marine invertebrates that evolved almost entirely during the Mesozoic and Cainozoic Eras. They deserve far more attention than paleontologists in the field and in the museum have devoted to them in the past.

ACKNOWLEDGMENTS

The writer wishes to record his gratitude to the New Zealand Geological Survey (Director, Mr R. W. Willett), which entrusted him with the description of the fossil decapod Crustacea of New Zealand, and to those in charge of the other institutions from which specimens were made available, including University of Auckland, Canterbury Museum, Dominion Museum, Otago Museum, University of Otago, Victoria University of Wellington. He wishes to thank Mr N. de B. Hornibrook (N.Z. Geological Survey) for micropaleontological age determinations of important specimens and Mr J. C. Yaldwyn (Dominion Museum, Wellington) for valuable information and the loan of specimens, Dr Mary Wade (University of Adelaide) and Miss J. Boyce (South Australian Museum) for help with the photographic work, and Miss S. Summer (University of Adelaide) for careful preparation of the typescript. Most of all he is indebted to Dr C. A. Fleming, Chief Paleontologist, New Zealand Geological Survey, who spared neither time nor effort in obtaining material and data, checking localities, ages, and documentation, and preparing the appendix.

PART I. THE FOSSIL DECAPOD CRUSTACEA OF NEW ZEALAND

SYSTEMATIC LIST OF NEW ZEALAND FOSSIL DECAPOD CRUSTACEA

Names	Ages	Registered Numbers (holotypes in bold type)
Fam. GLYPHEIDAE		
Glypheopsis antipodum n. sp. ..	Liassic	Otago Mus. **C.03.41**
Fam. MECOCHIRIDAE		
Mecochirus marwicki n. sp. ..	Kimmeridgian	DC **266**
„ ? sp.	L. Tithonian	DC 235, 236
Fam. CALLIANASSIDAE		
Callianassa awakina n. sp. ..	Otaian, U. Oligocene	DC 117, 189–93, **194**
„ *waikurana* n. sp. ..	Haumurian, Maestrichtian ..	DC **219**
„ sp. a	Haumurian, Maestrichtian ..	DC 220–1, DC 239 (?)
„ sp. b	Tongaporutuan, U. Miocene ..	DC 261
Ctenocheles cf. *maorianus* Powell ..	Castlecliffian, U. Pleistocene ..	DC 107, 109–111, 231, Vic. Univ. Zool. Dept.
Fam. PALINURIDAE		
Jasus flemingi n. sp.	Basal Altonian, L. Miocene ..	DC **203**
Fam. RANINIDAE		
Laeviranina perarmata n. sp. ..	Bortonian, M. Eocene	DC 233, **246,** 247, 250
Lyreidus elegans n. sp.	Altonian (DC 108), L. Miocene ..	DC 108, **123**
Fam. MAJIDAE		
Leptomithrax atavus n. sp. ..	Kapitean, Upper Miocene ..	DC 226, **253–255,** 256–258
„ *uruti* n. sp. ..	Tongaporutuan, U. Miocene ..	DC **175,** 195
„ *irirangi* n. sp. ..	?Opoitian, L. Pliocene	DC **223**
Paramithrax minor Filhol ..	Castlecliffian, U. Pleistocene ..	Dominion Mus.
Fam. CANCRIDAE		
Cancer novaezealandiae (Jacquinot and Lucas)	Opoitian, Waitotaran, Nukumaruan, Castlecliffian, Pliocene - Pleistocene	DC 102, 104, 114, 214, 216, 260, 263–264, Vic. Univ. Zool. Dept.
Fam. PORTUNIDAE		
Portunites granulifer n. sp. ..	Bortonian, M. Eocene	DC **232,** 234, 240–4, 248, 251
Ovalipes cf. *punctatus* (de Haan) ..	Castlecliffian, Pleistocene	DC 116, 215
„ sp. a.	Waitotaran, Upper Pliocene ..	DC 127–128
Fam. XANTHIDAE		
Menippe sp.	Hutchinsonian, U. Oligocene ..	DC 170–172
Pseudocarcinus sp.	Kapitean, U. Miocene-Pliocene ..	DC 238
Tumidocarcinus tumidus (H. Woodward)	Bortonian, M. Eocene ? Kaiatan or Runangan to Duntroonian, Upper Eocene to L. Oligocene	DC 120, 134, 138–9, 142, 145, 149, 150, 151–2, 154, 156–8, 178, 196, 209. ?208, ?227
„ *giganteus* n. sp. ..	Lillburnian to Tongaporutuan, U. Miocene	DC 132–3, 176, 180, **181**–4, 187–8, 197–9, 205, 210, 225
„ *dentatus* n. sp. ..	Duntroonian, L. Oligocene ..	DC 135–6, 140, **143,** 153, 185, Dominion Mus., and Adelaide Univ. Geol. Coll.
„ sp.	Altonian	DC 105, 186
Fam. GONEPLACIDAE		
Ommatocarcinus arenicola n. sp. ..	Otaian to Waiauan, Oligocene-Miocene	DC **155**
„ sp.	Awamoan, L. Miocene	DC 115
Galene proavita n. sp.	Clifdenian, M. Miocene	DC **129** + **130** + **204,** 131, 121, 122, 230
Fam. OCYPODIDAE		
Hemiplax hirtipes Heller	Subfossil	DC 173, Auck. Mus.
„ ?*major* n. sp.	Nukumaruan, Pleistocene ..	DC 228, **229,** 237
„ sp.	Waitotaran, U. Pliocene ..	DC 212

DESCRIPTIONS

Family GLYPHEIDAE

Genus GLYPHEOPSIS Beurlen, 1928

TYPE SPECIES: *Glyphea ornata* Quenstedt

Glypheopsis antipodum n. sp.

Pl. 2, Fig. 1

MATERIAL: One slightly flattened specimen showing the greater part of the carapace and three abdominal segments in dorsal view, also antennae and parts of the first pereiopods. Otago Museum No. C 03 41. (Coll. W. J. Sherry.)

OCCURRENCE: Ahuriri Flat, Clutha. (Ahuriri Flat is an old name for a locality 2 miles south-east of Glenoamaru, S179/461).

AGE: Liassic (Herangi Series), probably Ururoan, judged by the locality. (Information from Dr C. A. Fleming.)

DIAGNOSIS: Carapace subcylindrical, with a deep cervical, a shallow post-cervical and a moderately deep, U-shaped branchio-cardiac furrow; the post-cervical furrow bent downward at right angles a short distance behind the cervical furrow. The posterior and branchial regions of the carapace are deeply pitted; the anterior median portion is smooth between the keels.

DESCRIPTION: Carapace elongate and slender, with parallel sides in dorsal aspect. Cervical furrow deep, steeply inclined forward and downward, straight except for a slightly V-shaped median portion. The anterior part of the carapace is wide. Median keel straight, continuous, smooth, ending in a short rostrum. Lateral keels on the anterior portion of the carapace strong, granulated, the distance between the median and the first lateral keel equal to that between the first and second but less than that between the second and the lateral keel. The first keel is slightly curved inward at its anterior and posterior ends, the second and third are straight. The surface of the carapace is smooth between the ridges from the median line to the flank of the third keel which is granulated. The branchio-cardiac furrow is broadly U-shaped in dorsal view, deep and smooth. The post-cervical furrow is straight and indistinct in its median portion where it is marked mainly by stronger granulation along its anterior edge. It bends down very sharply near its anterior end, a short distance only behind the cervical furrow, to meet the branchio-cardiac furrow. The upper boundary line of the narrow field lying anterior to this junction and marked xω in fig. 19 - 8 is formed by a furrow, as in *G. pustulosa* (H. v. Meyer) and *G. ornata* (Quenstedt), but the field itself is not well preserved. The short median lobe between the post-cervical furrows is visible but not well marked off anteriorly. The portion of the carapace between the cervical and branchio-cardiac furrows is strongly granulated, while behind the branchio-cardiac furrow rounded pits between reticulate elevations dominate the sculpture. The posterior margin is marked by a wide sulcus and a weak ridge. The first abdominal segment is short, the tergum of the following segment is almost square, flattened dorsally, and relatively smooth, being ornamented only with a few widely and irregularly spaced pits. The third segment is similar but shorter. The pleura are marked off by longitudinal ridges and furrows. The merus, carpus, and propodus of the first pereiopod are stout, flattened, and granulated.

MEASUREMENTS: Length of carapace 30 mm, width about 13·5 mm, length from base of rostrum to cervical furrow 14 mm, lengths of abdominal segments 1–3 about 4, 7, and 5 mm, width of abdominal tergites about 9 mm.

COMPARISON: This species differs from *G. ornata* (Quenstedt), described from the Callovian, in its single median keel and the strong ornamentation of the carapace behind the cervical furrow. The position of the third anterior lateral crest and the conspicuous pitting behind the branchio-cardiac furrow distinguish it also from other species.

Family MECOCHIRIDAE

Genus MECOCHIRUS Germar, 1827

TYPE SPECIES: *Macrourites longimanatus* Schlotheim

Mecochirus marwicki n. sp.

Pl. 2, Fig. 2 a, b, 3; Text Fig. 1 a, b

MATERIAL: Remains of at least three individuals showing most of the body with appendages. Deposited by the Department of Geology, University of Auckland, in the collection of the New Zealand Geological Survey. Holotype No. DC 266.

OCCURRENCE: Klondyke Road, Waikato Heads, Grid Reference N51/326979, coll. B. H. Purser, Thesis locality 11 (N51/610).

AGE: Jurassic, Upper Heterian (approximately Kimmeridgian).

PRESERVATION: Carapace broken and distorted in two specimens, abdomen longitudinally and dorso-ventrally compressed in all three specimens, but appendages in almost undisturbed position in one of them.

DIAGNOSIS: A small species, with a medially furrowed rostrum with three teeth on lateral ridges; carapace with oblique granulated ridges on its anterior portion and fine transverse ridges on its posterior portions. First pereiopods long, spiny, subchelate and heterochelous, with long pointed dactylus.

DESCRIPTION: Carapace small (about 21 mm long), thin, and probably rather soft. The rostrum is styliform, about 3 mm long, with a median furrow and lateral ridges, each with three widely spaced teeth. Cervical furrow (e–e1) deep, semi-circular in its median portion, joined by the much less distinct branchio-cardiac furrow (a) with an acute angle above the faintly marked-off area ω. The branchio-cardiac furrow weakens rapidly and is not apparent dorsally. Post-cervical furrow (c) apparently indistinct, but the carapace is poorly preserved in its region. The two lateral rostral carinae continue on the anterior portion of the carapace for about one-half the length of the rostrum. Behind them, the continuation of the median rostral furrow is divided by a short median (meso-gastric) ridge, which is flanked by two granulated and elevated areas. Laterally, another granulated ridge extends forward and upward from the cervical furrow towards the base of the rostrum. The metagastric region is finely granulated; the rest of the carapace is covered with a network of ridges with peaks and valleys. The ridges become more pronounced and arranged more transversely on the posterior portion of the carapace.

The abdomen is strongly developed, but only the last three or four segments are well preserved. Their tergites are almost smooth, except for a weak granulation, particularly on the sixth segment. The pleura are rounded but with almost straight anterior margins. The telson is trapezoidal with slightly divergent weak lateral ridges and a faint median depression; the uropodes have strong longitudinal ridges and a diaeresis.

The third maxillipedes are visible but not well preserved. The first pereiopodes are long, as in the typical species of the genus. There is a distinct "knee" between the basi-ischium and

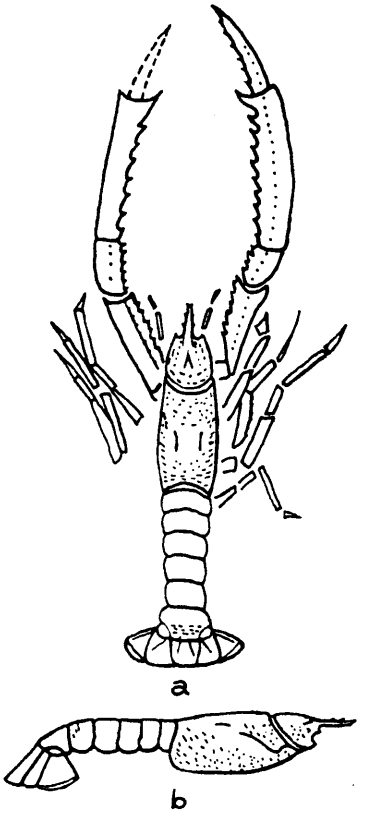


Fig. 1. *Mecochirus marwicki*. a – Carapace and abdomen restored, appendages shown as preserved. Nat. size. b – Lateral view of carapace and abdomen restored, Nat. size.

the merus, which is long and widened distally. Its inner and outer edges bear rows of spines. The carpus is short and barrel-shaped, with a granulated surface and several long spines. The propodus is very long, with a row of about 10 spines, which increase gradually in length distally and which are set along its inner and upper edge. The surface is finely granulated. The last tooth rises from the distal margin. It is short and stout on the right propodus but long and spinose on the left propodus of the holotype specimen. This condition could be described as subchelate and heterochelous. The dactylus (incomplete on the holotype but complete in another right first pereiopod) is very long (probably about two-thirds the length of the propodus), almost straight, ending in a needle-sharp point, and with about seven spinose teeth on its inner surface. They decrease in size towards the tip. The second pereiopod is short, barely reaching the carpus of the first when both are extended. It ends in a subchela with a long dactylus. The following two pairs are thinner but of about equal length, and directed forward and outward. The fifth pereiopod has the carpus, propodus, and dactylus directed backward and outward (in the holotype).

COMPARISON: The new species fits the description of the genus as given by H. Woods in 1927 (H. Woods, 1925–1931, p. 64). It is represented by a few species ranging from the Liassic to the Portlandian of western Europe. Among these, *M. clypeatus* (Carter) seems to be nearest to the new species in the shape of the carapace and abdomen. It is, however, the only species preserved without lateral compression and this may account for the similarity. The ornamentation of the carapace and first pereiopods is finer in *M. clypeatus*. In the type species *M. longimanatus* (Schlotheim) the ornamentation of the anterior portion of the carapace and of the pereiopods differs from that of the new species.

Mecochirus ? sp.

MATERIAL: Badly crushed and disjointed portions of the cephalothorax and abdomen of two specimens (DC 235, 236).

OCCURRENCE: Kawhia-Raglan Road, N73/655, GS 6712, coll. D. Kear and C. A. Fleming.

AGE: *Aulacosphinctoides* Zone, Upper Jurassic, Puaroan Stage (Lower Tithonian).

REMARKS: One of these two specimens (DC 236) shows five moderately well preserved rounded abdominal pleura and part of the flank of the thin carapace, with a strongly impressed cervical furrow and a ribbon-like branchio-cardiac furrow. This part of the carapace is also preserved in the other specimen where the branchial surface is seen to be rugose. The observable characters agree with those of *Mecochirus*, but in the absence of the distinctive first pereiopod and of the rostral portion of the carapace the generic placing of these specimens must remain in doubt.

Family CALLIANASSIDAE

Genus CALLIANASSA Leach, 1814.

TYPE SPECIES: *Cancer* (*Astacus*) *subterraneus* Montagu

Callianassa awakina n. sp.

Pl. 2, Fig. 4, 5; Text Fig. 2

MATERIAL: Three large and one small right chelae and one large left chela (DC 189–193 coll. C. A. Fleming); one large left chela (DC 117, coll. C. W. Washburne and J. Marwick). Most of the immovable finger is missing in all these specimens. A concretion contains the remains of at least four large chelae (DC 194).

OCCURRENCE: Awakino East S.D., Awakino–Mahoenui highway, cutting 3 miles east of road tunnel GS 5771, (DC 189–194), also road cutting near Mangaruha Creek, GS 2592 (DC 117).

HOLOTYPE: Specimen DC 194A.

STRATIGRAPHIC POSITION AND AGE: 100–200 ft below base of Mokau Group in upper part of Mahoenui Group (DC 189–194). DC 117 is from a similar horizon about half a mile to the southwest. Otaian, Upper Oligocene.

DIAGNOSIS: A *Callianassa* with a large, square, moderately biconvex propodus, ornamented with dorsal and ventral ridges and large elongate perforate bosses around the digital margin. Immovable finger with a spinose basal tooth, an external denticulate ridge, and two dorsal keels. Movable finger stout.

DESCRIPTION: Propodus square, in the holotype 18 mm long and high. Upper margin slightly convex, lower margin mostly straight, with gentle proximal slope. External surface convex, medially flattened; internal surface moderately convex, with a small concave area at the base of the immovable finger. Upper margin with a blunt ridge, which is well marked proximally and disappears distally. Lower margin with a pronounced, somewhat sinuous ridge, which is marked by a sharp furrow externally and by a line of about 25 small pits internally. There are also about 10 small widely spaced external pits along the ridge. At some distance below the upper edge there are 8–10 pits, mostly inconspicuous, on the inner surface in a gently sloping row, which ends near the digital articulation. The surface of the propodus is smooth and shiny, except for a number of oval rimmed sockets around the digital margin. On the inner surface, 3 or 4 are close to the margin, about 4 above the base of the immovable finger, while on the outer surface about 6 are scattered between the articulation and the base of the immovable finger. A sharp spine is present on the interdigital sinus, on the outer surface, followed by a row of granules extending to the upper external edge of the immovable finger. This is stout, triangular in external view and in transverse section, with two sharp ridges on its upper face. They end below the digital opening. The dactylus is thick, strong, and sharply pointed, with a sharp inner and a denticulate outer edge and a broadly rounded upper surface.

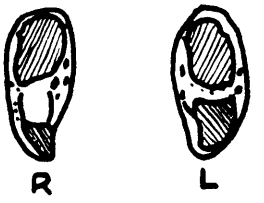


Fig. 2. *Callianassa awakina*. Distal view of palms of right chela (DC 189) and left chela (DC 117). Nat. size.

This species somewhat resembles *C. granulata* Withers (1926) from the Eocene Scotland Beds of Barbados, but differs in the lack of granulation.

The specific trivial name *awakina* is a latinised adjective.

Callianassa waikurana n. sp.

Pl. 2, Fig. 6

MATERIAL: One almost complete right chela (propodus and dactylus). Only external face visible. No. DC 219 (holotype).

OCCURRENCE: Waikura Stream, East Cape Peninsula, GS 6561 (N62/531); coll. H. W. Wellman, 1956.

AGE: Haumurian Stage, i.e. Upper Piripauan, Maestrichtian.

DIAGNOSIS: Chela small, subquadrate, external surface smooth except for a few scattered pits, dactylus curved, with basally broad and flat upper surface and a curved toothless cutting edge.

DESCRIPTION: Propodus subquadrate in outline, slightly longer (12 mm) than high (11 mm). Outer surface stongly convex, particularly in its upper part. Upper and lower margins straight, parallel, anterior and posterior margins converging slightly upward, lower proximal angle obtusely rounded, carinate, the carina extending from the base of the proximal articulation to the base of the fixed finger. This finger is short, strong, and broadly triangular in outline. The dactylus is short and curved, with a very flat upper surface, which is very wide at the base and tapers towards

the tip. The surface of the propodus is smooth except for a few scattered pits below the base of the dactylus and a row of widely spaced small pits above the lower edge. The dactylus has a curved cutting edge without teeth, and four or five pits above it.

This species does not resemble closely any other *Callianassa*.

Callianassa sp. a

Pl. 2, Fig. 7

MATERIAL: Two specimens represented by fragmentary right and left chelae, and other fragments associated with one specimen. (DC 220, 221). Probably also another fragmentary specimen (DC 239).

OCCURRENCE: Utakura River, Okaihau, North Auckland. In very hard, dark grey, well rounded pebbles embedded in a lighter grey matrix (DC 220, 221). Waitangi River (DC 239). Coll. F. G. Fitzgerald, 1925.

AGE: Probably Haumurian Stage, Maestrichtian. Pebbles and matrix are not believed to differ significantly in age.

DESCRIPTION: The incomplete material does not permit full description but a few observed characters are listed here for future reference.

In the left propodus length and height are equal, in the right propodus the height exceeds the length slightly. In both the straight upper margin converges towards the straight lower margin. The fingers appear to be short. The external surface of the left propodus shows two prominent longitudinal rows of pits, with 5–6 pits in each row extending from about the upper and lower levels of the articulation of the dactylus to the proximal margin of the propodus. The external surface of the right propodus shows an additional row extending back from the base of the finger. The internal surface of the left propodus shows a row of 7 well developed pits along the upper edge.

MEASUREMENTS: Length and height of left propodus about 15·5 mm. Length of right propodus 11·5 mm, height 12·5 mm.

Callianassa sp. b

Pl. 2, Fig. 8

MATERIAL: One large left chela, external surface only exposed, with fragments of another chela in close proximity. (DC 261.)

OCCURRENCE: Putangirua Creek, Palliser Bay, East Wellington, coll. D. Cowie, 1958.

AGE: Tongaporutuan, Upper Miocene.

DESCRIPTION: A large robust chela, biconvex, with sharp straight dorsal and ventral margins. Articulation of dactylus projecting above the base of the immovable finger, with only one large pit 1 mm behind the top margin of the projection. The rest of the outer surface is smooth except for an oblique row of small impressions, 5 mm in length, about 8 mm behind the base of the dactylus. The upper surface of the immovable finger is keeled, with a median tooth and an upturned pointed termination. Its outer surface and lower edge each bears a row of small pits. The dactylus is very stout and blunt, with an outer row of pits and a basal tooth.

MEASUREMENTS: Height of propodus 20 mm, length 22 mm, thickness about 9 mm, length of immovable finger 11·5 mm, height at base 5 mm, length of dactylus 15·4 mm, height at base about 7 mm.

REMARKS: This is a large and conspicuous form, which should be easily recognisable when further specimens are found. It is unlike any other *Callianassa* from New Zealand.

Another species of *Callianassa* which is unidentifiable was found in the Bortonian (Middle Eocene) of Green Valley, at crossing of main Palmerston Road, N. Otago (GS 2119, DC 218 coll. D. A. Brown, 1938). Fragments of legs and other parts of the body are preserved but the chelae are missing.

Genus CTENOCHELES Kishinouye

TYPE SPECIES: *C. balssi* Kishinouye

Ctenocheles cf. **maorianus** Powell

Pl. 2, Fig. 9–12

1948. *Ctenocheles maorianus* Powell, Rec. Auckland [N.Z.] Mus. 3 (6): 369, pl 68.
1955. *Ctenocheles maorianus* Powell, Dell, Rec. Dom. Mus. N.Z. 2 (3) : 149.

MATERIAL: From Victoria University Zoology Department: 10 fingers of the larger chela (3 right fixed, 1 left fixed, 3 right movable, 3 left movable), 8 fingers of the smaller chela. From N.Z. Geological Survey: 1 fragmentary propodus of a right smaller chela with fixed finger (DC 231), 2 fragmentary fingers of the right larger chela (DC 109, DC 107), and 2 fragmentary fingers (1 movable) of the right and 1 (immovable) of the left smaller chela (DC 110–111).

OCCURRENCE: Coastal section between Castlecliff and Kai Iwi, Wanganui.

STRATIGRAPHIC POSITION AND AGE: In or near Pinnacle Sand Formation; Kupe Formation, GS 4042; Lower Castlecliff Shellbed CU_2a, GS 4099; Upper Castlecliff Shellbed (Upper Marwicki Zone); Castlecliffian, Upper Pleistocene.

REMARKS: The fingers and chela are clearly recognisable as belonging to the genus *Ctenocheles*. The movable fingers are proximally dorso-ventrally compressed, but for the greater part of their length they are strongly laterally compressed. The cutting edge shows the usual rake-like straight row of sharply pointed teeth. Three to four short teeth are usually found between the long ones in the middle portion of the fingers of the larger chela but there may be up to six small teeth in the intervals on larger fingers. The propodus of the right chela is as described by Powell in the holotype of the Recent New Zealand species. The fingers of the smaller chela resemble those figured by Powell from the paratype and also those of *C. balssi* Kishinouye. They are rounded in section and their teeth are very small and conical but they also show alternations in size. There are numerous small pits on the surface. There are no grounds for a distinction between the living species and the fossil material but there is hardly enough of it preserved to assert that they must represent the Recent species. Not enough is known about the variability of the arrangement of the teeth on the fingers of the larger and smaller chelae in the living form for a comparison with that observed in the relatively large number of fossil fingers. In the circumstances it can be assigned only conditionally to the living species. The smaller fingers are 10–13 mm long, the length of the fixed finger of the only fragmentary chela is 22 mm.

Family PALINURIDAE

Genus JASUS Parker

TYPE SPECIES: *Palinurus lalandii* H. Milne Edwards

Jasus flemingi n. sp.

Pl. 1; Text Fig. 3

MATERIAL: One large specimen, almost complete, but anterior margin of carapace damaged. (DC 203, collected and presented by Mr Ulrich, Golden Bay Cement Works.)

OCCURRENCE: Tarakohe Marl Pit, Tarakohe, Golden Bay, Nelson.

AGE: Basal Altonian, Lower Miocene. (This age was confirmed by the examination of Foraminifera; personal communication from Mr N. de B. Hornibrook, 1953.)

DIAGNOSIS: A palinurid of the genus *Jasus*, differing from the Recent *J. verreauxi* (H. Milne Edwards) in the complete absence of spines on the abdominal tergites and in the presence of longitudinal furrows delimiting the pleura.

PRESERVATION: The specimen is preserved in its natural position on a slab of fine grey argillaceous sandstone. The carapace is dorso-ventrally somewhat compressed, particularly in its anterior portion where the inflated hepatical regions have collapsed on both sides, over-deepening their dorsal boundary furrows. The compression of the carapace makes it difficult to judge the original height of the projections (spines or tubercles) on its surface. Where the frontal portion has broken away, a faint section of the bases of the eye stalks is seen above the dorsal edge of the fused antennular bases. Portions of the left antennal and right antennular stalks are visible. Parts of the merus, carpus, and propodus of the first, second, third, and fourth pereiopods are preserved, all extended forward, but the first pair reaching downward and the fourth right leg flexed, while most of the right and part of the left fifth pereiopod extend outward and backward. The abdominal segments 1–6 are preserved, with some pleura slightly displaced owing to compression. The telson is not preserved. Some of the shell is present but it appears to have been thin as the matrix adheres normally and closely to its surface and there is no evidence of decalcification. The flattening of the posterior part of the carapace and of the abdomen, without major fracturing, suggests that the specimen was freshly moulted and incompletely calcified when it became embedded in the sediment. It has not been disturbed (except by compression due to compaction of the sediment) after embedding.

DESCRIPTION: Carapace subcylindrical, spinose, widening towards the branchial regions. Joint lateral cervical and median postcervical furrow, with longitudinal posterior extensions, developed as in other palinurids and well marked. Behind the (missing) rostrum one larger, two smaller, and one very large median spine or tubercle, flanked on each side by a row of two small and three large elevations, then by a pair of rows consisting of four spines alternating in size. Both these lateral rows are slightly convex towards the flanks. There was apparently a spinose crest or an inflated area above the hepatical regions which appear to have been spiny above and smooth below the periphery. The cardiac region behind the postcervical furrow shows two parallel rows of spines of varying size which continue the two lateral rows of the anterior region of the carapace, and two less regular lateral rows. The intestinal and branchial regions are covered with spines of varying sizes numbering not more than 50 on each side. They are only vaguely arranged in rows. There are no small spines or scales in the spaces between the individual larger ones. A wide smooth furrow is seen in front of the posterior margin, which is broken.

The abdominal segments are smooth, but very finely pitted, and covered with a network of fine anastomosing incised lines without spines or transverse furrows. Five sharp small teeth can be seen on the posterior margin of the pleura of the second segment, which ends in a somewhat sickle-shaped terminal spine (text fig. 3). Other segments had similar terminal spines. The abdominal pleura seem to have been set off from the tergites by longitudinal furrows. These are seen on all segments but not clearly owing to dorso-ventral compression during fossilisation.

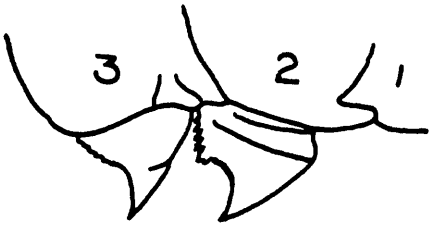


Fig. 3. *Jasus flemingi*. Pleura of abdominal segments 2 and 3. The tergites are crushed. Nat. size.

Basal antennular segment below the front arcuate, with anterior median spine. Antennal stalks strong and spiny, antennular stalks slender and smooth. First pereiopods strong, smooth, merus with a dorsal keel ending distally in a sharp spine. The merus of the first and second pereiopods in normal position extends to the level of the eye stalks. Carpus triangular in dorsal view, propodus with rounded edges. Pereiopods 2–5 about equal in width, rounded in section.

COMPARISON: This species belongs to the group of palinurids with a cylindrical carapace and with the antennular somite produced no further than the extremity of the rostrum. This group is now known as the genus *Jasus* Parker. Within it, as within other genera, a sharp distinction exists between species with and without transverse furrows on the abdomen; the new species obviously belongs to the latter division. This is represented in the living fauna by *J. verreauxi* Milne Edwards,

1851 (Syn.: *Palinurus hügeli* Heller 1862; see Pesta 1915). It is found in New Zealand and on the east coast of Australia from Tasmania to south Queensland. The new form differs from this species in the absence of spines on the abdominal tergites and in the presence of longitudinal furrows delimiting the pleura. The front is unfortunately missing; the antennular segment had a broadly curved (inverted U-shaped or horseshoe-shaped) anterior margin instead of being straight and widely divergent posteriorly and laterally as in the Recent species. The details of the spiny ornament of the carapace agree remarkably closely. There can be no doubt of the close relationship of the fossil species with the living *J. verreauxi*.

Family RANINIDAE

Genus LAEVIRANINA Lörenthey, 1929

TYPE SPECIES: *L. budapestinensis* Lörenthey.

Laeviranina perarmata n. sp.

Pl. 2, Fig. 13, 14; Text Fig. 4

MATERIAL: Four more or less damaged specimens; the holotype (DC 246) showing the carapace with only the left and posterior margins missing, and with remains of the second, third, and fourth pereiopods. Paratypes showing the median portion of the carapace (DC 247), parts of the carapace, pterygostome and sternum (DC 250) and the fronto-orbital and left antero-lateral margins, together with the right cheliped (DC 233).

OCCURRENCE: Snowdrift Quarry, Milburn, Otago (GS 2977, 6793), coll. H. W. Wellman, 1942, and N. de B. Hornibrook, 1957.

AGE: Bortonian (Middle Eocene).

DIAGNOSIS: A species of *Laeviranina* with a narrow rostrum, a faint post-frontal carina, long, strong and curved extra-orbital and antero-lateral spines pointing forward and very slightly outward, the distance between them on either side measuring one-third of the fronto-orbital width. Surface of carapace finely pitted, lateral margins finely granulate.

DESCRIPTION: Carapace strongly convex transversally and slightly convex longitudinally. Rostrum narrowly triangular, with a very faint median ridge and granulated ridges along the lateral margins. Inner portion of orbital margin curved, ending in a composite supra-orbital tooth. This is divided into two denticles by a long and deep gutter-like inner (first) supra-orbital furrow and consists of a short inner and a much larger conical outer spine, which is directed forward. Its inner margin continues the outer border of the first supra-orbital furrow. Its base widens laterally before reaching the second supra-orbital furrow, which is as strongly developed as the first. The inner supra-orbital furrows converge backward, the outer pair are parallel to the median line. The outer portion of the orbital margin is straight and the very long, straight, acicular extra-orbital spine rises from its external limit at only a little more than a right angle, so that it points only very slightly outward. The extra-orbital and antero-lateral spines are both curved, long and strong and nearly parallel. The distance from the base of the extra-orbital to that of the antero-lateral spine, measured at their mid-points, equals one-third of the fronto-orbital width. It is two-thirds of the distance from the antero-lateral spine (mid-point of base) to the point of greatest width of the carapace on its lateral margin.

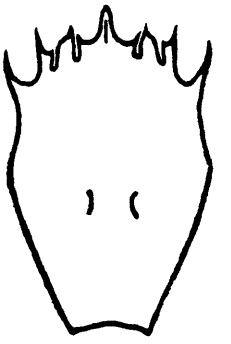


Fig. 4. *Laeviranina perarmata*. Restoration of carapace. Nat. size.

The fronto-orbital margin was 13·6 mm wide in the holotype (20 mm wide in the paratype); the carapace of the holotype was 20 mm wide and about 28 mm long.

The surface of the carapace is finely pitted, along the lateral margin it is finely granulate. The lateral "cardiac furrows" (impressions of the attractor epimeralis muscle) are faintly marked on the

inner and outer surfaces of the carapace. There is a faint post-frontal carina. The postero-lateral margins are angular. The pterygostomal region is bordered by a smooth elevated area ending inward in a crenulated step.

The propodus of the first cheliped is flat, very long, and narrow, with a strong stout spine directed forward at the distal end of its outer margin and four spines on its inner margin. The lower edge of the fixed finger arises at a right angle, the upper edge bears seven large saw-like teeth on its preserved proximal portion. They decrease in length outward from the third tooth. The dactylus is long, slender and curved, proximally with a granulated upper edge and a furrow.

COMPARISON: Four of the species of *Raninoides* described by Rathbun (1926) from the Eocene of Oregon and Washington were placed by Glaessner and Withers (1931) in the genus *Laeviranina* Lörenthey, together with five European species ranging from Lower to Upper Eocene. It differs from *Raninoides* H. Milne Edwards in greater relative width of the carapace and narrower fronto-orbital border, together with a shorter distance from the extra-orbital to the antero-lateral spine. Rathbun (1935) has since described another species, *R. ovalis* from the Lower Eocene of Alabama, in which the carapace is "about one and a half times as long as broad" and the fronto-orbital margin is less than two-thirds the width of the carapace, while in typical *Raninoides* it is only slightly less than the greatest width of the carapace. This species therefore also belongs to *Laeviranina*. The new species differs from it in its well developed lateral tooth. It is distinguished from *L. budapestinensis* Lörenthey and *L. fabianii* Lörenthey by its less pronounced post-frontal ridge, and from the last-named species also by its narrower supra-orbital notches. *L. perarmata* has a narrower fronto-orbital margin than *L. gottscheei* (J. Böhm), its lateral spine is larger than the extra-orbital spine and closer to it than to the point of maximum width of the carapace. Among the remaining species, *L. lewisana* (Rathbun) from the Eocene of Washington seems to be closest to the new species, which is, however, less convex transversely, with its lateral spine closer to the extra-orbital spine.

REMARKS: The new species seems to fit well into the line of evolution from the Cretaceous Raninidae through the Eocene *Laeviranina* to the Oligocene to Recent *Raninoides* (see Glaessner and Withers, 1931, p. 491). With more detailed information on the stratigraphic position and range of species available from micropaleontological studies, it may be rewarding to study quantitatively the steps in the simple and measurable bioseries involved in this morphogenetic sequence.

Genus LYREIDUS de Haan, 1841

TYPE SPECIES: *L. tridentatus* de Haan

Lyreidus elegans n. sp.

Pl. 2, Fig. 15, 16; Text Fig. 5

MATERIAL: Two carapaces. Holotype DC 123, Paratype DC 108.

OCCURRENCE: Tutaki S.D., Campbell Creek, GS 4719 coll. R. P. Suggate, 1948 (DC 123); Postal Creek, Oparara River, GS 4762 (DC 108), coll. H. W. Wellman and G. W. Grindley, 1948.

AGE: Upper Pareora or Southland Series (DC 123); Altonian (DC 108), Miocene.

DESCRIPTION: Carapace smooth, strongly convex transversally, slightly convex longitudinally. Fronto-orbital margin narrow, about one-half the width of the carapace or less. Antero-lateral margins blunt, diverging very slightly behind the extra-orbital tooth, then more strongly for the greater part of their length, ending at a single small flat lateral tooth which is directed forward and outward. It is placed at about two-fifths of the length of the carapace. The length is about 1·5–1·6 of the width in the holotype. The posterior lateral margin is marked on the posterior two-thirds of its length by a fine but sharp ridge, which extends to the lateral parts of the arched posterior

margin. It is very finely granulated. Most of the surface of the carapace is smooth but very finely pitted, with a faint granulation appearing behind the lateral tooth. The lateral cardiac furrows (attractor epimeralis muscle impressions) are seen as two almost straight lines about half-way between the lateral teeth and the posterior margin. The gastric apodeme pits are immediately behind the level of the lateral teeth. The front is not preserved. The pleura are granulated.

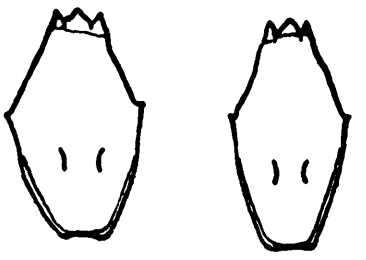


Fig. 5. *Lyreidus elegans*. Restoration of carapace. Left — specimen DC 123, right — specimen DC 108. Nat. size.

MEASUREMENTS: Width of holotype 17 mm, length (incomplete) 27 mm. Fronto-orbital width 8 mm. Width of paratype 9·5 mm, length (incomplete) 17·8 mm, fronto-orbital width 4·5 mm.

REMARKS: The species differs from *L. tridentatus* de Haan in the more posterior position of the lateral teeth and the much wider front-orbital margin and correspondingly less strongly converging antero-lateral margins. *L. bairdi* Smith and *L. channeri* Wood-Mason have two antero-lateral spines. *L. hungaricus* Beurlen (Middle Oligocene of Hungary) and the living species *L. politus* Parisi have none. The fossil *L. fastigatus* Rathbun from the Oligocene of the West Indies is represented only by a carpus. *L. alseanus* Rathbun from the Lower Oligocene of Washington is also very poorly preserved but is described as having two small teeth in front of the lateral spine. *L. elegans* is closest to and may be described as the ancestor of the living *L. tridentatus*, which is represented in Australian and New Zealand waters by *L. australiensis* Ward. This form, with a slightly broader carapace and sternum, was considered as a distinct species by Richardson and Krefft (1949) but as a synonym of *L. tridentatus* by McNeil, Sakai, and Powell (Powell, 1949; McNeil, 1953). The differences may have subspecific value.

Family MAJIDAE

Genus LEPTOMITHRAX Miers, 1876

TYPE SPECIES: *Paramithrax (Leptomithrax) longimanus* Miers

Leptomithrax atavus n. sp.

Pl. 3, Fig. 1; Text Fig. 6

MATERIAL: Holotype (DC 255), a cephalothorax without rostral spines, mostly preserved as an internal mould and inner shell layer, with parts of the outer layer near the posterior margin of the carapace and the left meso- and metabranchial regions where at least one barnacle was attached, also with fragments of the pereiopods and of the merus of the left cheliped. Paratypes: DC 253, a right cheliped (merus, carpus, and propodus, with the greater portion of the fingers missing); DC 254, a fragment of a very large propodus; DC 256, a cephalothorax, with some barnacles attached to the right mesobranchial region, left branchial regions and posterior portion missing, both fingers of the right chela preserved; DC 257–8, a cephalothorax, dorsal surface largely covered with balanid barnacles, with four fragmentary pereiopods and part of a finger; DC 226, a cephalothorax, part of left side concealed by hard matrix, with fragments of pereiopods.

OCCURRENCE: Road cutting 2 chains north of bridge over Makino River, on Stanley Road, GS 7203 (DC 253–8) coll. D. Rodley, 1958. The locality of specimen DC 226 is unknown but its preservation and matrix are not unlike those of spec. DC 253–8.

AGE: Kapitean (DC 253–8); Upper Miocene.

DESCRIPTION: Carapace oval in outline, with a sharp median crest and sloping flanks on the anterior half, regularly convex medially in antero-posterior direction, covered with spines and smaller tubercles, surface smooth between them, granulated near the posterior margin. Rostral (pseudo-rostral) spines broad at the base, incompletely preserved. Front narrow. Inter-antennular

spine long, vertical. Orbits well developed, supra-orbital ridge apparently narrow, not strongly spinose. Two supra-orbital fissures well developed. Inner supra-orbital spine transverse, outer supra-orbital spine directed upward and outward. Extra-orbital (post-orbital) spine more prominent, longer, pyramidal, with a small accessory spine closely behind its tip on the outer edge, and with a concave orbital face. The peripheral outline of the carapace shows one strongly developed hepatical and four equally spaced large branchial spines, the third marking the greatest width of the carapace. The fronto-orbital width (distance between extra-orbital teeth) is much less than one-half this width. Several larger spines mark approximately the boundary between meso- and metabranchial regions and a similar but straighter row extends across the meso- and epibranchial regions from the third branchial peripheral spine in medial and anterior direction. Six regularly spaced spines, in two anteriorly divergent rows flanking a deep median furrow, are found behind the rostrum and between the orbits. They are followed by five mesogastric spines. There are one urogastric and six cardiac tubercles of which the middle pair is the largest. The rest of the carapace is less prominently but closely tuberculate.

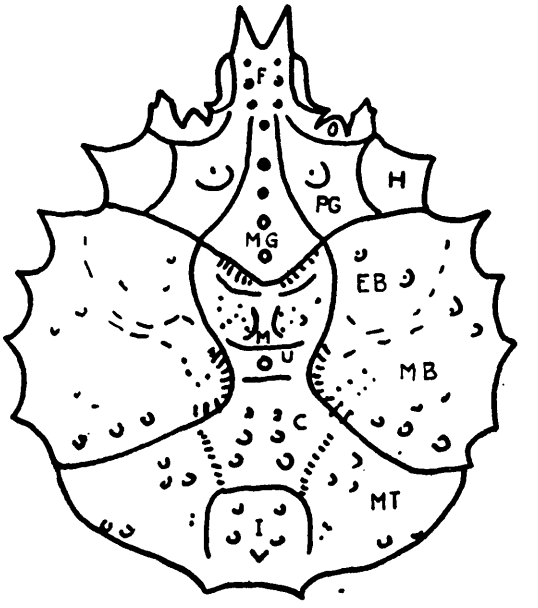


Fig. 6. *Leptomithrax atavus*. Restoration of carapace. Regions: F – frontal, O – orbital, H – hepatic, MG – mesogastric, M – metagastric, U – urogastric, C – cardiac, I – intestinal, PG – protogastric, EB – epibranchial, MB – mesobranchial, MT – metabranchial. Nat. size.

The pereiopods are long and strong, with the merus cylindrical. The chelipeds have the merus ornamented with a few scattered conical tubercles, the carpus angular in cross section but without definite sharp ridges, and with conical tubercles scattered over the outer surface, more densely spaced than on the merus. The propodus is rhombical in cross section, with blunt upper and lower margins, without tubercles but with a very fine granulation near the base of the fixed finger which is bent downward near its tip. The dactylus is long and strong, tapering very gradually.

MEASUREMENTS: Width of holotype between bases of lateral spines 60 mm, width between bases of hepatic spines 40 mm, length from orbit to posterior margin 58 mm, distance between extra-orbital spines 26 mm, width between bases of inner orbital spines 12 mm, height of carapace 27 mm, maximum diameter of merus of cheliped 11 mm; maximum height of large chela (DC 254) 35 mm. The width of the incompletely preserved specimen DC 256 (between the bases of the lateral spines) was about 67 mm, the width of its front (excluding supra-orbital ridges) is 9 mm.

Leptomithrax uruti n. sp.

Pl. 2, Fig. 17; Pl. 3, Fig. 2; Text Fig. 7

MATERIAL: Holotype (DC 175), a carapace, mostly well preserved as an internal mould, with fragments of one or two pereiopods. Paratype (DC 195), a small cephalothorax and abdomen, slightly crushed and deformed.

OCCURRENCE: Wray's Quarry, Uruti Road, 60 chains south of Uruti P.O.; GS 1139 (DC 175) coll. L. I. Grange, 1923. Upper Waitara (NE) S.D., 36 chains west of Rerekino Trig.; GS 2789 (DC 195) coll. H. J. Evans, 1940.

AGE: Urenui beds, Upper Tongaporutuan (DC 175, 195); Upper Miocene.

DIAGNOSIS: *L. uruti* differs from the other New Zealand Tertiary fossil species (*L. atavus* and *L. irirangi*) in its wider front and fronto-orbital margin, which is more than one-half the greatest

width of the carapace, in its more sub-triangular and less rounded carapace outline, in its more convex, inflated branchial regions, and more closely spinose ornamentation.

DESCRIPTION: Carapace subtriangular in outline, with a sharp median crest, strongly and regularly convex in antero-posterior direction, flanks sloping rather steeply in the hepatical region, convex across the branchial regions, closely covered with pointed spines and tubercles. The shell is smooth between them but partly granulated in the fronto-orbital and hepatic regions. Front wider than the distance to the first mesogastric spines. Rostral (pseudo-rostral) spines short, broad at the base, directed horizontally forward. Inter-antennular spine triangular, vertical. Orbits wide, with a strongly developed, convex, granulated, supra-orbital ridge. Inner supra-orbital spine transverse and very sharply pointed, outer supra-orbita (intercalary) spine separated from it by a deep fissure, oblique and triangular, directed downward and outward. Extra-orbital (post-orbital) spine strong, with a concave orbital face and a distinct accessory spine behind its tip. Two distinct hepatic spines on the peripheral margin, followed by three sharp mesobranchial spines, the third of which marks the greatest width of the carapace. The fronto-orbital width (distance between extra-orbital teeth) exceeds one-half of this width. The arrangement of larger spines on the surface of the carapace does not differ significantly from that in *L. atavus*.

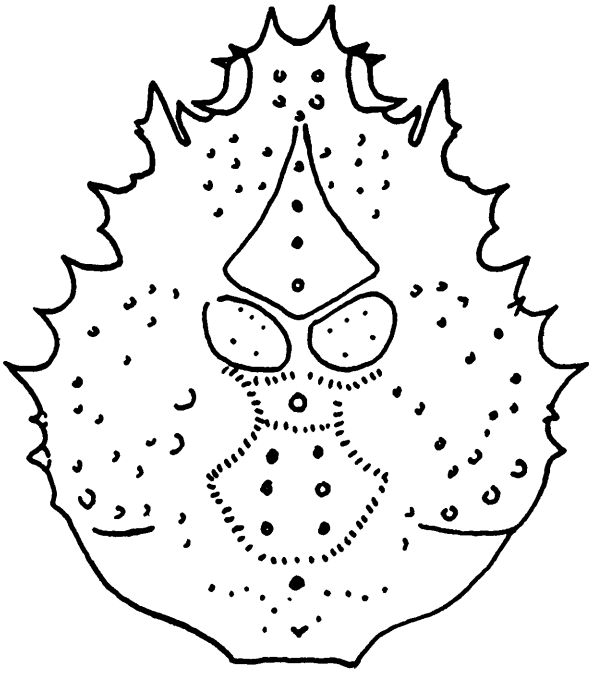


Fig. 7. *Leptomithrax uruti*. Restoration of carapace. ×2·5.

Basal antennal joint with two prominent teeth directed obliquely outward. Abdomen (female ?, DC 195) with deep longitudinal grooves bordering a convex median portion equal in width to the lateral parts. Terminal segment triangular. Lateral portion of sternum smooth.

MEASUREMENTS: Length of holotype 30 mm, width between bases of lateral spines 26 mm, width between bases of hepatic spines 19·5 mm, fronto-orbital width (distance between extra-orbital spines) 15 mm, width between bases of inner orbital spines 8 mm, width of front 5 mm, height of carapace 11 mm.

The specific trivial name *uruti* is an indeclinable noun.

Leptomithrax irirangi n. sp.

Pl. 3, Fig. 3, 4; Text Fig. 8

MATERIAL: One carapace, largely decorticated and abraded, with some of the antennar region and the epistome preserved (DC 223).

OCCURRENCE: From shell rock on road sidings outside HMNZS *Irirangi* Naval Radio Station, coll. T. Hosking, 1953 (N132/501).

AGE: "Probably from Waiouru Reef-bearing Sandstone, approximately Opoitian (Lower Pliocene)", information from Dr C. A. Fleming.

DIAGNOSIS: This species differs from *L. atavus* in its flatter carapace, which lacked a median crest, and in its relatively wider front; from *L. uruti* in its flatter carapace, more rounded outline, narrower fronto-orbital margin, and relatively shorter mesogastric region.

DESCRIPTION: Carapace broadly oval in outline, gently convex in antero-posterior and transverse directions. Rostral (pseudo-rostral) spines missing, probably short and solid and not sloping downward. Inter-antennular spine vertical, triangular in section, with a concave anterior face. Front wide, with a sharply incised median groove extending back from the anterior notch. Orbits well developed, supra-orbital ridge wide, curved in antero-posterior direction. Inner supra-orbital fissures strongly converging posteriorly. Outer supra-orbital (intercalary) spine with wide base, outer supra-orbital fissures opening forward, extra-orbital spine wide at its base, cupped inside, extending beyond the inner supra-orbital spine, and with a weak accessory spine behind its point on its outer edge. The outline of the hepatic lobe is almost rectangular. It shows one very strong hepatic spine, possibly accompanied by a very weak accessory spine. Three large branchial spines follow after a wide smooth concave interval, the third marking the greatest width of the carapace. Several larger spines are arranged on the posterior portion of the mesobranchial regions. Two tubercles mark the ends of the posterior margin. There are three pairs of tubercles on the rostrum between the orbits, followed by three or four mesogastric spines. The posterior meso- and metagastric regions are worn. One strong uro-gastric and two symmetrically placed cardiac spines can be seen. The rest of the carapace is covered with widely spaced tubercles and a fine granulation.

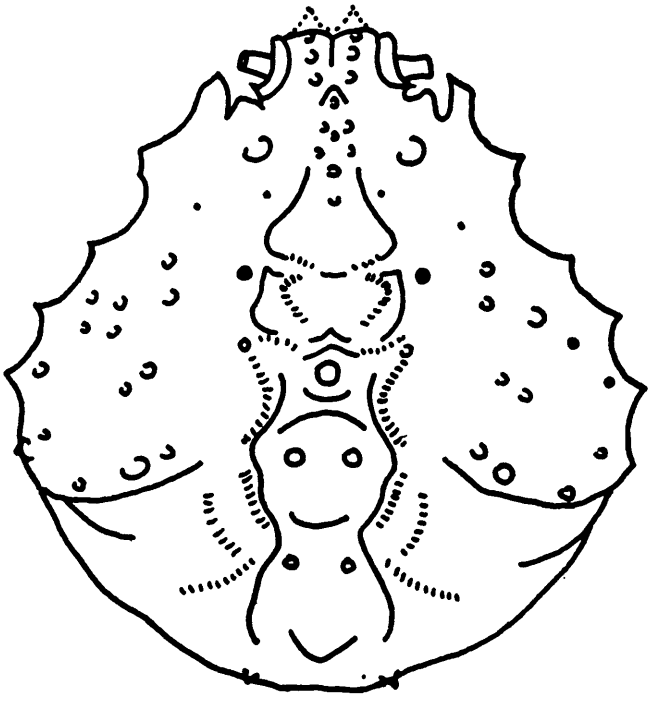


Fig. 8. *Leptomithrax irirangi*. Restoration of carapace with eye stalks partly preserved. Nat. size.

Two spines are present on the pterygostome, one near the hepatic notch and the other inward from the first branchial peripheral spine. There are four sub-hepatic spines. The eye stalks are short and round.

MEASUREMENTS: Length of carapace 82 mm; width between bases of lateral spines 76 mm, between hepatic spines 48 mm, between extra-orbital spines 31 mm, between bases of inner orbital spines 18 mm; width of front 11 mm; height of carapace 25 mm.

The specific trivial name *irirangi* is an indeclinable noun.

Family CANCRIDAE

Genus CANCER Linnaeus, 1758

TYPE SPECIES: *C. pagurus* Linnaeus

Cancer novaezealandiae (Jacquinot and Lucas)

Pl. 3, Fig. 5, 6

1853. *Platycarcinus novae-zealandiae* Jacquinot and Lucas, Voy. Pole Sud, Zool., vol. 3, Crust., p. 34, pl. 3, fig. 6.
1929. *Cancer novae-zealandiae* (Jacquinot and Lucas), Chilton and Bennett, Trans. N.Z. Inst. 59: 744.
1950. *Cancer novae-zealandiae* (Jacquinot and Lucas), Benson and Finlay, Trans. roy. Soc. N.Z. 78: 269–70.

MATERIAL: One male specimen showing median, posterior, and right lateral portions of carapace, abdomen, proximal portions of all pereiopods and distal portions of claws (DC 114). One dactylus of right cheliped (DC 102). Two dactyli of left cheliped (DC 104, 216). One fixed finger of left

cheliped (Victoria Univ. Zool. Dept.). Fragmentary right and left chelae and part of left dactylus (DC 260).

OCCURRENCE: Nukumaru Beach, Wanganui, GS 4114 (DC 102) coll. C. A. Fleming, 1945. Castlecliff (Tainui Shellbed), GS 4104 (DC 104) coll. C. A. Fleming, 1945. Mangaotoro S.D., 80 chains at 360° from Trig. W, GS 5694 (DC 114) coll. A. R. Lillie, 1940. 2½ miles north of Parnassus, Hawkswood S.D., GS 2827 (DC 214). Jed River, Marlborough, GS 2839 (DC 216) coll. H. E. Fyfe, 1934. E bank, Ruamahanga R., Gladstone, N162 (DC 260), coll. D. Cowie. Coastal section between Castlecliff and Kai Iwi (Victoria Univ. Zool. Dept.). Te Aute, Hawke's Bay, GS 833 (DC 263–4) coll. A. Hamilton.

AGE: Opoitian, Lower Pliocene (DC 114); Waitotaran, Pliocene (DC 263–4); Nukumaruan (Lower Pleistocene) (DC 260); Nukumaruan, Hautawan Substage, Lower Pleistocene (DC 214, 216); Castlecliffian, Mid-Pleistocene (DC 104 and Victoria Univ. Zool. Dept.). Benson and Finlay (1950) have recorded the species from a subfossil (post-Tertiary) concretion, possibly from the mud of Auckland Harbour.

REMARKS: The preserved parts of the Pliocene specimen (DC 114) agree closely with *C. novaezealandiae*, particularly the wide carapace, its fine close granulation, indistinct regions, short, slightly projecting and moderately crenulated antero-lateral lobes; also the granulation of the postero-lateral margin and the ornamentation of the chelae as far as it is visible. No differences between it and the living form have been detected. The carapace was about 105 mm wide and 63 mm long. The dactylus (DC 104) was about 21 mm long and the articulation 12 mm high. It has strong granules and tubercles in irregular rows on the upper and a few blunt teeth on the lower surface and is very strongly curved.

Family PORTUNIDAE

Genus PORTUNITES Bell, 1858

TYPE SPECIES: *P. incertus* Bell

Portunites granulifer n. sp.

Pl. 3, Fig. 7; Text Fig. 9

MATERIAL: One almost complete carapace with a fragmentary right cheliped and proximal portions of pereiopods (Holotype, DC 232). Also an external mould of the median part of a carapace (DC 234) and three more or less incomplete specimens in concretions (DC 240, 241, 243), carapace fragments (DC 243, 252) and chelae (DC 242, 244, 248, 251).

OCCURRENCE: Snowdrift Quarry, Milburn, Otago, GS 2977, 6793, coll. H. W. Wellman, 1942, and N. de B. Hornibrook, 1957.

AGE: Bortonian, Middle Eocene.

DIAGNOSIS: A species of *Portunites* with a wide carapace, four small frontal teeth, three blunt conical tubercles on the branchial regions, with two additional lateral branchial tubercles, and strongly crested chelae.

DESCRIPTION: Carapace wider than long, greatest width (between lateral spines) near centre of length. Front apparently with four widely spaced small teeth (seen in specimen DC 243, but damaged in all specimens). Orbits large, upper margin with a small notch and a

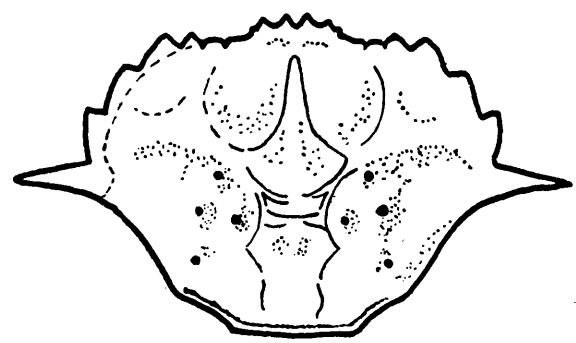


Fig. 9. *Portunites granulifer*. Restoration of carapace. Nat. size.

projection directed forward and upward close to the external frontal tooth, followed by a smooth supra-orbital rim with two fissures. Extra-orbital tooth triangular in cross section, followed by three flat, pointed antero-lateral teeth of which the second is the largest, and a long, conical, sharply pointed lateral spine, which is directed outward and upward.

Postero-lateral margin nearly straight, marked by a weak ridge for about two-thirds of its length behind the lateral spine. A raised border above the large vaulted portion above the last pereiopods extends as a sinuous granulated ridge above the posterior margin.

The mesogastric, protogastric, urogastric, and cardiac regions are individually inflated and well marked. The anterior portion of the mesobranchial regions is raised to form an anteriorly convex ridge extending to the lateral spines. Medially it bends back to the side of the mesogastric field, where it is raised to form a bluntly conical tubercle. A stronger tubercle is situated a little to the side and behind the first; a third one is opposite the urogastric-cardiac furrow. There is another weaker pair of tubercles on the branchial regions behind the second pair, half way between the lateral extension of the cardiac region and the postero-lateral margin. The surface of the carapace is evenly granulated, with a slight concentration of granules on the larger tubercles.

The irregularly pentagonal upper surface of the carpus of the cheliped bears a strong oblique ridge with a branch leading to the tooth at the distal end of the inner edge. The short strong propodus has a flat upper surface bounded by two curved ridges and strong oblique median crests on both the inner and outer surface.

COMPARISON: The new species resembles very closely *P. triangulum* Rathbun from the Oligocene of Washington and Oregon. It differs only in details of surface sculpture, such as the absence of larger granules in front of the branchial ridge and the presence of a posterior (fourth) branchial tubercle. The frontal teeth seem to be smaller in the new species. The relation between these two forms is obviously closer than that with other species of the genus.

MEASUREMENTS OF HOLOTYPE: Length of carapace 40 mm, width between tips of lateral spines 65 mm, width of front 10·5 mm, width of orbits 7 mm, anterior length of lateral spine 8 mm; length of propodus of chela 20 mm, height about 15 mm, thickness about 9 mm.

Genus OVALIPES Rathbun, 1898

TYPE SPECIES: *Cancer ocellatus* Herbst

Ovalipes cf. **punctatus** (de Haan)

Pl. 3, Fig. 8

1833, *Corystes (Anisopus) punctata* de Haan, Fauna Japonica, Crust., p. 13; 1835 ibid. p. 44, pl. 2, fig. 1.
1834. *Platyonichus bipustulatus* Milne Edwards, Hist. Nat. Crust., vol. 1, p. 437, pl. 17, fig. 7–10.
1929. *Ovalipes bipustulatus* (Milne Edwards), Chilton and Bennett, Trans. roy. Soc. N.Z. 59: 755.
1930. *Ovalipes punctatus* (de Haan), Rathbun, Bull. U.S. nat. Mus. 152: 24, pl. 5–8.

MATERIAL: Dactylus of right cheliped (DC 215). Fixed finger of left cheliped (DC 116). Fingers of right cheliped, coll. J. C. Yaldwyn.

OCCURRENCE: Ohope Beach, Bay of Plenty, GS 3893 (DC 215) coll. J. Healy, 1946; Kidnapper S.D., face of high terrace of Maraetotara River GS 5315 (DC 116) coll. T. Grant Taylor, 1951. Doubtless Bay sand hills, on surface with subfossil bird bones (information from Mr J. C. Yaldwyn).

AGE: Castlecliffian, Pleistocene (DC 215, 116); subfossil (coll. J. C. Yaldwyn).

REMARKS: The specimens listed above are very similar to Australian and New Zealand Recent material of this widespread species. Differences in the size of teeth and shape of spines on the fingers are minor and cannot be evaluated taxonomically without extensive investigations of the variability of the living species. While it will be desirable to base final conclusions on more completely preserved material, the present fragmentary fossil specimens prove that either the living species or a very closely related form existed in the Pleistocene.

Ovalipes sp. a

Pl. 3, Fig. 9

MATERIAL: Two fragmentary fingers of the right chela (DC 127–128).

OCCURRENCE: Teviotdale S.D., Lower Waipara River, GS 4997 coll. D. R. Gregg, 1949.

AGE: Waitotaran, Upper Pliocene.

REMARKS: This material, which is too fragmentary for a specific description, indicates the occurrence of a new species of the genus *Ovalipes* in the Pliocene. The shape of the fingers resembles that of the corresponding parts of *O. punctatus* but there are considerable differences in the ornamentation. In *O. punctatus* there are five granulated ridges on the corresponding finger. In the Pliocene specimen the upper outer ridge is smooth, the lower outer ridge is faintly granulated, the upper inner ridge is coarsely granulated. The main difference is seen in the lower inner and lower ridges where the ornament is formed, from the level of the base of the finger to that of the third large tooth, by more or less discontinuous, pronounced, straight, transverse ridges rather than by rounded granules. They seem to continue the pattern of the stridulating ridge at the base of the chela of *O. punctatus*. The pits for tufts of hair occupy similar positions in both forms. The height of the immovable finger at its base is 14·5 mm.

Family XANTHIDAE

Genus MENIPPE de Haan, 1833

TYPE SPECIES: *Cancer rumphii* Fabricius

Menippe sp.

Pl. 3, Fig. 10

MATERIAL: One complete and one fragmentary right immovable finger (DC 170, 171), and one fragment of a right dactylus (DC 172), coll. McKay.

OCCURRENCE: Hutchinson's Quarry, Oamaru, GS 172, coll. A. McKay, 1876.

AGE: Hutchinsonian (at type locality), uppermost Oligocene.

DESCRIPTION: Notwithstanding their fragmentary nature, these fingers are very distinctive and seem to prove definitely the occurrence of the genus *Menippe* in New Zealand. They are indistinguishable from the immovable fingers of the larger chela of *M. almerai* Via (1941) from the Upper Eocene of Spain. As in the species described by Via, the shell is up to 4 mm thick. There are two large, widely separated teeth and a trace of a third (distal) tooth. The first commences at the base of the finger. It is long and wide and has a flat surface, which is slightly depressed in the centre. The second tooth forms a step at a much lower level than the first one and is smaller.

REMARKS: The genus *Menippe* has fossil representatives in the Middle Eocene of the Paris Basin, Upper Eocene of Spain, Upper Miocene of Florida and Fiji, and the Pleistocene of North America.

Genus PSEUDOCARCINUS H. Milne Edwards

TYPE SPECIES: *Cancer gigas* Lamarck

Pseudocarcinus sp.

Pl. 3, Fig. 11

MATERIAL: One dactylus of the right larger claw (DC 238).

OCCURRENCE: South side of Goldsborough-Kumara Road, 1 mile west of Goldsborough (GS 4588), coll. R. P. Suggate and H. W. Wellman, 1948.

AGE: Kapitean, uppermost Miocene to Pliocene.

DESCRIPTION: This finger is about 68 mm long, (measured along a straight line), with about 10 mm missing at the tip. Its greatest width at the base is about 9 mm. It is gently curved inward and downward, and compressed (higher than wide) throughout its length. It has a blunt tooth near its broken base; another one may have been present. The rest of the lower margin bears a vaguely dentate edge.

REMARKS: This genus of giant crabs, which had not been described as a fossil before, also occurs in the Miocene of Melbourne, Victoria, where it has been found in beds equivalent to the lower beds at Royal Park, Balcombian (specimen forwarded by Mr E. D. Gill, National Museum of Victoria) and in the Lower Pliocene of Adelaide, Aldinga and Surveyor's Point near Port Vincent, South Australia (Adelaide University collections).

Genus TUMIDOCARCINUS n. g.

TYPE SPECIES: *Harpactocarcinus tumidus* Woodward

DIAGNOSIS: A genus of the Xanthidae resembling *Harpactocarcinus* but differing in the strongly inflated shape of the carapace, the absence or slight development of antero-lateral marginal spines and the absence of tuberculation on the upper edge of the propodus of the cheliped. The differences from *Xanthopsis* are the greater length of the antero-lateral margin and the absence of elevated bosses on the carapace.

DISTRIBUTION: Middle Eocene (Bortonian)?, Upper Eocene (Kaiatan or Runangan) to Upper Miocene (Tongaporutuan) of New Zealand. Oligocene to Lower Miocene (Janjukian, Longfordian) of south-eastern Australia.

TAXONOMY: The great range in size of the representatives of this genus, its unusually long time range, and the obvious differences in the shape of the antero-lateral margin of the carapace suggest that more than one species is present in the available material. The fact that most of the Miocene specimens are about twice the size of the Oligocene individuals can hardly be due to accidents of preservation or collecting. It must be assumed that phylogenetic increase in size has taken place. It was not accompanied by any important change in the ratio of length to width of the carapace, which can be plotted as a straight line without significant deviations. There may be a slight change in the dorsal curvature of the carapace, but flattening of the fossils by compaction, with or without fracturing, makes it unsafe to use measurements of height, apart from the difficulty of exposing homologous points on the lower surface on which such measurements could be based.

A valid taxonomic distinction can be established on the distance between the frontal teeth. In one group of specimens the distance between the median teeth is less than that between the median and lateral teeth, while in the other group the teeth are approximately evenly spaced across the frontal margin. In addition, the regions of the carapace are not inflated in this second group, the median portion is flatter and the sub-marginal area is more steeply inclined. This group is confined to the Miocene. In the group with close-set median frontal teeth the regions may be slightly inflated, the carapace is more evenly vaulted, particularly in transverse direction, and the branchiostegites are less steeply inclined.

Another distinction can be based on the antero-lateral margin which is either granulate as in the type species or slightly dentate. All specimens with dentate margins come from the Lower Oligocene while specimens with granulated margins occur in the Eocene, Oligocene, and Miocene. All specimens with dentate antero-lateral margins belong to the group with close-set median frontal teeth. The forms with dentate and granulate margins co-exist in the Duntroonian Wharekuri Greensand of the Waitaki River (Oligocene). Their differences should be considered as specific, as there are no transitions from one type to the other such as would be expected in intra-specific variants, nor is there any suggestion of correlation with sex or age.

REMARKS: The typical species ranges from Eocene to Oligocene (Duntroonian). The Miocene species ranges from Lillburnian to Tongaporutuan. Unfortunately, no well preserved specimens are available from the interval between Waitakian and Clifdenian (higher part of Oligocene to lower part of Miocene). Only two specimens of *Tumidocarcinus*, which are not specifically identifiable, are available from the Altonian. They are:

DC 105, dactylus of a left chela, Otumahana S.D., Huia Stream, GS 4771, Altonian, coll. H. W. Wellman, 1948.

DC 186, fragments of female abdomen, third maxillipeds, a left cheliped, and pereiopods, without carapace. Komiti (= Pakaurangi) Point, Kaipara Harbour, GS 451, Altonian, coll. S. H. Cox 1880.

OCCURRENCE OF *Tumidocarcinus* IN AUSTRALIA: A well preserved specimen from Longford, Gippsland, near the type locality of the "Longford Substage" (Crespin 1943), which corresponds to the Awamoan to Altonian of New Zealand, is in the Museum of the Geological Survey of Victoria. The frontal and posterior margins of this specimen are somewhat crushed. It belongs certainly to *Tumidocarcinus tumidus*. The late Dr T. H. Withers compared this specimen and also one of the New Zealand Miocene specimens with the holotype of the species in the British Museum (Natural History) and considered them conspecific.

Other specimens from the Janjukian micaceous marls of the oil shaft at Lakes Entrance in Gippsland, Victoria, were described by Crespin (1947). The new species "*Harpactocarcinus*" *victoriensis* Crespin is based on the partly preserved carapace of the holotype and a paratype described as a carapace preserved chiefly as an internal mould. It is said to differ from "*H.*" *tumidus* in that the carapace is covered entirely with fine granulations. "There is also a difference in shape of the petalloid markings on the carapace of *H. victoriensis* (only visible on paratype) and *H. tumidus*. The area between the tips of the two petals are broadly V-shaped in the former and broadly U-shaped in the latter" (Crespin 1947, p. 22). These differences are due to the partly decorticated state of the Victorian specimens. Photographs show that only a thin layer of shell remains on the paratype. In the present material from New Zealand the attachment scars of the posterior gastric muscle are arranged, in internal moulds which are still covered with a thin layer of shell (e.g. DC 176) as in "*H.*" *victoriensis*, and on the outer surface of the carapace (e.g. the holotype, DC 205, or the Longford specimen) approximately as shown in Woodward's drawing (1876, pl. 7). Similarly, a slight decortication produces the impression of more even granulation. Actually, "*H.*" *tumidus* is granulated all over the carapace, the granulation being coarser on the posterior part. This can be seen in photographs of the Victorian specimens. As the front and posterior margin are not well preserved and the transverse curvature is not known, their relationship to *T. giganteus* cannot be ascertained.

Tumidocarcinus tumidus (Woodward)

Pl. 4, Fig. 1, 2; Pl. 6, Fig. 5, 6; Text Fig. 10

1876. *Harpactocarcinus tumidus* H. Woodward, Quart. J. geol. Soc. Lond. 32 : 51, pl. 7.
1882. *Harpactocarcinus tumidus* H. Woodward, A. McKay, N.Z. geol. Surv. Rep. geol. Explor. 1881, [14]: 74.
1912. *Harpactocarcinus tumidus* H. Woodward, P. Marshall, Handb. Region. Geol., vol. 7, pt. 1, H. 5, p. 24.
1914. *Harpactocarcinus tumidus* H. Woodward, F. Chapman, Australasian Fossils, p. 248, fig. 120c.
1917. *Harpactocarcinus tumidus* H. Woodward, J. Henderson, N.Z. geol. Surv. Bull. n.s. 18: 94.
1929. *Harpactocarcinus tumidus* H. Woodward, M. F. Glaessner, Foss. Catal., pt. 41, p. 206. (The age is here given as "Paleocene", an erroneous interpretation of statements in Woodward, 1876.)
?1947. *Harpactocarcinus victoriensis* I. Crespin, Proc. roy. Soc. Vict. 59: 21, pl. 4.

AGE AND OCCURRENCE OF THE HOLOTYPE: Woodward refers to the locality of the holotype, which is in the British Museum (Natural History), No. 59539, as Woodpecker Bay near Brighton, Ototaran Series. Hector (in Woodward, 1876, p. 53) refers to Seal Rocks, which lie off the south end of the bay. McKay's (1877, p. 111) and Hector's (1876, p. 53) accounts of the stratigraphic positions of the crabs collected show that they came from beds now known to be Runangan to Duntroonian in age, and McKay's specimen (DC 120) has been dated as Whaingaroan by Foraminifera (N. de B. Hornibrook, pers. comm.).

MATERIAL: 14 more or less well preserved specimens and several fragments, mostly chelipeds. (DC 120, 134, 138–9, 145, 151–2, 154, 156–8, 178, 196, 209, ?227 and one specimen from Canterbury Museum).

OCCURRENCE: Brighton, SW Nelson, Woodpecker Bay, GS 31 (DC 120) coll. A. McKay, 1874; Wharekuri, Waitaki River, GS 486, (DC 134, 138–9, 142, 145, 149, 151–2, 154, coll. A. McKay, 1880); Cobden S.D., Port Elizabeth Beach, GS 4873 (DC 156–8, coll. H. W. Wellman and M. Gage 1949); Fishing Rock, Wharekuri, Waitaki River, GS 1341 (DC 178, 196, coll. P. Marshall); coast ¼ mile north of Limestone Creek, Brighton S.D., GS 3676 (DC 209) coll. H. W. Wellman, 1945; Raincliff, South Canterbury (Canterbury Mus., coll. M. C. Gudex). "Cobden Limestone, Greymouth", GS 35 (DC 227, coll. A. McKay, 1873).

AGE: Bortonian-Kaiatan (Cant. Mus.), Runangan (DC 156–8), Whaingaroan (DC 120), Duntroonian; Middle Eocene ?, Upper Eocene, Lower Oligocene.

DESCRIPTION: Carapace large, strongly convex both in longitudinal and transverse direction, with the steepest declivity towards the front. The width of the frontal margin is about one-quarter of the width of the carapace. There are four stout, long, widely spaced frontal teeth, which are directed forward rather than downward. The distance between the median teeth is slightly less than that between the median and the lateral frontal teeth. The orbits are small, the supra-orbital margin is without fissures. The extra-orbital tooth is conical and strong. The antero-lateral margin is evenly curved, with a thickened, evenly granulated ridge. The lateral angle of the carapace is bluntly rounded. A slight indentation of the postero-lateral margin is often seen behind the lateral angle, due to the lateral extension of a rudimentary branchio-cardiac furrow crossing the margin. The postero-lateral margin is not marked by any ridge or keel; it is convex in dorsal aspect as well as in posterior view. A sharp ridge extends above the bases of the last pereiopods. The posterior margin is arched and indistinctly ridged.

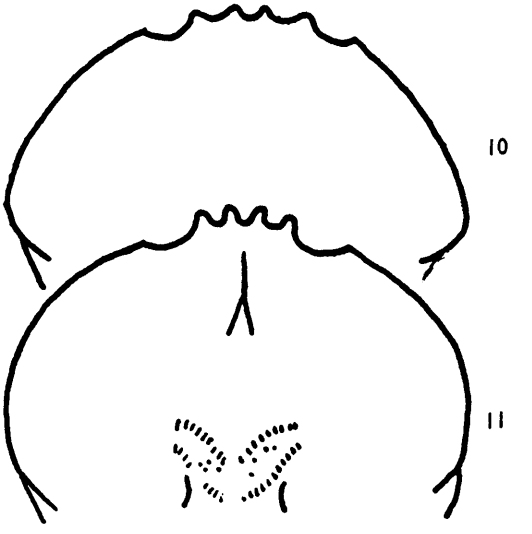


Fig. 10. *Tumidocarcinus tumidus*. Outline of anterior portion of carapace, showing front and orbits. (DC 156). Nat. size.

Fig. 11. *Tumidocarcinus giganteus*. Outline of anterior portion of carapace, showing front and orbits (DC 176). Nat. size.

The surface of the carapace is finely granulated along the frontal, orbital, and antero-lateral margins, finely pitted on the anterior half, and more coarsely granulated on the posterior half. The regions of the carapace are unmarked, except for the slightly inflated cardiac and metabranchial regions. Lateral urogastric furrows (in which the muscle impressions of the attractor epimeralis are situated), cardiac, and intestinal furrows are visible as depressed zones, posterior gastric and mandibular muscle attachments are also present as reticulate markings on the external and internal surface of the carapace but are not depressed. A wide, faintly depressed, transverse zone across the branchial regions in some specimens corresponds in position to the branchio-cardiac furrow. A shallow median groove may be present on and behind the front, particularly on internal moulds.

The sub-marginal area is wide, granulated, with a marked sub-hepatic swelling. The pterygostomes are narrow, with marginal granulated ridges. The sternum has smooth shallow grooves on the main segment separating papillate elevated areas. The first two male abdominal segments are very short, the third occupies the entire space between the bases of the last pereiopods, the last is the longest and ends in the middle of the main sternal segment.

The holotype is male, not female as Woodward had stated. The female abdomen is now known to be much wider throughout and much longer, extending between the first pereiopods and to the anterior margin of the sternum.

The chelae are very strong. In male individuals, the right chela is usually larger, as it is also in at least one female. In one or two specimens the left chela is larger. The propodus of the larger claw is inflated, with rounded upper and lower margins, which are convex in external view. The fingers are strong; the immovable finger is bent downwards. Its upper edge bears a row of strong teeth of which the first two have flattened crushing surfaces corresponding to similar flattened teeth on the long, curved dactylus. The other teeth vary in size and are pointed. The surface of the propodus is only faintly pitted, not granulated or ridged. The smaller chela is similar in the shape of the propodus and fingers but the teeth are apparently all sharp-edged.

The pereiopods are incompletely preserved. All meropodites are broadly oval in section. Those of the last pair are found normally lying above the preceding pair.

The holotype, of which an excellent plaster cast is available, shows clearly the granulate antero-lateral margin of the carapace. The frontal teeth are drawn in the type figure with the distance between the median teeth much less than that between median and lateral teeth. These teeth seem to have been damaged in the course of subsequent preparation. The carapace is evenly vaulted transversely. These observations show that the group possessing these characters, i.e., the Eocene to Lower Oligocene specimens with granulate antero-lateral margins, but not those with denticulate margins, represent the type species. The stratigraphically younger forms, which also have granulated margins but evenly spaced frontal teeth and a transversely flattened carapace and which reach much larger size, are here distinguished as a new species.

MEASUREMENTS (cast of holotype): Width 74 mm, length 70 mm, front 18 mm, orbits 8 mm, height of right propodus 30 mm, height of left propodus 20·5 mm.

Tumidocarcinus giganteus n. sp.

Pl. 5, Fig. 1, 2; Pl. 6, Fig. 1–4; Pl. 7, Fig. 1, 2; Text Fig. 11

MATERIAL: 14 specimens, mostly well preserved. DC 181 (holotype), DC 132–3, 176–7, 180–4, 187–8, 197–9, 205, 210, 225 (paratypes).

OCCURRENCE: Mimi S.D., GS 4660 (DC 132) coll. L. I. Grange, 1922; Gorge of Tangarakau River, North Island (DC 133); Rail and road cuttings, Mangaone Valley, Pouato S.D., Tangarakau District, GS 1422 (DC 176, 180, 187–8, 199, 210) coll. P. Marshall; east bank of Wanganui River about 12 miles below Taumarunui (DC 177, chela only) coll. F. D. Gemmel, 1925; Sect. 2B, Block 8, Maraekowhai, Pouatu S.D. (DC 181) coll. L. Bossard; Kohuratai District, Pouatu S.D. (DC 182) coll. H. A. Ellis; Tangarakau District (DC 183–4); Pouato S.D., Tahora, on road 6 chains north of accommodation house (DC 197) coll. L. I. Grange, 1923; Moki Road, Pouato S.D. (DC 198); Cliff at coast, 200 yards north of mouth of Dovedale Stream, north Canterbury (DC 205) coll. G. M. Smart, 1953; Patten Ck., 2 miles south of Mokihinui River (DC 225) coll. H. W. Wellman, 1946.

AGE: Lillburnian (DC 176, etc.) to Tongaporutuan (DC 225), Middle and Upper Miocene.

DIAGNOSIS: A species reaching a very large size, up to 138 mm length and 146 mm width of the carapace, with the larger chela up to 103 mm high; the carapace somewhat flattened transversely, with four frontal teeth evenly spaced; posterior margin of the carapace not marked by a granulated ridge.

DESCRIPTION: The carapace is similar in shape to that of *T. tumidus* but appears to be more flattened in the centre and the meta-branchial regions are slightly less inflated. The granulations on the surface of the carapace and on the antero-lateral margins are identical. The sub-marginal area slopes a little more steeply downward. The four frontal teeth are evenly spaced. The orbits and the posterior margin are as in *T. tumidus*. The right chela reaches an enormous size but resembles

the larger chela of the type species in shape of propodus and fingers. The finger tips are often coloured black; the rest of the shell is dark brown in some specimens and pale yellow in others.

MEASUREMENTS OF HOLOTYPE: Length of carapace 117 mm, width 22 mm, height 59·5 mm, distance between frontal teeth 9 mm, orbit 11 mm, height of right propodus about 61 mm, height of left propodus 32·4 mm. Height of right propodus of largest chela 103 mm.

Tumidocarcinus dentatus n. sp.

Pl. 6, Fig. 7, 8

MATERIAL: Seven mostly well preserved specimens, DC 143 (holotype), 135, 136, 140, 153, 185, one specimen in the Dominion Museum, Wellington, and one in the Adelaide University Geology Department collection.

OCCURRENCE: Wharekuri, Waitaki River, GS 486, coll. A. McKay, 1880.

AGE AND STRATIGRAPHIC DISTRIBUTION: Wharekuri Greensand, Duntroonian, Oligocene.

DIAGNOSIS: This species differs from *T. tumidus* in its denticulate antero-lateral margin of the carapace, the regions of which are slightly more pronounced and more convex, particularly on internal moulds.

DESCRIPTION: The antero-lateral margins of the carapace bear two short and wide tooth-like projections on each side, between the extra-orbital and the strong lateral teeth. From the lateral teeth a more or less pronounced ridge or buttress extends backward, ending on the epi-branchial swelling. The distance between the median frontal teeth is much less than that between the median and lateral frontal teeth. Apart from the greater inflation of the regions of the carapace, the ornamentation of its surface and of the abdomen and the characters of the appendages are as described for *T. tumidus*.

REMARKS: A comparison with *Xanthopsis quadrilobatus* (Desmarest) suggests that the epi-branchial swelling in *Tumidocarcinus* is homologous with the lateral tooth of *Xanthopsis*. The postero-lateral margin in *T. dentatus* is longer and less convergent backward than in *Xanthopsis* and the frontal dentation is also different.

MEASUREMENTS OF HOLOTYPE: Length of carapace not including frontal teeth 54·7 mm, width of carapace behind antero-lateral teeth 59·8 mm, width of front 15·2 mm, distance between median frontal teeth 4 mm, distance between median and lateral frontal teeth 5 mm, width of orbits 7·8 mm.

Family GONEPLACIDAE

Genus OMMATOCARCINUS White, 1852

TYPE SPECIES: *O. macgillivrayi* White

Ommatocarcinus arenicola n. sp.

Pl. 7, Fig. 3; Text Fig. 12b

MATERIAL: One specimen (internal mould), showing the entire carapace, part of the right cheliped and proximal parts of the pereiopods, preserved in sandstone. DC 155.

OCCURRENCE: Mt. Brown, Waipara River GS 66, coll. A. McKay.

AGE: Within the interval from Otaian to Waiauan, upper part of Oligocene to middle part of Miocene.

DESCRIPTION: The carapace is trapezoidal. The front is truncated, with a median notch and basal (inner orbital) notches. The supra-orbital margin is sinuous, convex over the greater part but laterally concave. It ends in a strong extra-orbital spine which is directed forward and outward, and which marks the greatest width of the carapace. The width of the front is between one quarter and one fifth of the width of the carapace. The antero-lateral margins are sub-parallel and end in a protuberance which is directed upward and outward. The postero-lateral margins converge. The posterior margin is wide and straight. The median part of the carapace is flat in side view, sloping forward more steeply and backward more gently. Between the lateral protuberances the surface of the carapace is perfectly flat. The regions of the carapace are not marked on the internal mould which is slightly abraded. A transverse elevated zone extends inward from the lateral protuberances and well defined lateral longitudinal crests are visible on the branchial regions in front of the bases of the last pereiopods. These crests diverge anteriorly.

The propodus of the right cheliped is long and slender. The fingers are not visible. In the first three periopods the merus is compressed; the carpus is short and rounded, with a distinct upper distal spine.

MEASUREMENTS: Length of carapace 22·4 mm, maximum width of carapace at base of extra-orbital spine 32·2 mm, width of front 7·3 mm, orbit about 11·5 mm wide, length of extra-orbital spine 3·7 mm, distance between bases of lateral protuberances 31·4 mm, length of posterior margin 12 mm.

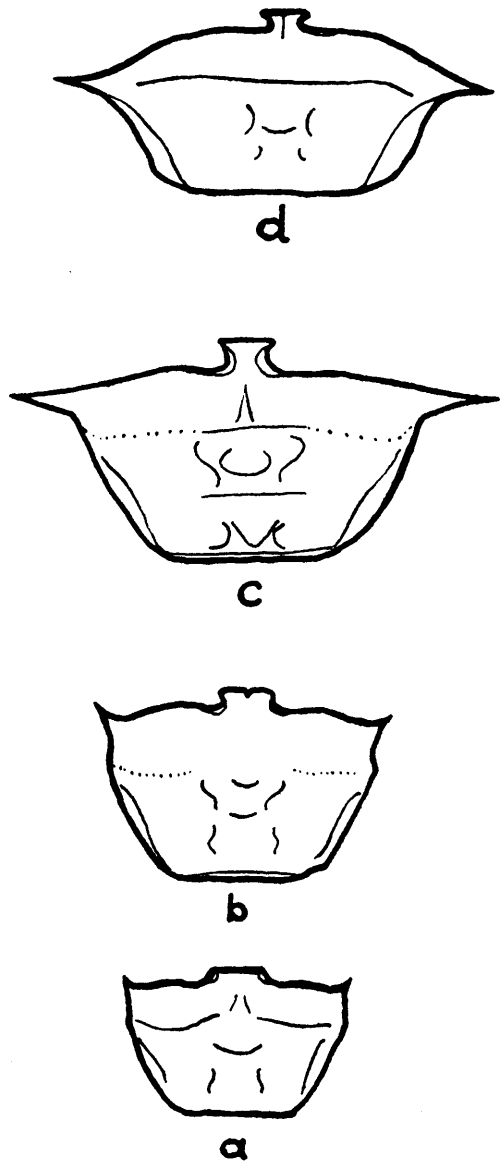


Fig. 12. Comparison of carapace shape in: a – *Goneplax rhomboides* (Linnaeus), b – *Ommatocarcinus arenicola* Glaessner, c – *O. corioensis* (Cresswell), d – *O. macgillivrayi* White. Nat. size. (a, after Bachmayer; b, drawn from holotype; c, specimen from the Miocene of Murgheboluc, Victoria, from the Cudmore Collection in the National Museum of Victoria; d, after White.

REMARKS: This species resembles *O. corioensis* (Cresswell) which is common in the Balcombian (Middle Miocene) of Australia, and the living species *O. macgillivrayi* White from Queensland and New Zealand and *O. pulcher* Barnard from East Africa. A comparison of the outlines of the carapace and claws in these species shows a gradation suggestive of an evolutionary lineage. The new species is closer in the shape of its carapace to the less specialised genus *Goneplax* Leach, but the front is more like that of *Ommatocarcinus*, to which the species is assigned as an early primitive form.

A small fragment of the distal part of a left propodus of a cheliped (DC 115) can be tentatively assigned to *Ommatocarcinus* sp. as it shows the distinctive outline and section of the claws of

this genus. It came from Oamaru S.D., Beach at Three Roads, GS 5665 (coll. M. Gage, 1947), and its age is Awamoan (uppermost Oligocene or Lower Miocene).

Genus GALENE de Haan, 1835

TYPE SPECIES: *G. bispinosa* Herbst

Galene proavita n. sp.

Pl. 7, Fig. 4, 5; Text Fig. 13

MATERIAL: A cephalothorax with male abdomen, right cheliped, and bases of pereiopods, with the front of the carapace damaged (holotype: DC 129, 130, 204); a cephalothorax with the shell partly preserved (DC 131); a fragmentary right cheliped (DC 121); a cephalothorax with right chela and leg fragments (DC 230); possibly also a complete carapace of a young specimen (DC 122). Coll. H. W. Wellman and G. W. Grindley (all except DC 230).

OCCURRENCE: Postal Creek, Oparara River, GS 4752 (DC 121–2); Otumahana S.D., Bellbird Stream, GS 4773 (DC 129–31, 204). The locality of DC 230 is unknown.

AGE: Clifdenian, Miocene.

DIAGNOSIS: A *Galene* with two weak antero-lateral lobes, transverse and longitudinal branchial crests, and very fine granulation of the carapace; chelipeds without tubercles.

DESCRIPTION: The carapace is wider than long, flat in the middle, sloping more strongly forward than backward or toward the sides. The front is wide; it was probably truncated but it is damaged. The orbits are small, the granulated supra-orbital margin has a single fissure. The antero-lateral margins are regularly curved. They are divided by a weak hepatic indentation into two lobes and end in a strong lateral spine, which is rounded in cross section and directed mainly laterally. The postero-lateral margins are long, straight, distinctly converging and finely granulated. The posterior margin is straight and ridged. Its length exceeds one-third of the width of the carapace, or one-half of it if the margins above the bases of the last pereiopods are included. The surface of the carapace is very faintly granulated. The regions are not clearly marked. The urogastric and cardiac regions are indicated by the attachment areas of the attractor epimeralis muscle; the anterior tip of the mesogastric tongue is faintly visible. There are two pairs of ridges on the carapace. A transverse pair extends in a slightly sinuous curve from the lateral spines towards the gastric regions, and a longitudinal pair extends from above the bases of the last pereiopods forward and slightly outward.

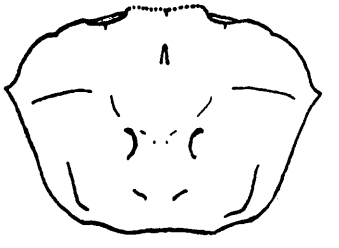


Fig. 13. *Galene proavita.* Restoration of carapace. Nat. size.

The sternum is faintly granulated, mainly in its anterior portion, and pitted. The abdominal segments are free, the second and third apparently reaching the bases of the last pereiopods. Their surface is smooth but shows widely spaced pits.

The chelipeds are strong, the carpus is triangular in dorsal view and finely granulated, with a strong, blunt, internal tooth. The propodus is strongly convex, particularly in the middle of the inner and outer surfaces, with its upper edge rounded and its lower edge flattened proximally but compressed distally. Both edges converge proximally, the dorsal margin is unornamented. The fingers have denticulate edges. The dactylus is longer than the distance from the carpal to the digital articulation. The pereiopods are strong, with compressed meropodites.

REMARKS: This form resembles *Pseudorhombila* as well as *Galenopsis* A. Milne Edwards. It differs from *Galenopsis typicus* A. Milne Edwards in the absence of a median post-frontal depression and of elevated epigastric regions, in the presence of longitudinal ridges on the branchial regions and of transverse ridges extending from the lateral spines. The lower margin of the propodus of the cheliped is straight and the fingers are long. The legs are strong. It differs from *Pseudorhombila patagonica* Glaessner, which it resembles in its outline and small orbits, in the absence of the strong antero-lateral teeth and in the presence of only one supra-orbital fissure. It also resembles *Carcinoplax*

H. Milne Edwards, particularly in its outline and the shape of its anterio-lateral margin, but in *C. antiquus* (Ristori) the antero-lateral tooth is stronger and the orbits are longer. The chelipeds are different in this genus. The new species differs from *Galene bispinosa* Herbst in the fine granulation of the margins of the carapace and of the chela, the absence of distinct antero-lateral teeth and in the weaker chelae of the male. These differences do not appear to exclude it from the genus *Galene*, which has been reported previously from the Miocene of Taiwan (Formosa) and from the Pliocene of Indonesia. It differs from *G. granulifera* Lin from the uppermost Miocene of Taiwan in its greater relative width, much wider front, and less strongly marked regions of the carapace.

MEASUREMENTS: Length of carapace 36 (28) mm, width 53 (38) mm, front 11·6 (9·5) mm, orbit 6·7 (5·2) mm, maximum length of chela and length of dactylus 23 mm, maximum height of chela 18 mm. The figures in parentheses refer to the paratype DC 131, the others to the holotype.

Family OCYPODIDAE

Genus HEMIPLAX Heller, 1865

Type species: *Cleistostoma ? hirtipes* Heller

Hemiplax hirtipes Heller

?1853. *Cleistostoma ? hirtipes* Jacquinot and Lucas, Voy. Pole Sud, Zool. vol. 3, Crust. p. 69.
1865. *Hemiplax hirtipes* Heller, Reise d. Novara, Crust., p. 40, pl. 4, f. 3.
1929. *Hemiplax hirtipes* (Jacquinot and Lucas), Chilton and Bennett, Trans. N.Z. Inst. 59: 759, (see discussion of authorship of this species).

MATERIAL: 23 specimens in concretions, in various stages of abrasion (Auckland Museum). One well preserved cephalothorax with fragments of legs, DC 173.

OCCURRENCE: Otago Harbour (raised beach); possibly also from Kaipara Harbour (DC 173).

AGE: Post-Pleistocene.

REMARKS: These specimens agree in all observable characters with the Recent species.

Hemiplax ? major n. sp.

Pl. 7, Fig. 6; Text Fig. 14

MATERIAL: One cephalothorax with the front and antero-lateral margins of the carapace damaged, parts of pereiopods and chelipeds preserved (DC 229, holotype); one fragmentary carapace (DC 228) (coll. C. A. Fleming and M. T. Te Punga); two specimens showing fragments of the ventral side and claws (DC 237, coll. C. A. Fleming).

OCCURRENCE: Pakihikura Bridge, Rangitikei River, GS 4191 (N139/502).

AGE AND STRATIGRAPHIC POSITION: Lateral equivalent of Mangahou Siltstone, 80 ft below Pakihikura Tuff. Upper Nukumaruan, Lower Pleistocene.

DESCRIPTION: This species resembles closely *H. hirtipes* but it grows to a much larger size and its

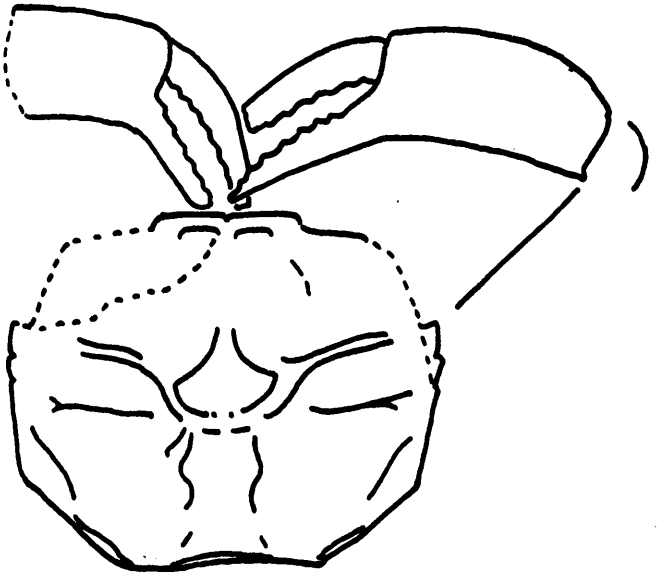


Fig. 14. *Hemiplax major*. Partial restoration, based on all available specimens. Antero-lateral margins not preserved and not restored.

carapace is narrower. The ratio of length to width is 1 : 1·5 in *H. hirtipes* and 1 : 1·2 in *H. major*. The extra-orbital tooth is not preserved but the two following antero-lateral teeth are like those of *H. hirtipes* in shape and position. The regions of the carapace are also similar, and so are the proportions of the chelae and the angle at which the immovable finger of the left chela diverges from the lower edge of the propodus.

MEASUREMENTS: Width of carapace 52 mm, length 42 mm, width of front about 20 mm, length of propodus of right cheliped to base of dactylus 30 mm, maximum height of chela 16 mm.

REMARKS: The poor preservation of these specimens makes their identification somewhat uncertain, but it seems worth while to draw attention to the occurrence in the Pleistocene of a large crab resembling *Hemiplax* that appears to be unknown in the living fauna of New Zealand.

A poorly preserved cephalothorax of a small crab, about 14 mm long and 20 mm wide, was found in the Waitotaran (Pliocene) of Matarua Creek, Mangahao S.D. (GS 2811, DC 212), coll. J. Marwick, 1942. It has been tentatively identified as *Hemiplax* sp.

PALEO-ECOLOGICAL OBSERVATIONS

A discussion of the ecology of the fossil decapod Crustacea based entirely on museum specimens can hardly be satisfactory. A careful investigation of the relations of these fossils to the sediment and to other elements of the fauna is required and must be based on field observations. No such observations have been made on the fossil decapod Crustacea of New Zealand. Some casual observations made in the course of their systematic study are, however, thought worth recording.

An extraordinary assemblage of crustacean remains from Waiau-ua River (DC 159–169, coll. J. Buchanan, 1867), of Tertiary age, consists of hundreds of fragments of legs of decapoda, most likely pagurids, together with a few carapace fragments of *Cancer*. They are preserved in a hard concretionary nodule, which also contains scattered but complete small molluscan shells. This assemblage of fossil remains suggests the remnants of a meal of a crab-eating animal, possibly a seal. In my experience it is unique.

Another unique occurrence is the preservation of several specimens of *Leptomithrax atavus* with the median portion of the carapace covered with balanid barnacles. The completeness of the skeletons of some of these individuals suggests that they carried the barnacles when alive, as many spider crabs carry Anthozoa, Bryozoa, or sponges attached to their backs.

The abundance of *Tumidocarcinus* is remarkable, particularly as it corresponds to similar occurrences of the apparently related genus *Xanthopsis* in the Eocene and Oligocene. Formations containing it have often been referred to as "crab-beds" by field geologists.

The occurrence of fossil crabs in concretions is not uncommon though not fully explained. The concretions containing *Raninoides* and *Portunites* in the Snowdrift Quarry, Clarendon, Otago, are found as pebbles in a basal conglomerate of Duntroonian (Oligocene) age, derived from the Bortonian (pers. comm. from Dr C. A. Fleming, based on H. W. Wellman's field observations). Other crabs belonging to *Callianassa*, *Tumidocarcinus* and *Leptomithrax* are also preserved in concretions, and so are the subfossil *Hemiplax*.

STRATIGRAPHIC DISTRIBUTION AND FAUNAL RELATIONS

MESOZOIC

The few available Mesozoic decapod Crustacea give no more than a very small sample of the fauna that must have existed at that time.

	N.Z. Stage	Standard Stage	Fauna
U. Cret.	Haumurian	Maestrichtian	*Callianassa waikurana*, *C.* sp. a.
U. Jur.	Ohauan Heterian	L. Tithonian L. Kimmeridgian	*Mecochirus* ? sp. *Mecochirus marwicki*
L. Jur.	..	..	*Glypheopsis antipodum*

The three known genera are well known elements of the respective Mesozoic faunas of other parts of the world, and their occurrence in New Zealand, though it extends their geographic range, was not unexpected.

CAINOZOIC

The distribution of decapod Crustacea in the Cainozoic, shown in Table 1, is based on the now generally accepted division of that stratigraphic interval into regional stages. No Tertiary decapods older than Bortonian are known and the earlier stages are therefore omitted. Correlation of the regional stages with the stages of the standard European time scale is still to some extent uncertain. General agreement exists about the placing of the Bortonian in the Middle Eocene, the Kaiatan and Runangan in the Upper Eocene, and the Whaingaroan to Otaian in the Oligocene, but there is little evidence for more detailed correlation. Divergent opinions still exist on the placing of the six stages from Hutchinsonian to Waiauan. Modern micropaleontological work on the pelagic and larger Foraminifera is providing a new basis for inter-regional correlation, but the foundations have not yet been securely laid in Europe where the standard scale of stages was first developed. It seems best, therefore, to indicate the possible range of datings based on various lines of argument by placing the New Zealand scale against the European scale according to Hornibrook's work (1958), which appears to give the earliest datings compatible with available evidence, as well as against another scale based on the work of Drooger (1956) and others, which gives the youngest possible ages for the stratigraphically important microfossils on which tentative correlations can be based.

Eocene to Oligocene

The Eocene-Oligocene fauna is dominated by *Tumidocarcinus tumidus*, which occurs in considerable numbers, ranging from Middle or Upper Eocene well into the Oligocene (Duntroonian), where it is accompanied by *T. dentatus*. In the Bortonian, *Laeviranina perarmata* is associated with *Portunites granulifer*. This association is not uncommon in the Lower Tertiary. Different species represent it in the Lower Eocene London Clay and in the Middle and Upper Eocene of Hungary. It occurs also in the Eocene and Oligocene of the Pacific coast of North America (Oregon and Washington). In the Oligocene, *Laeviranina* was replaced by its descendant *Raninoides*. *Raninoides* ? *araucanus* (Philippi) and *Portunites* ? *araucanus* (Philippi) were described from the late Oligocene or early Miocene of Chile. *Tumidocarcinus* occurs outside New Zealand only in Australia. As it is a conspicuous and relatively common fossil, its absence from the well known European and American Tertiary faunas cannot be due to accidents of collecting or preservation. It must be recognised as an endemic element of the regional fauna, probably derived from the widespread *Xanthopsis* stock. It would be surprising indeed if no further endemic decapod Crustacea were to be found in the Lower Tertiary of the New Zealand region.

Late Oligocene to Miocene

Tumidocarcinus survives into the Miocene, evolving by size increase and other minor changes into *T. giganteus*. The details of this change are obscured by the absence of this genus in the interval from Waitakian to Clifdenian, with the exception of fragmentary specimens from the Altonian. The few Australian specimens come from the "Janjukian" Lakes Entrance Formation of Gippsland (Oligocene) and probably from the Longford Limestone (Lower Miocene).

There are other links between the New Zealand and Australian Oligocene to Miocene decapod faunas, but as the study of the Australian fauna is still in progress, they can be indicated only in general terms.

Lyreidus occurs in the Gambier Limestone at Mt. Gambier, South Australia (late Oligocene to early Miocene), *Pseudocarcinus* is found in the Balcombian and Lower Pliocene, and *Ommatocarcinus* is widely represented by the species *O. corioensis* in the Balcombian (probably equivalent

of the Clifdenian). Two elements of the New Zealand Miocene fauna are unknown from the Australian Tertiary. They are *Galene* and *Leptomithrax* (and in addition *Jasus*, the preservation of which must be considered quite exceptional). *Calappa* is common in the Australian and European Miocene but not known from New Zealand.

Pliocene to Pleistocene

In the Pliocene and Pleistocene we find remains of a different assemblage, which is distinguishable from the living fauna only by comparatively minor changes in some species. A new and apparently extinct species represents the genus *Hemiplax* in the Nukumaruan (Lower Pleistocene), and this genus and also *Ovalipes* are represented in the Pliocene by forms that cannot be assigned to the living species. *Cancer novaezealandiae* and *Ctenocheles maorianus* are represented by fragmentary material, which, if it does not prove the identity of the fossil with the recent species, at least does not indicate significant differences. The first-named species occurs in the Pliocene and Pleistocene, the second appears to be represented in the Upper Pleistocene. The genus *Ctenocheles* occurs in the Australian Miocene and Upper Eocene. After this work had been completed, Mr J. C. Yaldwyn forwarded a specimen of *Paramithrax minor* Filhol from the Castlecliffian of Castlecliff, Wanganui (Dominion Museum). This species occurs living in Australian and New Zealand waters.

TABLE 1. Stratigraphic Distribution of Tertiary Decapod Crustacea in New Zealand

PLEISTOCENE			WANGANUI	Castlecliffian	*Ctenocheles* cf. *maorianus*, *Cancer novaezealandiae*, *Ovalipes* cf. *punctatus*, *Paramithrax minor*
				Nukumaruan	*Cancer novaezealandiae*, *Hemiplax major*, indet. chelae
PLIOCENE				Waitotaran	*Ovalipes* sp., *Hemiplax* sp., *Cancer novaezealandiae*
				Opoitian	*Cancer novaezealandiae*, *Leptomithrax ririangi*
MIOCENE	Sarmatian	Sarmatian	TARANAKI	Kapitean	*Leptomithrax atavus*, *Pseudocarcinus* sp.
				Tongaporutuan	*Callianassa* sp. b, *Tumidocarcinus giganteus*, *Leptomithrax uruti*
	Tortonian	Tortonian	SOUTHLAND	Waiauan	*Tumidocarcinus giganteus*
		Helvetian		Lillburnian	*Tumidocarcinus giganteus*
	Helvetian	Burdigalian		Clifdenian	*Galene proavita*
		Aquitanian		Altonian	*Jasus flemingi*, *Lyreidus elegans*, *Tumidocarcinus* sp.
	Burdigalian		PAREORA	Awamoan	*Ommatocarcinus* sp., indet. chelae
	Aquitanian			Hutchinsonian	*Menippe* sp.
				Otaian	*Callianassa awakina*
OLIGOCENE			LANDON	Waitakian	Indet. chelae
				Duntroonian	*Tumidocarcinus tumidus*, *Tumidocarcinus dentatus*
				Whaingaroan	*Tumidocarcinus tumidus*
UPPER EOCENE			ARNOLD	Runangan	*Tumidocarcinus tumidus*, indet. chelae
				Kaiatan	? *Tumidocarcinus tumidus*, indet. chelae
MIDDLE EOCENE				Bortonian	*Laeviranina perarmata*, *Portunites granulifer*, ? *Tumidocarcinus tumidus*, *Callianassa* sp.

SUMMARY OF THE HISTORY OF THE DECAPOD CRUSTACEA OF NEW ZEALAND

Not enough is known of the Mesozoic decapod fauna of New Zealand to distinguish it from that of other regions. From early Tertiary time we find characteristic features that gradually approach some of the distinctive characters of the present fauna. The still small number of these fossils gives us only a vague outline of faunal history but this seems worth recording. The characteristic widespread genera of the warm nummulitic seas (*Lophoranina*, *Harpactocarcinus*, *Xanthopsis*) are absent. The occurrence of the large extinct xanthid genus *Tumidocarcinus* in the Eocene to Miocene of New Zealand and in the mid-Tertiary of Australia gives the first indication of a distinctive zoogeographical province. In the Miocene we find ancestral forms of several genera that occur at present in the Indo-Pacific Region (*Ommatocarcinus*, *Lyreidus*, *Galene*). The last-named genus is no longer present in New Zealand waters. The fossil species representing the other genera are probably ancestral to some species now living in the New Zealand area. These forms could thus be considered as endemic.

Another characteristic element of the present New Zealand fauna, the oxyrhynchous crab *Leptomithrax*, is shown to be endemic, at least since late Tertiary time, by its appearance in the Upper Miocene. The earlier history of the Oxyrhyncha is obscure, few of their fossil representatives having been compared in sufficient detail with living genera. The known Pliocene and Pleistocene crabs appear to have differed from living forms only to a minor degree, but it is noteworthy that at least one Pleistocene species of the genus *Hemiplax* appears to have become extinct.

The Tertiary decapod Crustacea from Fiji as described by Rathbun have nothing in common with those now known from New Zealand (with the exception of a species of *Menippe* in the Pliocene).

PART 2. EVOLUTION AND TAXONOMY OF THE DECAPOD CRUSTACEA

There is general agreement that the classification of a group of organisms should reflect their genetic relations as far as these can be deduced from their morphology. Characters believed to indicate closer or more remote relationships are selected for comparison, and their development in different groups is interpreted as more primitive or more advanced. In the zoological classification of decapod Crustacea such characters are often selected from structures of the mouth parts and antennae, the gills, and the other appendages. The paleontologist contributes one criterion of incontestable significance, the appearance of various taxa in time, and adds extinct taxa that must be considered and placed in the system. He uses different characters as the basis for classification if those used in zoology (e.g. gills) are not preserved in fossils. This, however, does not place the fossils outside the zoological system but simply introduces additional characters, which may be less convenient in zoological classification but which are not necessarily less significant genetically and taxonomically and must be integrated in the general systematics of the group.

In fossil decapod Crustacea the carapace and abdomen are most frequently preserved and show significant patterns, also the chelae of crabs and lobsters, and often the rostral, antennar and mouth parts. Unfortunately, these parts are often thoughtlessly destroyed in collecting or preparation by inexperienced workers, or they are left unexposed in the matrix and undescribed in published specimens. This leaves the characters of the carapace and abdomen as the main sources of information on the genetic relations of the decapod Crustacea of the past. The evolution of these parts of the skeleton can be demonstrated by the sequence of fossils in time and by their morphological analysis. The results of the placing of fossils in their proper relationship with living forms are often surprising. The ingenious and detailed "proof" of the origin of crabs from homarid lobsters (presented by Bouvier, 1897) was shown to be baseless by the discovery of a morphological sequence from extinct Triassic Macrura to extinct primitive Liassic Brachyura that existed before either the supposed ancestor or its supposed descendant had appeared on the scene. The separation of the living Raninidae from other crabs, carefully argued by Bourne, conflicts with the fact that their ancestry can be traced to Lower Cretaceous crabs that are very close to Oxystomata. They may belong to the Family Calappidae, though this family later evolved adaptations different from those of the Raninidae.

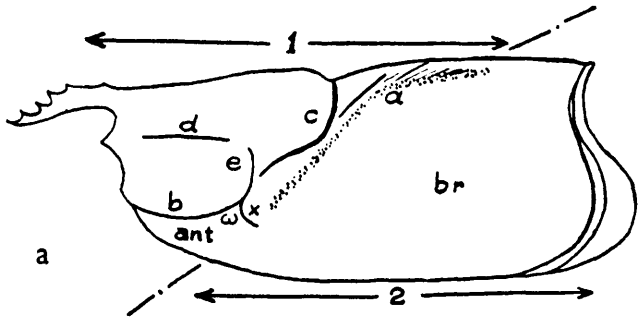
The reluctance of some systematic zoologists to relinquish traditionally established systems for the shifting grounds of evolutionary paleontology is understandable, but it must be challenged by paleontologists making thorough comparative morphological studies of both fossil and living material.

EVOLUTION OF THE CARAPACE

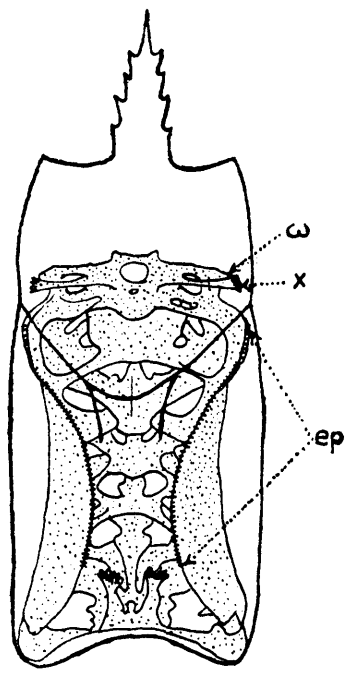
THE CARAPACE AND THE INTERNAL SKELETON

In the decapod Crustacea five segments of the head and eight segments of the thorax form a cephalothorax. It is covered by the carapace (fig. 15), which is an extension of the dorsal integument of the head. Its flanks form the external cover of the branchial chamber and are referred to as the branchiostegite. Externally, only the appendages show the position of the original segments, but internally the head is not entirely fused with the thorax. The cephalic portion of the integument overgrows the thoracic portion dorsally and some or all of the thoracic tergites are lost. The thorax segments are crowded together dorsally in a reduced space between the posterior boundary of the

head and the first abdominal somite. The thoracic sternites and the lateral portions of the thorax integument form parts of the endoskeleton and remain functional, serving as attachments of the muscles and as supports for the articulation of the thoracopods and their branchial appendages. The first three pairs of thoracopods are developed as maxillipeds and are somewhat reduced in size. The remaining pairs form pereiopods (including chelipeds) and their size, particularly that of the first pair, is increased. The differentiation in the relative sizes of their basal joints and muscles affects directly the corresponding parts of the remaining thoracic skeletal elements and indirectly the carapace. The strengthening of the anterior pereiopods, outweighing the small reduction of the



a



b

Fig. 15. Relations of carapace and internal skeleton in the lobster, *Homarus vulgaris*.
a – lateral view of carapace. 1, cephalic portion; 2, thoracic portion; ant, anterior chamber; br, branchiostegite; a, branchiocardiac furrow; c, post-cervical furrow; e, cervical furrow; b, antennal furrow; d, gastro-orbital furrow; ω, projection covering mandibular joint; x, area of attachment of "adductor testis" muscle (internal).
b – diagrammatic dorsal view of internal skeleton, with outline of carapace. ep, dorsal edge of epimeral fold, with attachment of attractor epimeralis muscle shown by cross hatching; x, calcified portion of adductor testis muscle; ω, mandibular articulation.

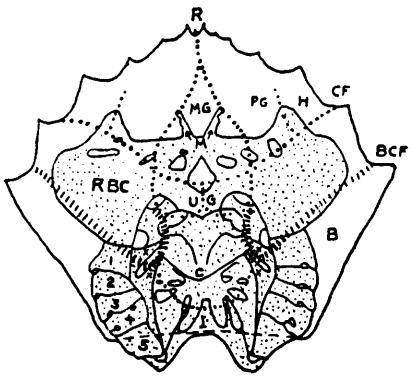


Fig. 16. Relations of carapace and internal skeleton in the crab *Dromia*. R, rostrum; CF, cardiac furrow; BCF, branchio-cardiac furrow; M•mandibular supports; RBC, anterior roof of branchial chamber (inclined forward and inward); 1–5 endopleurites corresponding to pereiopods. The attachment of the attractor epimeralis muscle to the carapace is indicated diagrammatically by cross hatching. From its anteriorly directed median parts the muscle fibres extend obliquely downward and backward to the four projections (x) of the endoskeleton; from its lateral parts they extend downward to the crest of the branchial roof (postero-lateral parts of branchial chamber walls not shown). Major regions of the carapace outlined by dotted lines. MG, mesogastric; UG, urogastric; C, cardiac, I, intestinal; B, branchial; PG, protogastric; H, hepatic. Redrawn from Glaessner, 1933.

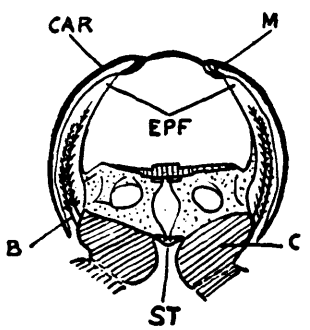


Fig. 17. *Astacus fluviatilis*. Transverse section of cephalothorax. CAR, carapace; ST, sternum; B, branchiae; C, coxa of pereiopod; EPF, epimeral fold; M, attractor epimeralis muscle. After Netz, redrawn from Glaessner 1933.

maxillipeds, tends to push the anterior ventral border of the thorax forward, reducing the space occupied by the posterior cephalic somites and, at the same time, increasing the size of the branchial chamber.

The existence of more or less distinct "regions" delimited by furrows on the surface of the carapace of decapod Crustacea (fig. 16) and certain relations of these regions to the position of internal organs were recognised by the earliest observers (Desmarest, H. Milne Edwards, and others). When it was found that these relations were only very general and superficial, efforts were made to establish homologies between these sculptural elements of the carapace as developed in different families and genera, without reference to the internal structure of the cephalothorax (Boas 1880, Bouvier 1897, Van Straelen 1925). Such attempts were not altogether successful as it was impossible to recognise in this manner parallel or convergent evolution that led to similar surface patterns in different phyletic groups. Moreover, the true nature of the carapace in Decapoda and in Malacostraca generally, was often misunderstood.

The simplest part of the carapace is the *branchiostegite*, which covers the flanks of the thorax and the gills. Its ventral and posterior margins are free. Its boundary against the median portion of the carapace is marked by the *branchio-cardiac furrow*. A band of muscles follows this furrow. Schmidt (1915) has shown in his studies on *Astacus fluviatilis* that this is the *attractor epimeralis* muscle connecting the carapace with the internal skeleton, i.e., with the upper margin of the epimeral fold (fig. 17). This parallelism between a furrow and a muscle band led some authors to the wrong generalisation that the furrows of the carapace in Decapoda are generally connected with muscles or "membranes".

No furrows can exist behind the branchio-cardiac furrow because a smooth internal surface of the branchiostegite is essential for the free circulation of water in the gill chamber. For the same reason no muscles can be attached to the branchiostegite.

The anterior end of the branchiostegite is formed by a small triangular convex area approaching with its anterior pointed end the base of the antenna. It does not cover any gills, but in the Macrura it protects the epipodite or scaphognathite of the maxilla, the swift movements of which expel the water from the gill chamber. An arched furrow (designated by Bouvier as "*sillon inférieur*" or "i") often marks the boundary between this *anterior chamber* and the gill chamber.

The attachment areas of muscles are recognisable on the inner surface of the carapace in all decapod Crustacea by their fine reticulation. On the external surface these areas are often slightly depressed but in some cases they are elevated. The most important groups of muscles attached to the carapace are the attractor epimeralis, mandibular, gastric, and a small portion of the thoraco-abdominal muscles. The muscles of the thoracic appendages are attached to the internal skeleton and do not reach the carapace.

Among the *mandibular muscles* the most important are the *adductor posterior* and the *adductor lateralis mandibulae*. There is considerable variation in the development of these muscles. In the genera *Astacus*, *Homarus* and *Palinurus* the posterior muscle is very strong, its area of attachment covering a considerable part of the lateral internal surface of the carapace in front of the main transverse furrow. In the Brachyura and Galatheidea this muscle is very weak and the lateral adductor muscle which is attached to the antero-lateral wall of the carapace occupies more space on its surface.

Of all the numerous external gastric muscles (Mocquard, 1883) only the group of the *gastricus posterior* is attached to the carapace. As a rule it is connected with two small calcareous projections of its internal wall (apodemes) close to the median line and recognisable from the outside as a pair of minute pits. The anterior gastric muscles are attached to the lower surface of the rostrum or, in the Brachyura, to small flat calcareous projections situated underneath the epigastric regions of the carapace.

One bundle of fibres of the *thoraco-abdominal muscles* reaches the inner surface of the carapace on each side. It is attached near the posterior margin of the carapace, between the median line and the attractor epimeralis. In the Brachyura the external swelling corresponding to its area of attachment is known as the "intestinal region".

The rudimentary *adductor testis* muscle (formerly described as "dorsoventralis posterior", Grobben, 1917) is important for the study of homologies of furrows on the carapace of the Decapoda. It can hardly be of any functional value. Grobben considered it as the muscle that in primitive Malacostraca effected the closing of the bivalved carapace, but Siewing (1956, p. 144) is uncertain about this homology. However that may be, this muscle was not affected by any further adaptive modifications or changes in relative position. It is a narrow transverse band connecting a projection of the fused sternal segments of the cephalon with the lateral wall of the carapace. This area of attachment has a definite relation to the position of the attractor epimeralis and to the branchio-cardiac furrow. The epimeral fold of the internal skeleton of the thorax, which forms the gill chamber, ends near the bases of the first thoracic appendages, and so does the attractor epimeralis, which is attached to the crest of this fold. The endosternite of the second maxilla lies anteriorly to the epimeral fold. Its external margin is bent downward so that together with the overlapping portion of the carapace it forms the roof and outer wall of the "anterior chamber" (see p. 38). The transverse adductor muscle is found just above this endosternite. Its attachment area lies in the obtuse angle between the obliquely rising epimeral fold and the horizontal roof of the anterior chamber. Where the furrows on the carapace are well developed it is visible externally, in the obtuse angle between the branchio-cardiac furrow and its lowest anterior branch, i, which marks off the vaulted outer wall of the anterior chamber.

In many Macrura the anterior part of the carapace possesses another important feature, which can be used as a point of reference in establishing homologies. This is a peculiar knob, which was noticed by Boas and referred to by this author as ω. It is easily seen that this knob marks the position of the external mandibular joint. This is formed by a heavily calcified hook of the endosternite of the mandibular segment articulating with a projection of the mandibula.

MORPHOLOGY AND EVOLUTION OF THE CARAPACE FURROWS

The various furrows on the carapace of the Decapoda are not equal in their morphological significance. Three of them are of the greatest importance in phylogeny and classification. They are referred to as *transverse furrows*, and the terms *cervical*, *post-cervical* and *branchio-cardiac* are applied to them. In the letter notation of carapace furrows that was introduced by Boas (1880) and modified, not altogether successfully, by Bouvier (1897) and van Straelen (1925), e-e_1 is the cervical, a (and b_1, formerly "hepatic") the branchio-cardiac, and c the post-cervical furrow. The following subsidiary furrows were also included in the letter classification: d – gastro-orbital, b – antennal, i – inferior. Some subsidiary furrows apparently originated as depressions between convex areas of the carapace. They were formed independently, either to accommodate large masses of muscle such as the adductor lateralis mandibulae, or to fit over the cylindrical basal joints of the antennae, or simply as a means of strengthening the carapace. A conspicuous triangular sulcus surrounds the mesogastric region in *Pemphix*, many Brachyura, and many Galatheidea. It is faintly marked in some Thalassinidea and Glypheidea. A taxonomic unit (Section Gastralida) was proposed for those groups in which the mesogastric sulcus is well developed (Beurlen and Glaessner 1930) but later work indicated that it is not a consistently important character.

The carapace furrows should not be confused with the "lineae". The latter are more or less straight, weakly calcified, narrow zones of the carapace of some decapods. Lineae are developed in some Penaeidea (*Parapenaeus*, *Carpopenaeus*), Thalassinidae ("*linea thalassinica*"), Paguridae, Galatheidae ("*linea anomurica*") and Homolidae, "*linea homolica*". They are independent of the furrows and regions and extend from the anterior to the posterior margin of the carapace. It is certain that they facilitate moulting; the median suture of the Nephropsidae, Glypheidea, and Pemphicidae and the pterygostomial suture of the Brachyura are therefore also "lineae". Their homology is uncertain and it is probable that they were acquired independently in different lineages. They indicate a remarkable reappearance in the decapod skeleton of the "facial sutures" of the trilobites.

Fig. 18. Evolution of the carapace in Nephropsidea

1. *Lissocardia silesiaca* H. v. Meyer. Triassic. After Assmann.
2. *Eryma bedelta* (Quenstedt). Jurassic. After Woods.
3. *Klytia ventrosa* H. v. Meyer. Jurassic. Original drawing.
4. *Enoploclytia leachi* (Mantell). Cretaceous. After Mertin.
5. *Palaeophoberus suevicus* (Quenstedt). Jurassic. After Glaessner.
6. *Hoploparia longimana* (Sowerby). Cretaceous. After Woods.
7. *Paraclytia boetticheri* Mertin. Cretaceous. After Mertin.
8. *Palaeohomarus hemprichi* Mertin. Cretaceous. After Mertin.
9. *Homarus vulgaris* H. Milne Edwards. Recent. Original drawing.
10. *Nephrops norvegicus* L. Recent. Original drawing.
11. *Astacus fluviatilis* Fabricius. Recent. Original drawing.

Fam. Erymaidae: 1–4. Fam. Nephropsidae: 5–10. Fam. Astacidae: 11.

For explanation of letters see text. In drawings from previously published figures these letters have been added.

Fig. 19. Evolution of the carapace in the Glypheocarida (Glypheidea + Pemphicidea), Anomocarida (Caridea + Thalassinidea + Paguridea), Palinura (Eryonidea + Scyllaridea) and Brachyura (Dromiacea).

1. *Pseudoglyphea spinosa* (Assmann). Triassic. After Assmann.
2. *Litogaster tiefenbachensis* Assmann. Triassic. After Assmann.
3a. *Pseudopemphix albertii* (H. v. Meyer). Triassic. After Glaessner.
3b. *Pseudopemphix fritschi* Wüst. Triassic. After Scheffen.
4a, b. *Pemphix sueuri* (H. v. Meyer). Triassic. After Glaessner.
5. *Mecochirus longimanatus* (Schlotheim). Jurassic. Modified after Beurlen and van Straelen.
6. *Meyeria ornata* (Phillips). Cretaceous. After Woods.
7. *Paraglyphea prestwichi* (Carter MS, Woods). Jurassic. After Woods.
8. *Glypheopsis cretacea* (McCoy). Cretaceous. After Woods.
9. *Magila latimana* Oppel. Jurassic. After Oppel.
10. *Schlueteria tetracheles* Fritsch. Cretaceous. Reconstruction, from holotype.
11. *Gebicula exigua* Alcock. Recent. After Alcock.
12. *Alpheus malleodigitatus* Bate. Recent. After Coutière.
13. *Coenobita perlata* H. Milne Edwards. Recent.
14a, b. *Eocarcinus praecursor* Withers. Jurassic. After Withers.
15a, b. *Prosopon mamillatum* H. Woodward. Jurassic. After Withers.
16. *Homolopsis edwardsi* Bell. Cretaceous. Reconstruction, from topotype.
17. *Dromiopsis rugosa* (Schlotheim). Danian. From topotype.
18. *Tetrachela raiblana* Glaessner. Triassic. After Glaessner.
19. *Eryon* sp. Jurassic. After Woods.
20. *Polycheles andamanensis* Alcock. Recent. After de Man, from van Straelen.
21. *Palaeopalinurus glaessneri* Bachmayer. Jurassic. Reconstruction, from holotype and paratype specimens. The unornamented areas believed to represent carapace furrows are marked by stippling.

22a, b. *Palinurus vulgaris* Latreille. Recent. Original drawings.

For explanation of letters see text. In drawings from previously published figures, these letters have been added or altered.

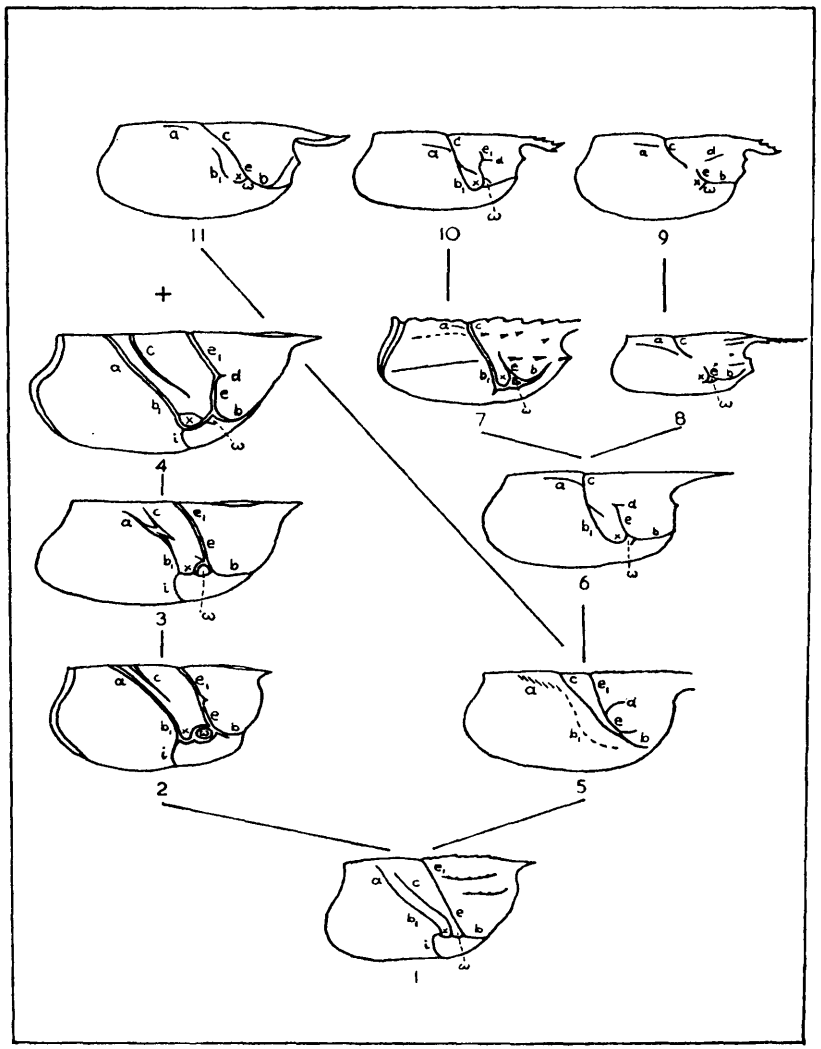


Fig. 18.

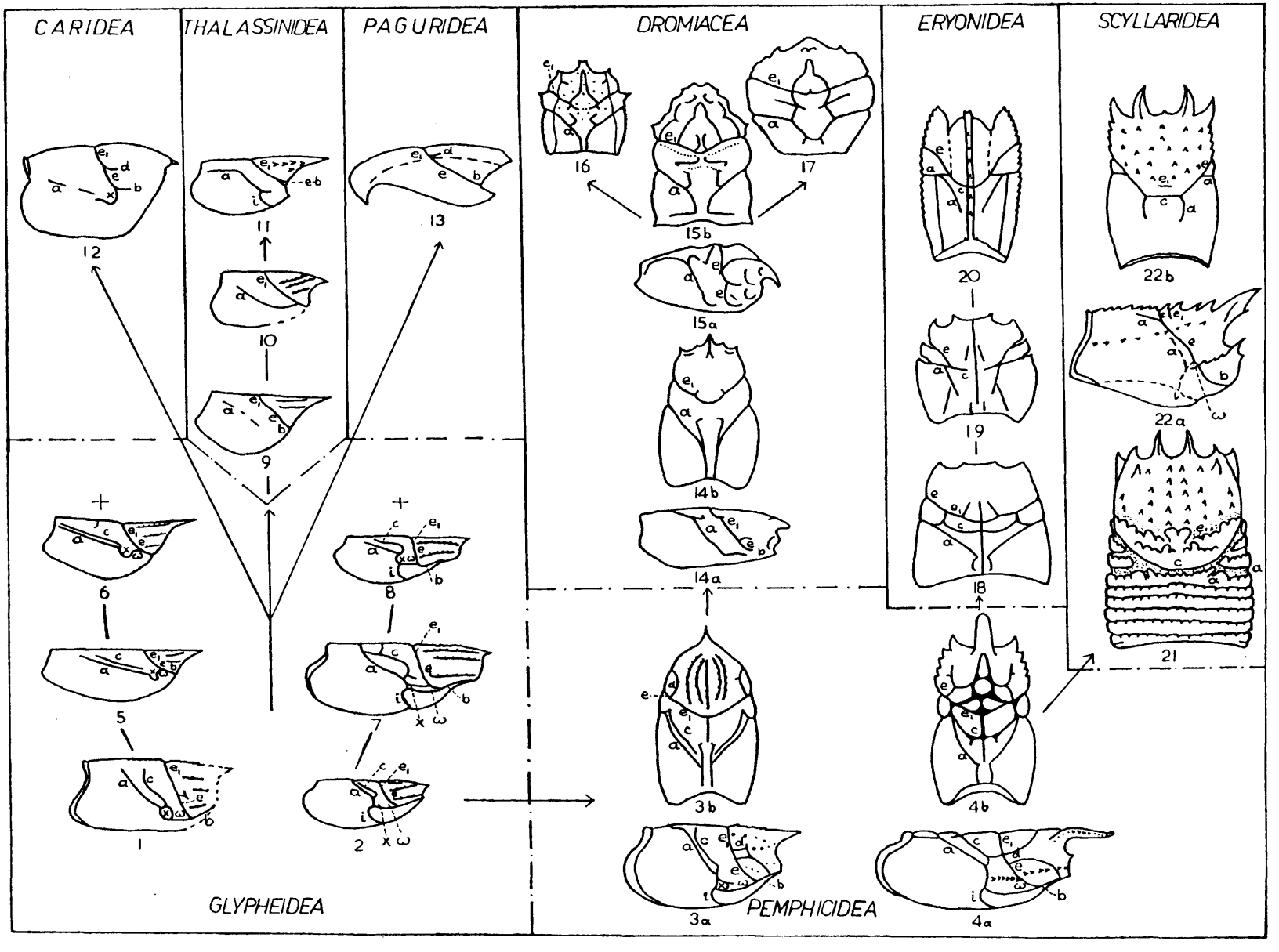

CARIDEA
THALASSINIDEA
PAGURIDEA
DROMIACEA
ERYONIDEA
SCYLLARIDEA
GLYPHEIDEA
PEMPHICIDEA

Fig. 19.

There is a marked tendency in the course of decapod evolution for the number of transverse furrows to be reduced by fusion or gradual obliteration. The correct identification of the remaining portions of the system of furrows in advanced forms is a task of vital importance for the recognition of phylogenetic relations and for the taxonomy of this order. Boas, who was the first to use the comparative morphology of the carapace furrows as a basis for the classification of recent and fossil decapods, recognised that the conspicuous single transverse furrow of *Homarus* and *Nephrops* ("c") was not homologous with the first transverse furrow of *Eryma* ("e_1"), but some later authors wrongly rejected this observation. It is now possible to review the early work in the light of the great increase in paleontological material which proves beyond doubt that the primitive condition of the furrow system is one in which three transverse furrows exist, as in all known Triassic Reptantia. At the same time the study of homologies can be placed on a much firmer basis by relating the system of furrows to points of reference which were discussed above, i.e., the fixed segmental muscle attachments and the mandibular joint. The details of the process of carapace evolution in the decapods as revealed by comparative morphology cannot be discussed here, but the diagrammatic figures showing the phylogenetic trends in Nephropsidea (fig. 18), Glypheocarida, Anomocarida, Brachyura and Palinura (fig. 19) indicate the value of the method and the results obtained.

There is still some doubt about homologies and evolution in the Scyllaridea and Galatheidea, for which groups more morphological information on recent and fossil forms is required.

Boas's and Bouvier's notation of furrows, although somewhat inconvenient, is here retained for purposes of comparison. A symbol "x" for the known or inferred position of the adductor testis muscle attachment is added.

The morphological change in the carapace furrows reflects the following basic morphogenetic trends in decapod Crustacea. The crowding, partial obliteration, and fusion of furrows on the flanks of the cylindrical carapaces of typical "Macrura Reptantia" is caused by the forward expansion of the anterior ventral thoracic portion of the carapace, which has been explained above as a result of the differentiation of the appendages of the cephalothorax. At the same time, as the non-functional tergal portions of the thoracic somites are reduced, the branchio-cardiac furrow extends back towards the posterior border of the carapace. Where the cephalothorax is dorso-ventrally flattened this process is somewhat modified, as the lateral expansion of the carapace creates the necessary additional space for the gill chambers and muscles. In the Brachyura (fig. 16) the reduction of the abdomen necessitates a change from the primitive cylindrical to a conical shape of the thoracic skeletal elements. This means that the dorsal edges of all thoracic segments are crowded together and moved forward. The attractor epimeralis muscle is concentrated in two small arcuate masses near the centre of the carapace, where its roughened attachment areas are clearly visible internally and externally at the sides of the urogastric and cardiac regions. The forward and lateral extension of this muscle is broken up into thin strands or altogether lost, and, parallel with this development, the main branchio-cardiac furrow disappears gradually.

ORIGIN OF CARAPACE FURROWS

The origin of the carapace furrows can be traced back from the most primitive decapods of the Triassic, in which the furrows are strongly developed, to Mysidacea and other more primitive Malacostraca (Glaessner 1957).

TRIASSIC REPTANTIA: In all Triassic Reptantia three transverse furrows cross the middle part of the carapace. The third or branchio-cardiac furrow is V-shaped. It ends laterally at the boundary between the gill chamber and the anterior chamber. The first or cervical sulcus has a curved connection with the upper boundary of this chamber ending below the base of the antenna. The lateral portion of the second or post-cervical furrow is either parallel to the other furrows and reaches the margin of the anterior chamber at an angle as in *Lissocardia* (fig. 18) and the Erymaidae, or it joins the lower end of the branchio-cardiac furrow as in *Pseudoglyphea*, *Litogaster*, *Pseudopemphix*, and *Pemphix* (fig. 19). In the first case it may be assumed that the lateral mandibular joint lies in

front of the lower (lateral) end of the post-cervical furrow while the adductor testis muscle was attached to the carapace behind this furrow, as both these reference points must lie above the anterior chamber and can neither coincide with, nor be crossed by, furrows. In the second case a distinction has to be made between different genera. In *Pseudoglyphea* the knob ω can be observed between two branches of the cervical furrow. The attachment area of the muscle corresponds to an area bounded by a semi-circular extension of the branchio-cardiac furrow, which is joined by the post-cervical furrow above the attachment area. In *Litogaster* the position of the two points is not easily recognisable on the surface but the shape and position of the furrows makes them closely comparable with those in *Pseudoglyphea.* In *Pseudopemphix* a small, well defined area above the posterior corner of the anterior chamber must be considered as the muscle attachment. This genus is very rare and a detailed examination of the test cannot be made without damaging specimens. The position of ω in this genus is found by comparing it with the closely related *Pemphix*, in which the actual position of the external mandibular articulation is known. It is covered by the second lateral large inflated area, which occupies the entire space between the transversal furrows (cervical and laterally fused post-cervical and branchio-cardiac furrows). The position of the adductor testis muscle in *Pemphix* is unknown.

MYSIDACEA: The first furrow in the Mysidacea and the only furrow known in the Euphausiacea are laterally bifurcating, enclosing between their branches the body of the mandible. These forms possess no real branchial chamber and for this reason do not develop any "anterior chamber". The position of this furrow points to its homology with the cervical groove of the Decapoda. In some of them, e.g., *Palinurus*, the mandible occupies the same relative position. In dorsal aspect this furrow is straight in the Mysidacea but U- to V-shaped in the Euphausiacea. The last transversal furrow of the Mysidacea ends laterally anterior to the bases of the first thoracopods and extends along the anterior margin of the first thoracic somite. From the median end of the epimeral fold it extends backward in a narrow U-shaped loop, which closes medially in front of the first free thoracic tergite. This furrow is undoubtedly homologous with the branchio-cardiac groove of the Decapoda. Some Mysidacea possess an intermediate transverse furrow. In *Eucopia* it appears to join laterally the branchio-cardiac furrow. In *Boreomysis* the two are parallel, and published figures show the intermediate furrow ending laterally between the bases of the maxillulae and maxillae. The cervical sulcus is well developed in a number of Pygocephalomorpha.

SYNCARIDA: In the Anaspididae a transverse furrow is observed, ending laterally between the segments of the mandible and the maxillula. Calman (1896) considered it as homologous with the cervical furrow of the Mysidacea and decapods, and others agreed with this. Its relation to the mandible indicates that it is not the boundary between the head and the thorax. Later, however, Calman (1909, p. 163) considered it "quite probable" that it is the posterior boundary of the head, invoking in support of this assumption a "forward displacement of the lateral plates of the anterior thoracic somites" in some other Malacostraca, but there is no evidence of such displacement in the Syncarida.

PHYLLOCARIDA: In some recent phyllocarids the boundary between the head and

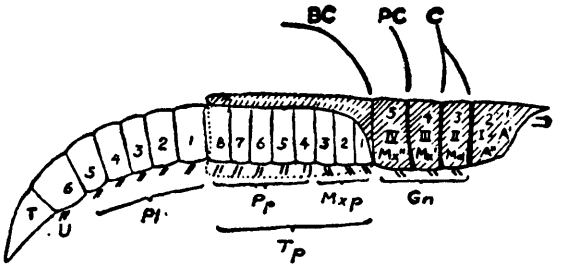


Fig. 20. Diagram showing position of carapace furrows in relation to segmentation in Malacostraca. Cephalic portion and dorsal part of carapace shaded, outline of carapace shown in dotted line, thoracic portion and abdomen blank, position of appendages shown by letters. Segments of cephalon: I–IV after Snodgrass, beginning with antennal segment A″; 1–5 alternative numbering including antennular segment A′. Thoracic segments: 1–8. Abdominal segments: 1–6 and T (telson). Gnathocephalic appendages (Gn): mandibula (Md), maxillula (Mx′), maxilla (Mx″), thoracopods (Tp), maxillipeds (Mxp), pereiopods (Pp). Abdominal appendages: pleopods (Pl), uropods (U). Carapace furrows in relation to segments: cervical (C), post-cervical (PC), branchio-cardiac (BC).

the thorax is marked by a line on the carapace. Behind this line the carapace overlaps the free thoracic somites. The attachment area of the carapace adductor muscle is adjacent to this line. Manton (1934) has shown that in *Nebalia* this muscle is maxillary in origin. The line is homologous with the branchio-cardiac furrow in decapods.

The conclusion drawn from these observations is that the three primary transverse carapace furrows in Malacostraca originated as segmental boundaries (fig. 20). Their relation to the gnathocephalic appendages and to the first thoracic somite is fixed and definite. The first or cervical transverse furrow is related to the mandibular segment and is probably originally its posterior boundary (II–III according to Snodgrass, 1937, 3–4 according to the count of cephalic segments accepted by other authors). The second or post-cervical furrow is related, in the position of its lateral end, to the segments of the maxillulae and maxillae (III–IV or 4–5). The third or branchiocardiac furrow is definitely the posterior boundary of the maxillary segment (IV–V or 5–6), which is also the posterior boundary of the cephalic region.

THE REDUCTION OF THE ABDOMEN

In free-swimming decapods the abdominal appendages (pleopods) are the main organs of locomotion (Fig. 21a). In addition, females carry their eggs attached to them, and other adaptations connected with reproduction are developed from them. A sudden contraction of the strong flexor muscles of the abdomen and a forward movement of the tail fan produce, in the Macrura, a most effective flight movement in a backward direction. In benthonic forms this is the only part played by the abdomen in connection with locomotion, which in the normal forward direction is obviously slowed down by this unwieldy appendage. It is not surprising, therefore, that it becomes reduced in many "Decapoda Reptantia" (Fig. 21b). This reduction affects mainly the relative size of the abdomen. It is never completely lost, its terminal somite (telson) always remains, and fusion of segments occurs only to a minor extent. The reduction may take place in various other ways. In the burrowing Thalassinidea, calcification of the integument is reduced and the abdominal pleura are gradually lost. This occurs also in the Paguridea but here the shape of the abdomen becomes gradually adapted to concealment in gastropod shells, with consequent loss of symmetry. Some descendants of the Paguridea become freely mobile and acquire a stronger calcification and a crab-like habitus but they do not regain the primary symmetry of the abdomen. In the evolution of the Galatheidea the abdomen is in the earlier stages not reduced in size but closely folded against the sternum. This is possible only in conjunction with a reduction of the last

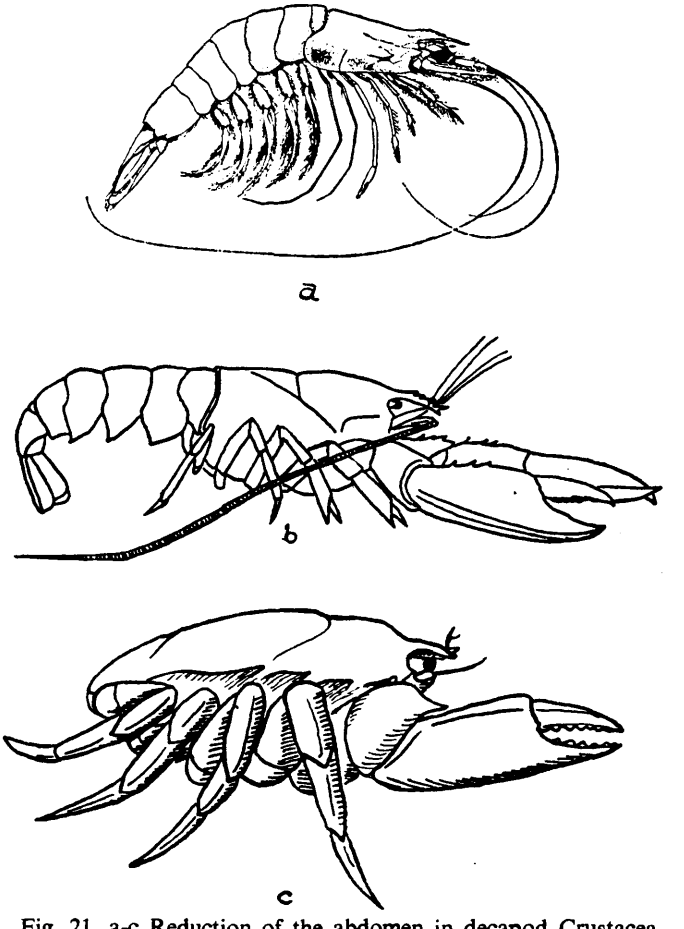


Fig. 21. a-c Reduction of the abdomen in decapod Crustacea. a–*Parapenaeopsis gracillima*, b–*Homarus vulgaris*, c–*Carcinus maenas*.

thoracic somite, which becomes movable. Observations on *Galathea strigosa* show that the epimeral fold of the last thoracic somite is reduced to such an extent that only the attachment areas of the branchiae and the articulation of the abdomen remain. The fifth pereiopods thus lose their firm support and the attachment areas of their muscles and become unable to fulfil their original function as organs of locomotion. They are modified to cleaning brushes for the gills. In the crab-like descendants of the Galatheidae, the Porcellanidae, the inflexion of the abdomen is complete but the fifth pereiopods are not restored to their former size.

In the Brachyura the entire abdomen is progressively and rapidly reduced. The inflexion of this reduced abdomen is possible without loosening the framework of the last thoracic somite. In the early stages of the evolution of the Brachyura (Dromiacea) this somite is reduced and shifted in connection with a general structural alteration of the internal skeleton but it remains firmly attached to the preceding somites. At this stage little space is available for it, and for this reason the fifth and occasionally also the fourth pereiopods are shifted dorsally and reduced in size. Their function changes from locomotion to the carrying of protective foreign objects. In contrast to the Galatheidea, however, nothing is lost, the sternum is unaffected and the epimeral fold remains intact. This makes it possible for the last thoracic somites to expand again as soon as the reduction of the abdomen and its inflexion are complete (Brachyrhyncha, Fig. 21c). The last pereiopods can even attain a higher degree of specialisation (swimming legs of the Portunidae). At the typically brachyuran stage the abdomen has finally lost its primary locomotive function and only plays some part in reproduction. It is interesting to note that the highly complex abdominal muscles are reduced in the early Megalopa-stage of *Carcinus*, in which the abdomen is still long (Daniel, 1931).

EVOLUTIONARY TRENDS IN THE BRACHYURA

A thorough study of the evolution of the Brachyura on the basis of detailed comparative examination of morphogenesis of the skeleton has yet to be undertaken. Only a very brief general outline of present views can be presented here in support of their classification. Withers (1932) has revealed one of the "missing links" in invertebrate evolution in the form of the Liassic *Eocarcinus*, which connects beyond doubt the most primitive known Brachyura with an extinct group of macrurous Crustacea, the Triassic Pemphicidea. Later (1951) he was able to trace this line further through the Prosoponidae of the Middle Jurassic to those of the Cretaceous. I have summarised the knowledge of Jurassic Brachyura (Glaessner, 1933) and described the morphology of the furrows and muscle insertions on the carapace, which occupy an important place among the taxonomic characters of the fossil crabs. Beurlen (1933) expressed different views on the evolution of the early Brachyura, according to the doctrine of "explosive" origin of new types, but the disagreement concerns interpretations rather than the course of evolution. Few new relevant data have been published since, but abundant new late-Jurassic Brachyura have been collected and are reported to be under examination. It seems to have taken the Brachyura the long span of Jurassic time, about 30 million years to consolidate their organisation on the level of the Dromiacea. The real advance to higher levels of organisation and concomitant "adaptive radiation" commenced only in the Cretaceous.

After the complete establishment of the fully brachyuran characters of the cephalothorax and abdomen, further evolutionary steps in the morphology of the crabs affect parts of the skeleton different from those that were altered in the process of evolving the Brachyura from their macruran ancestors. Changes in the carapace, furrows, and regions still continue, but major evolutionary steps occur in the fronto-orbital region and mouth parts, in close relation to advancements in respiration and sensory functions. The shape of the carapace, though still undergoing evolution along several divergent lines (Oxyrhyncha, Brachyrhyncha), is subject to adaptive changes, which may be convergent. Future work on the evolution of the crabs should be based more on the morphogeny of the anterior portion of the cephalothorax, in addition to that of the dorsal surface of the carapace, which is often the only part described in detail, particularly in Cretaceous crabs.

Only a few general remarks on genetic relationships suggested by our present knowledge of fossil crabs are added, and unsolved problems are outlined.

The oldest Oxystomata are found in the Lower Cretaceous (*Necrocarcinus, Orithopsis*). They are characterised, apart from their mouth parts, which are often undescribed in fossils, by an elongate or hexagonal carapace with a distinctive pattern of regions. A prominent continuous mesogastric and cardiac ridge is a characteristic feature of this pattern. The branchio-cardiac furrow is often well marked. An origin of the Oxystomata from the family Homolidae among the Dromiacea seems feasible though it is as yet undemonstrated. It may be that the oxystomatous condition or grade of organisation has been reached independently by descendants of different Dromiacea in the Cretaceous. Bourne (1922) had argued from comparative studies on recent material that the Raninidae could not have originated from Dromiacea and had separated them from all other crabs as Gymnopleura. However, their earliest Lower Cretaceous representatives (*Notopocorystes*) are closer to *Necrocarcinus* than to their living typical raninid descendants, with which they are linked by abundant fossil material. Their phylogenetic relations with the earliest Oxystomata are thus strongly supported by paleontological data. The Paleocene *Camarocarcinus arnesoni* Holland and Cvancara (1958) was recently described as a raninid but it is clearly an oxystomatous crab close to *Necrocarcinus*.

This genus has been placed in the family Calappidae, which is remarkably well represented by fossils, probably because the burrowing habits of some genera facilitate fossilisation.

The history of the remaining family of the Oxystomata, the Leucosiidae, is difficult to trace. It is not known before the Tertiary, and is then represented by living genera. Beurlen (1930) has mentioned similarities between *Calappilia* and the Leucosiidae.

The Oxyrhyncha or spider crabs are also unrepresented before the Tertiary except by unidentifiable fragments. The pointed rostrum (correctly though inconveniently distinguished by Balss from the more conspicuous paired lateral rostral spines, which constitute, strictly speaking, a "pseudorostrum"), and the prominent mesogastral-cardial ridge, together with the elongate cephalothorax, place this group much closer to the Oxystomata than to the Brachyrhyncha, but it is more advanced in the organisation of its mouth parts.

The Cancridae and the more primitive Atelecyclidae differ from Brachyrhyncha in their narrow front and prominent mesogastric-cardiac ridge and other characters. Rathbun has placed the Upper Cretaceous genus *Avitelmessus* in the family Atelecyclidae; it appears also to be closely related to the Dakoticancridae. This may indicate an independent origin of the Cancridae from Dromiacea. I have separated them from the Brachyrhyncha as Cancriformia (Glaessner, 1929).

The remaining true Brachyrhyncha comprise mainly the Portunidae, the Xanthidae and Goneplacidae, and the Ocypodidae and Grapsidae.

The Xanthidae are known from the Cretaceous but their early representatives mostly lack distinctive carapace patterns and throw little light on their relationships. Certain early Xanthidae resemble Dynomenidae; their origin may well have been among the Dromiacea. They are one of the most abundant and most strongly differentiated groups of living crabs. Abundant fossil material of the Xanthidae and the closely related Goneplacidae and Geryonidae generally supports phylogenetic and taxonomic conclusions based on living representatives.

Fossil Grapsidae are rare, while their recent representatives are abundant inhabitants of the littoral zone. They give no significant indication of their origin. Their littoral habitat appears to have adversely affected their chances of preservation in the sediment.

The Portunidae are characterised by a peculiar adaptation to fast swimming by means of a transformation of the last pereiopod. This was clearly a successful evolutionary step, leading to wide distribution and considerable taxonomic differentiation in this group during the Tertiary. The Cretaceous origins of this family are obscure. The distinctive swimming legs are found in *Carcineretes* Withers (probably Maestrichtian), which was considered by Beurlen as representing a different family on account of its carapace which is unlike that of the Portunidae. A similar carapace was found in *Ophthalmoplax* Rathbun, but here the last pereiopods are unknown and the carapace also resembles that of *Archaeopus*. Withers has compared *Carcineretes* with the controversial living genus *Cymopolia*. The available evidence is insufficient for a decision on whether the swimming adaptation was acquired convergently or whether the Portunidae are

derived from the Carcineretidae. Whether in this case the origin of the Portunidae was from xanthoid crabs as claimed by Beurlen (1930) or independently from Dromicea is uncertain.

This leaves the Ocypodidae to be discussed. Beurlen (1930) has combined them with the aberrant deep-sea Retroplumidae in a "Tribe" (= Section) Ocypodoida, and Via (1957) has in a recent preliminary note expressed agreement. The Ocypodidae are crabs with square carapaces ("Catometopa"), distinguished from the Goneplacidae by their narrow front and long eye stalks. If *Ophthalmoplax* and *Archaeopus* belong to this group, then its considerable age and independent origin are rightly claimed, but this rests at present only on the square carapace and narrow front with large orbits in these Cretaceous genera. References to *Goniocypoda* from the Neocomian are erroneous, "*G. sulcata*" Carter being based on a subfossil *Macrophthalmus*. The Eocene genus *Goniocypoda* was placed in the Hexapodinae by Glaessner and Rao (in press). The alternative possibility of a closer relation between the Oxypodidae and Goneplacidae still exists.

In this brief review of the evolution of the Brachyura a number of problems has been pointed out on which evidence either is insufficient because of lack of fossils or could be brought to light by more detailed study of available paleontological material. They are (1) the detailed morphology of Jurassic crabs and the possibility of finding ancestral forms of different later lineages among them, (2) the Lower Cretaceous crabs, which are imperfectly known, particularly those above the level of the Dromiacea, (3) the Upper Cretaceous Dakoticancridae including *Avitelmessus grapsoideus* Rathbun and their relation to a group of large-eyed American crabs comprising *Archaeopus antennatus* Rathbun, "*Plagiolophus*" *vancouverensis* (Woodward), *Carcineretes* and *Ophthalmoplax*. Within this incompletely known group may lie the key to the genetic relationships of the Dorippidae and other Oxyrhyncha, the Ocypodidae and possibly the Portunidae. Pending these investigations, the picture of a strongly radiating monophyletic evolution of the Brachyura which I proposed in 1930 still stands, with only minor modifications (fig. 22). The classification that follows does not seem to be in conflict with present paleontological evidence.

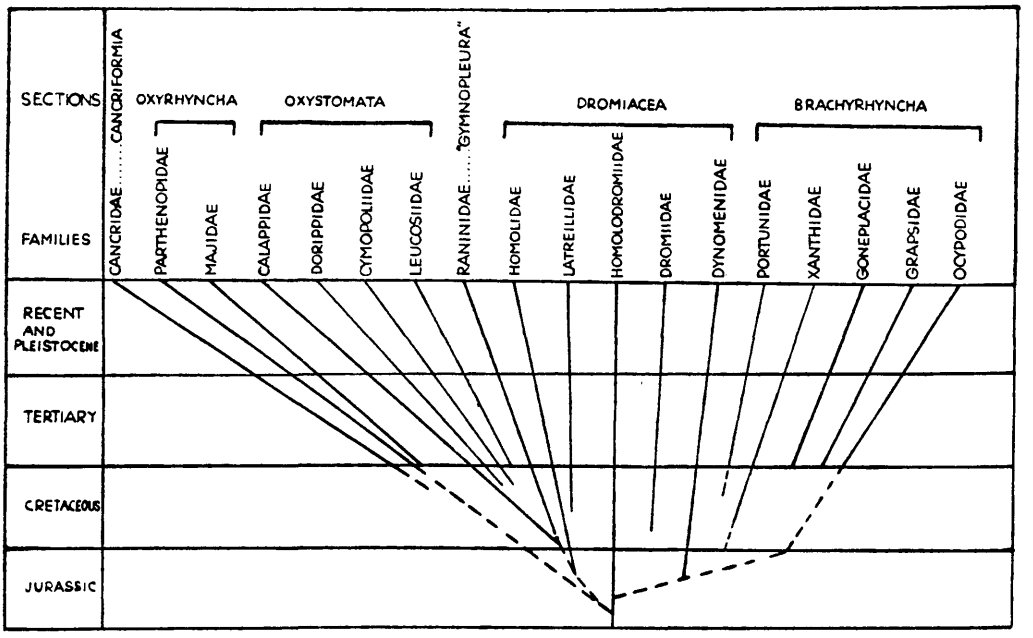


Fig. 22. Genetic relations and stratigraphic distribution of the most important families of Brachyura. After Glaessner 1932.

OUTLINE OF THE CLASSIFICATION OF DECAPOD CRUSTACEA

A reclassification of the decapod Crustacea based on the results of phylogenetic studies on both recent and fossil material was proposed by Beurlen and Glaessner (1930). This formed the basis of recent reviews of the Order Decapoda in paleontological texts such as the chapter by Chernyshev

in the Russian edition of Zittel's "Principles of Palaeontology" (1934) and Roger's contribution to Piveteau's "Traité de Paléontologie" vol. 3, 1953. Later investigations have led to minor modifications of this classification and it is therefore desirable to re-state it now briefly in its amended form.

The new classification which for the first time took full account of known paleontological data, replaced the Suborders Natantia and Reptantia (which were established about 80 years ago to replace the grouping into Macrura, Anomura and Brachyura introduced by H. Milne Edwards in 1834), by a division based on morphology and phylogeny rather than on common types of adaptation. These new Suborders were the Trichelida comprising the Divisions Penaeidea, Stenopodidea (of which no fossil representatives are known) and Nephropsidea and the Heterochelida. Beurlen (1930) had drawn attention to the importance of the occurrence of three pairs of chelate legs in the Trichelida and had argued that they could not have been acquired by primarily benthonic forms. He adduced much evidence in favour of an independent acquisition of adaptation to pelagic life of the geologically much younger second group of the "Natantia", the Caridea (= Eucyphidea).

This new grouping has since received valuable support from zoological observations. Burkenroad (1939) who studied the branchial structures found that the Caridea differ from the Penaeidae and "Reptantia". He concluded "The significance of this difference of branchial patterns is not immediately apparent except insofar as it may provide still further evidence against acceptance of the category Natantia". On the basis of a detailed study of the larvae of decapod Crustacea, Gurney (1942) came to the conclusion that the Penaeidea have only a remote relationship to the Caridea and are more closely allied to the Nephropsidea. Beurlen (1930) has shown that the following characters of the Caridea make their derivation from Penaeidea unlikely: Number of chelae, shape of rostrum and carapace in primitive forms such as the Palaemonoida and Crangonoida, short abdomen, wide pleura of the second abdominal somite. The Caridea appear much later than the Penaeidea. The later Nephropsidea remain distinct from all other "Reptantia". It has now become evident that the extinct family Erymaidae is directly related to the earlier representatives of the Nephropsidea although the two lines of evolution are divergent (Glaessner, 1932, p. 119; Mertin 1941, p. 158; J. T. Woods, 1957, p. 156) (see fig. 18). There is no longer any good reason for the previously suggested separation of the Erymaidae as a "Tribe Paranephropsidea" and therefore the proposed named "sections" of the Trichelida ("Nectochelida", "Herpochelida") become redundant.

A study of fossil representatives of the Axiidae (*Magila* and *Schlüteria tetracheles* Fritsch, see Mertin 1941, p. 196; the conclusion that this species belongs to the Axiidae was reached independently, but left unpublished, by the present writer) does not support Gurney's statement, based on the study of larvae, that they are scarcely separable from Nephropsidea. It supports the view that they are direct descendants of the extinct Glypheocarida. This important Section of fossil Decapoda represents an ancestral group of non-nephropsid "Reptantia" and provides the key to relations which could not have been deduced from the characters of any living decapods, larval or adult. That the Thalassinidea (and with them the Paguridea) are derived from the Glypheidea can be shown by a comparison of important characters of the carapace, the rostrum, the abdomen and the pereiopods. Beurlen's arguments in favour of a derivation of the Caridea from the same ancestral group are convincing, notwithstanding their adaptive deviation in the direction of the "Natantia". Further studies have brought more evidence for the contention that the most primitive representative of the Palinura, the remaining "Anomura" and the early Brachyura approach the extinct Triassic Pemphicidea very closely in important structural features.

The morphological similarities between the Glypheidea and Pemphicidea rate high enough to justify inclusion of both in the Section Glypheocarida. The separation of *Pemphix* and its descendants ("Section Gastralida") from the Glypheidea is no longer considered desirable, mainly as a result of the recognition (Glaessner, 1932) of the close relations between *Pemphix* and *Pseudopemphix* and between this genus and *Litogaster* or *Pseudoglyphea*. Separate Sections Anomura s. str. (including Galatheidea and Hippidea but excluding Thalassinidea and Paguridea) and Brachyura are retained

in preference to their formerly proposed inclusion as "tribes" in a new "Section Heterura", which is now abandoned.

The resulting major classification (omitting some taxa that are of no paleontological importance) is presented in the following synopsis (*designates extinct groups).

I. Suborder Trichelida Beurlen and Glaessner, 1930
  1. Section Penaeidea Bate, 1888 (2 families) (Permian?-Recent)
  ?2. Section Stenopidea Bate, 1888 (No fossil representatives are known)
  3. Section Nephropsidea Alcock, 1901
    *1. Fam. Clytiopsidae Beurlen, 1928, Triassic
    *2. Fam. Erymaidae van Straelen, 1924, Jurassic-Cretaceous
    3. Fam. Nephropsidae Stebbing, 1893, Jurassic-Recent.
    4. Fam. Astacidae Hagen, 1870, Lower Cretaceous-Recent
    5. Fam. Parastacidae Huxley, 1878, Pleistocene-Recent

II. Suborder Heterochelida Beurlen and Glaessner, 1930
  *1. Infraorder Glypheocarida Beurlen and Glaessner, 1930
    1. Section Glypheidea van Straelen, 1924
      1. Fam. Glypheidae Winckler, 1883, Triassic-Eocene
      2. Fam. Mecochiridae van Straelen, 1925, Jurassic-Cretaceous
    2. Section Pemphicidea Beurlen and Glaessner, 1930
      1. Fam. Pemphicidae van Straelen, 1928, Triassic
  2. Infraorder Anomocarida Beurlen and Glaessner, 1930
    1. Section Thalassinidea Dana, 1852 (5 families) Jurassic-Recent
    2. Section Paguridea Henderson, 1888 (5 families) Jurassic-Recent
    3. Section Caridea Dana, 1852 (7–8 superfamilies) Jurassic-Recent
  3. Infraorder Palinura Borradaile, 1907
    1. Section Eryonidea de Haan, 1841
      *1. Fam. Coleiidae van Straelen, 1924, Triassic-Jurassic
      *2. Fam. Eryonidae Dana, 1852, Jurassic-Cretaceous
      3. Fam. Polychelidae Beurlen and Glaessner, 1930, Jurassic-Recent
    2. Section Scyllaridea Stebbing, 1904
      1. Fam. Palinuridae Gray, 1847, Jurassic-Recent
      2. Fam. Scyllaridae Bate, 1888, Cretaceous-Recent
  4. Infraorder Anomura H. Milne Edwards, 1834 (emend. Beurlen 1930)
    1. Section Galatheidea Henderson, 1888
      1. Fam. Galatheidae Dana, 1852, Jurassic-Recent
      2. Fam. Porcellanidae Henderson, 1888, Cretaceous-Recent
    2. Section Hippidea de Haan, 1849
      1. Fam. Albuneidae Stimpson, 1858, Tertiary-Recent
      2. Fam. Hippidae Stimpson, 1858, Recent
  5. Infraorder Brachyura Borradaile, 1907
    1. Section Dromiacea de Haan, 1839
      1. Superfamily Dromiidea Alcock, 1899
        1. Fam. Prosoponidae v. Meyer, 1860, Jurassic-Recent
        2. Fam. Dromiidae Alcock, 1899, Cretaceous-Recent
        3. Fam. Dynomenidae Ortmann, 1892, Jurassic-Recent
        *?4. Fam. Dakoticancridae Rathbun 1917, Cretaceous
      2. Superfamily Homolidea Alcock, 1899
        1. Fam. Homolidae Henderson, 1888
        2. Fam. Latreillidae Alcock, 1899, Cretaceous-Recent
    2. Section Oxystomata de Haan, 1841
      1. Fam. Dorippidae Dana, 1852, Cretaceous-Recent
      2. Fam. Calappidae Alcock, 1896, Cretaceous-Recent
      3. Fam. Leucosiidae Dana, 1852, Tertiary-Recent
    (Section Gymnopleura Bourne, 1922)
      4. Fam. Raninidae Dana, 1852, Cretaceous-Recent
    3. Section Oxyrhyncha Latreille, 1803 (emend. H. Milne Edwards, 1834)
      1. Fam. Majidae Alcock, 1899, Tertiary-Recent
      2. Fam. Inachidae Alcock, 1895, Tertiary-Recent
      3. Fam. Parthenopidae Alcock, 1895, Tertiary-Recent
    4. Section Cancriformia Glaessner, 1929
      1. Fam. Atelecyclidae Ortmann, 1893, Cretaceous?-Recent
      2. Fam. Cancridae Ortmann, 1893, Tertiary-Recent
    5. Section Brachyrhyncha Borradaile, 1907
      *?1. Fam. Carcineretidae Beurlen, 1930, Upper Cretaceous
      2. Fam. Portunidae Dana, 1852, Tertiary-Recent
      3. Fam. Xanthidae Alcock, 1898, Cretaceous-Recent
      4. Fam. Potamonidae Ortmann, 1896, Tertiary-Recent
      5. Fam. Geryonidae Colosi, 1924, Cretaceous-Recent
      6. Fam. Goneplacidae Dana, 1851, Tertiary-Recent
      7. Fam. Pinnotheridae H. Milne Edwards, 1852, Tertiary-Recent
      8. Fam. Grapsidae Dana, 1852, Tertiary-Recent
    (Section Ocypodoida Beurlen, 1930)
      9. Fam. Retroplumidae Gill, 1894, Tertiary-Recent
      10. Fam. Ocypodidae Ortmann, 1894, Tertiary-Recent

REFERENCES

BENSON, W. N.; FINLAY, H. J. 1950: A Post-Tertiary Micro-fauna in a Concretion Containing *Cancer novae-zealandiae*. *Trans. roy. Soc. N.Z. 78 (2–3)* : 269–70.

BEURLEN, K. 1930: Vergleichende Stammesgeschichte. *Fortschr. Geol. 8* : 317–586.

——— 1933: Zur Entfaltung der Brachyuren und zur Frage der explosiven Formenbildung überhaupt. *Zbl. Miner. Geol. Paläont., B, 8* : 473–9.

BEURLEN, K.; GLAESSNER, M. F. 1930: Systematik der Crustacea Decapoda auf stammesgeschichtlicher Grundlage. *Zool. Jb. 60* : 49–84, figs.

BOAS, J. E. V. 1880: Studier over Decapodernes Slaegtskabsforhold. *Skr. Vidensk.* Selsk. *(6), 1.*

BOURNE, G. C. 1922: The Raninidae, a Study in Carcinology. *J. Linn. Soc. (Zool.) 35* : 25–78, Pl. 4–7.

BOUVIER, E. L. 1897: Sur l'Origine Homarienne des Crabes; Étude Comparative des Dromiacés Vivants et Fossiles. *Bull. Soc. philom. Paris, (8), 8* : 34–110, pls.

BURKENROAD, M. D. 1939: Some Remarks upon Non-Penaeid Decapoda. *Ann. Mag. nat. Hist., Ser. 11, 3* : 310–8.

CALMAN, W. T. 1896: On the Genus Anaspides and Its Affinities with Certain Fossil Crustacea. *Phil. Trans. 38* : 787, 802, 2 pl.

——— 1909: Crustacea. *In:* Lankester, "Treatise on Zoology", (7). Black, London.

CRESPIN, I. 1943: The Stratigraphy of the Tertiary Marine Rocks in Gippsland, Victoria. *Bull. Min. Resour. Surv., Aust., 9 (Palaeont. Ser. 4)* : 1–101.

——— 1947: A Fossil Crab from the Lakes Entrance Oil Shaft, Gippsland, Victoria. *Proc. roy. Soc. Vict. n.s. 59 (1)* : 20–2, pls.

DANIEL, R. J. 1931: The Abdominal Muscle System of the Shore Crab (*Carcinus maenas*) and of the Zoea I and Megalopa Stages. *Proc. biol. Soc. Wash. 45.*

DROOGER, C. W. 1956: Transatlantic Correlation of the Oligo-Miocene by Means of Foraminifera. *Micropaleontology 2 (2)* : 183–92.

ETHERIDGE, R., JUN.; MCCULLOCH, A. 1916: Sub-fossil Crustaceans from the Coasts of Australia. *Rec. Aust. Mus. 11* : 1–14, Pl. 1–7.

FINLAY, H. J.: MARWICK, J. 1940: The Divisions of the Upper Cretaceous and Tertiary in New Zealand. *Trans. roy. Soc. N.Z. 70 (1)* : 77–135.

GLAESSNER, M. F. 1929: Crustacea Decapoda. *Foss. Cat. 1 (41)* : 464 pp.

——— 1930: Beiträge zur Stammesgeschichte der Dekapoden. *Palaeont. Z. 12* : 25–42.

——— 1932: Zwei Ungenügend Bekannte Mesozoische Dekapodenkrebse. *Pemphix sueuri* (Desm.) und *Palaeophoberus suevicus* (Quenstedt.) *Palaeont. Z. 14* : 108–21, Textf. 6.

——— 1933: Die Krabben der Juraformation. *Zbl. Miner. Geol. Paläont., B, 3* : 178–91, Textf.

——— 1957: Evolutionary Trends in Crustacea (Malacostraca). *Evolution 11* : 178–84.

GLAESSNER, M. F.; WITHERS, T. H. 1931: On London Clay Crabs of the Family Raninidae. *Ann. Mag. nat. Hist., Ser. 10, 8* : 484–493, Pl. 20, 21.

GROBBEN, K. 1917: Der Schalenschliessmuskel der Dekapoden Crustaceen, Zugleich ein Beitrag zur Kenntnis Ihrer Kopfmuskulatur. *S.B. Akad. Wiss. Wien 126 (1)* : 472–94, 1 pl.

GURNEY, R. 1942: "Larvae of Decapod Crustacea" Ray Society, London, 306 pp.

HOLLAND, F. D.; CVANCARA, A. M. 1958: Crabs from the Cannonball Formation (Paleocene) of North Dakota. *J. Paleont. 32 (3)* : 495–505, Pl. 74, figs.

HORNIBROOK, N. DE B. 1958: New Zealand Upper Cretaceous and Tertiary Foraminiferal Zones and Some Overseas Correlations. *Micropaleontology 4 (1)* : 25–38, Pl. 1, t. 1–2.

MCKAY, A. 1877: Reports Relative to Collections of Fossils made on the West Coast District, South Island. *N.Z. geol. Surv. Rep. geol. Explor. 1873–4,* [*8b*] : 74–115.

MCNEIL, F. 1953: Carcinological Notes No. 2. *Rec. Aust. Mus. 23* : 89–96.

MANTON, S. M. 1934: On the Embryology of the Crustacean *Nebalia bipes. Phil. Trans. B, 223* : 163–238, Pl. 20–26.

MERTIN, H. 1941: Decapode Krebse aus dem Subhercynen und Braunschweiger Emscher und Untersenon, sowie Bemerkungen über einige verwandte Formen in der Oberkreide. *Nova Acta Leopold, n.s. 10 (68)* : 152–257, 30 figs. 8 pls.

MOCQUARD, F. 1883: Recherches Anatomiques sur l'Estomac des Crustacés Podophthalmaires. *Ann. Sci. nat., Zool., Ser. 6, 16*: 1–311, Pl. 1–11.

PESTA, O. 1915: Bemerkungen zu einigen Langusten (Palinuridae) und Ihrer Geographischen Verbreitung. *S.B. Akad. Wiss. Wien, I, 124* : 1–10, pls.

POWELL, A. W. B. 1949: New Species of Crustacea from New Zealand of the Genera *Scyllarus* and *Ctenocheles* with Notes on *Lyreidus tridentatus. Rec. Auckland Inst. Mus. 3 (6)* : 368–71, Pl. 68.

RATHBUN, M. J. 1926: The Fossil Stalk-eyed Crustacea of the Pacific Slope of North America. *Bull. U.S. nat. Mus. 138* : 1–149, pls.

——— 1935: Fossil Crustacea of the Atlantic and Gulf Coastal Plain. *Spec. Pap. geol. Soc. Amer. 2* : 1–160, pls.

RICHARDSON, L. R.; KREFFT, S. 1949: *Lyreidus australiensis* Ward (Brachyura, Gymnopleura) from Cook Strait. *Tuatara 2 (2)* : 69–71.

SCHMIDT, W. 1915: Die Muskulatur von *Astacus fluviatilis* (*Potamobius astacus* L.) Ein Beitrag zur Morphologie der Decapoden. *Z. wiss. Zool. 113* : 165–251, figs.

SIEWING, R. 1956: Untersuchungen zur Morphologie der Malacostraca (Crustacea). *Zool. Jb., Anat. Ontog., 75 (1)*: 39–176, 72 Textf.

SNODGRASS, R. E. 1938: Evolution of the Annelida, Onychophora, and Arthropoda. *Smithson. misc. Coll. 97 (6).* 159, pp., 54 fig.

VAN STRAELEN, V. 1925: Contribution a l'Étude des Crustacés Décapodes de la Période Jurassique. *Mém. Acad. R. Belg. Cl. Sci. 7.*
VIA, L. 1941: Los Crangejos Fosiles de Cataluna. *Bol. Inst. geol. Esp. 55* : 55–127, 8 fig. 11 Pl.
——— 1957: Contribution à l'Étude Paléontologique des Ocypodoida, Beurlen. *C. R. Acad. Sci., Paris, 245* : 553–4.
WITHERS, T. H. 1926: Decapod Crustaceans (*Callianassa*) from the Scotland Beds of Barbados. *Geol. Mag. 63 (741)* : 104–8, pls.
——— 1932: A Liassic Crab, and the Origin of the Brachyura. *Ann. Mag. nat. Hist. Series 10, 9* : 313–23, Pl. 9, 10.
——— 1951: Some Jurassic and Cretaceous Crabs (Prosoponidae). *Bull. Brit. Mus. (nat. Hist)., Geol. 1(b)* : 173–94, pl. 15–17.
WOODS, H. 1925–1931: "A Monograph of the Fossil Macrurous Crustacea of England". Palaeontographical Society, London, 122 pp., 27 pls.
WOODS, J. T. 1957: Macrurous Decapods from the Cretaceous of Queensland. *Mem. Qd. Mus. 13 (3)* : 155–75, pls.

APPENDIX 1. CATALOGUE OF SPECIMENS

1. New Zealand Geological Survey Collection

Numbers with prefix DC refer to the New Zealand Geological Survey register of fossil Crustacea. The catalogue includes all specimens referred to in the text of this bulletin. For more detailed data on locality and age see Appendix 2.

DC 102 *Cancer novaezealandiae* (Jacquinot and Lucas), GS 4114, Nukumaru (S137/539), Nukumaruan.
DC 104 *Cancer novaezealandiae* (Jacquinot and Lucas), GS 4101, Castlecliff (N137/496). Castlecliffian.
DC 105 *Tumidocarcinus* sp. indet. GS 4771, Huia Stream (S18/564). Altonian.
DC 107 *Ctenocheles* cf. *maorianus* Powell, GS 4042, Kai Iwi (S137/495). Castlecliffian.
DC 108 *Lyreidus elegans* Glaessner, Paratype, GS 4762, Postal Creek (S12/516). Altonian.
DC 109–111 *Ctenocheles* cf. *maorianus* Powell, GS 4099, Castlecliff (N137/494). Castlecliffian.
DC 114 *Cancer novaezealandiae* (Jacquinot and Lucas), GS 5694, Mangaotoro S.D. (N150/479). Opoitian.
DC 115 *Ommatocarcinus* sp., GS 5665, Three Roads, Oamaru (S136/696). Awamoan.
DC 116 *Ovalipes* cf. *punctatus* (de Haan), GS 5315, Maraetotara R. (N135/522), Castlecliffian.
DC 117 *Callianassa awakina* Glaessner. Paratype, GS 2592, Awakino Valley (N91/14). Otaian.
DC 120 *Tumidocarcinus tumidus* (Woodward), topotype. GS 31, Woodpecker Bay (S37/495), Whaingaroan.
DC 121–2 *Galene proavita* Glaessner. Paratypes. GS 4752, Postal Creek (S12/521). Clifdenian.
DC 123 *Lyreidus elegans* Glaessner. Holotype. GS 4719, Campbell Creek (S32/594), Upper Pareora or Southland Series.
DC 127–8 *Ovalipes* sp., GS 4997, Lower Waipara (S68/192). Waitotaran.
DC 129–30 *Galene proavita* Glaessner. Holotype (part, see DC 204), GS 4773, Bellbird Stream (S18/566). Clifdenian.
DC 131 *Galene proavita* Glaessner. Paratype. GS 4773, Bellbird Stream (S18/566). Clifdenian.
DC 132 *Tumidocarcinus giganteus* Glaessner. Paratype. GS 4660 Mimi S.D. (N100/16). ?Lower Tongaporutuan.
DC 133 *Tumidocarcinus giganteus* Glaessner. Paratype. Tangarakau Gorge (N100/21). ?Upper Southland Series.
DC 134 *Tumidocarcinus tumidus* (Woodward), GS 486 Wharekuri (S117/489). Duntroonian.
DC 135 *Tumidocarcinus dentatus* (chela of DC 185).
DC 136 *Tumidocarcinus dentatus* Glaessner. Paratype. GS 486, Wharekuri (S117/489). Duntroonian.
DC 137–9 *Tumidocarcinus tumidus* (Woodward). GS 486, Wharekuri (S117/489). Duntroonian.
DC 140 *Tumidocarcinus dentatus* Glaessner. Paratype, GS 486, Wharekuri (S117/489). Duntroonian.
DC 142 *Tumidocarcinus tumidus* (Woodward). GS 486, Wharekuri (S117/489). Duntroonian.
DC 143 *Tumidocarcinus dentatus* Glaessner. Holotype, GS 486, Wharekuri (S117/489). Duntroonian.
DC 145 *Tumidocarcinus tumidus* (Woodward), GS 486, Wharekuri (S117/489). Duntroonian.
DC 149–52 *Tumidocarcinus tumidus* (Woodward). GS 486, Wharekuri (S117/489). Duntroonian.
DC 153 *Tumidocarcinus dentatus* Glaessner. Paratype, GS 486, Wharekuri (S117/489). Duntroonian.
DC 154 *Tumidocarcinus tumidus* (Woodward). GS 486, Wharekuri (S117/489). Duntroonian.
DC 155 *Ommatocarcinus arenicola* Glaessner. Holotype, GS 66, Mount Brown (S68/251). Otaian-Waiauan.
DC 156–8 *Tumidocarcinus tumidus* (Woodward). GS 4873, Point Elizabeth (S44/737). Runangan.
DC 159–69 ? Paguridea (indet.), GS 321, Waiau-ua River (?S55). ? Wanganui Series.
DC 170–2 *Menippe* sp. GS 172, Hutchinson's Quarry (S136/821). Hutchinsonian.
DC 173 *Hemiplax hirtipes* Heller. Mangakura, Tauhoa S.D. (N33). ? Holocene.
DC 175 *Leptomithrax uruti* Glaessner. Holotype, GS 1139, Uruti (N99/500). Tongaporutuan.
DC 176 *Tumidocarcinus giganteus* Glaessner. Paratype, GS 1422, Mangaone Valley (N110/12). Lillburnian.
DC 177 *Tumidocarcinus* sp. Wanganui R. (N111/498). ? Altonian.
DC 178 *Tumidocarcinus tumidus* (Woodward), GS 1341, Wharekuri (S117/492). Duntroonian.
DC 180 *Tumidocarcinus giganteus* Glaessner, GS 1422. Paratype, Mangaone Valley (N110/12), Lillburnian.
DC 181 *Tumidocarcinus giganteus* Glaessner. Holotype. GS 7555, Pouatu S.D. (N110/28). ?Lillburnian.
DC 182 *Tumidocarcinus giganteus* Glaessner. Paratype. GS 7554, Pouatu S.D. (N110/29). Tongaporutuan.
DC 183–4 *Tumidocarcinus giganteus* Glaessner. Paratypes. Probably Pouatu S.D. (N110). Lillburnian-Tongaporutuan.
DC 185 *Tumidocarcinus dentatus* Glaessner. Paratype, GS 486, Wharekuri (S117/489). Duntroonian.
DC 186 *Tumidocarcinus* sp. GS 451, Pakaurangi Point (N28/545). Altonian.
DC 187–8 *Tumidocarcinus giganteus* Glaessner. Paratypes, GS 1422, Mangaone Valley (N110/12). ? Lillburnian.
DC 189–93 *Callianassa awakina* Glaessner. Paratypes, GS 5771, Awakino Valley (N91/517). Otaian.
DC 194 *Callianassa awakina* Glaessner. Holotype, GS 5771, Awakino Valley (N91/517). Otaian.
DC 195 *Leptomithrax uruti* Glaessner. Paratype, GS 2789, Upper Waitara S.D. (N100/22). Tongaporutuan.
DC 196 *Tumidocarcinus tumidus* (Woodward). GS 1341, Wharekuri (S117/492). Duntroonian.
DC 197 *Tumidocarcinus giganteus* Glaessner. Paratype, GS 7556, Tahora (N110/30). ? Tongaporutuan.
DC 198 *Tumidocarcinus giganteus* Glaessner. Paratype, GS 7557, Moki Road (N110/31). ? Tongaporutuan.
DC 199 *Tumidocarcinus giganteus* Glaessner. Paratype. GS 1422, Mangaone Valley (N110/12). Lillburnian (?).
DC 203 *Jasus flemingi* Glaessner. Holotype. Tarakohe Marl Pit (S8/498). Lower Altonian.
DC 204 *Galene proavita* Glaessner. Holotype (part, see also DC 129–30), GS 4773. Bellbird Stream (S18/566). Clifdenian.
DC 205 *Tumidocarcinus giganteus* Glaessner. Paratype. Dovedale (S68/722). Waiauan.
DC 208–9 *Tumidocarcinus tumidus* (Woodward). Coast, Brighton S.D. (S37/579). Duntroonian.
DC 210 *Tumidocarcinus giganteus* Glaessner. Paratype. GS 1422, Mangaone Valley (N110/12). Lillburnian (?).

DC 211 *Tumidocarcinus tumidus* (Woodward). Plaster cast of Holotype. Woodpecker Bay, Brighton (S37/495). Whaingaroan-Duntroonian.
DC 212 *Hemiplax* sp. GS 2811, Mangahao S.D. (N149/479). Waitotaran.
DC 214 *Cancer novaezealandiae* (Jacquinot and Lucas), GS 2827, Parnassus (S55/23). Nukumaruan.
DC 215 *Ovalipes* cf. *punctatus* (de Haan). GS 3893, Ohope (N69/501) Castlecliffian.
DC 216 *Cancer novaezealandiae* (Jacquinot and Lucas), GS 2839, Jed River (S62/98). ?Nukumaruan.
DC 218 *Callianassa* sp. GS 2119, Green Valley (S146/534). Bortonian.
DC 219 *Callianassa waikurana* Glaessner. Holotype. GS 6561, Waikura Stream (N62/531). Haumurian.
DC 220–1 *Callianassa* sp. a. Utakura R. (N15/498). Haumurian.
DC 223 *Leptomithrax irirangi* Glaessner. Holotype. Irirangi (N132/501). Opoitian.
DC 225 *Tumidocarcinus giganteus* Glaessner, GS 3642, Patten Creek (S24/506). Tongaporutuan.
DC 226 *Leptomithrax atavus* Glaessner, Paratype. Locality unknown.
DC 227 ?*Tumidocarcinus tumidus* (Woodward), GS 35, Cobden (S44/465) Whaingaroan-Duntroonian.
DC 228–9 *Hemiplax major* Glaessner. Holotype. (229), and paratype. GS 4191, Pakihikura Bridge (N139/502). Nukumaruan.
DC 230 *Galene proavita* Glaessner. Locality unknown.
DC 231 *Ctenocheles* cf. *maorianus* Powell. Castlecliff (N137/512). Castlecliffian.
DC 232 *Portunites granulifer* Glaessner. Holotype. GS 2977, Snowdrift Quarry (S172/520). Bortonian.
DC 233 *Laeviranina perarmata* Glaessner. Paratype. GS 2977, Snowdrift Quarry (S172/520). Bortonian.
DC 234 *Portunites granulifer* Glaessner. Paratype. GS 2977, Snowdrift Quarry (S172/520). Bortonian.
DC 235–6 *Mecochirus* ? sp. GS 6712, Kawhia-Raglan Road (N73/655). Puaroan.
DC 237 *Hemiplax major* Glaessner. Paratype, GS 4191, Pakihikura Bridge (N139/502). Nukumaruan.
DC 238 *Pseudocarcinus* sp. GS 4588, Goldsborough (S51/583). Kapitean.
DC 239 *Callianassa* ? sp. a. GS 1175, Waitangi River (N15/499). Haumurian.
DC 240–5 *Portunites granulifer* Glaessner. Paratypes. GS 2977, Snowdrift Quarry (S172/520). Bortonian.
DC 246 *Laeviranina perarmata* Glaessner. Holotype. GS 2977, Snowdrift Quarry (S172/520). Bortonian.
DC 247 *Laeviranina perarmata* Glaessner. Paratype. GS 2977, Snowdrift Quarry (S172/520). Bortonian.
DC 248–9 *Portunites granulifer* Glaessner. Paratype. GS 2977, Snowdrift Quarry (S172/520). Bortonian.
DC 250 *Laeviranina perarmata* Glaessner. Paratype. GS 2977, Snowdrift Quarry (S172/520). Bortonian.
DC 251–2 *Portunites granulifer* Glaessner. Paratype. GS 2977, Snowdrift Quarry (S172/520). Bortonian.
DC 253–4 *Leptomithrax atavus* Glaessner. Paratypes. GS 7203, Makino River (N119/503). Kapitean.
DC 255 *Leptomithrax atavus* Glaessner. Holotype, GS 7203, Makino River (N119/503). Kapitean.
DC 256–8 *Leptomithrax atavus* Glaessner. Paratype, GS 7203, Makino River (N119/503). Kapitean.
DC 260 *Cancer* cf. *novaezealandiae* (Jacquinot and Lucas). Gladstone (N162/803). Nukumaruan.
DC 261 *Callianassa* sp. b. GS 5485, Putangirua Creek (N168/568). Tongaporutuan.
DC 263–4 *Cancer novaezealandiae* (Jacquinot and Lucas), GS 5833, Te Aute (N141/494). Waitotaran.
DC 266 *Mecochirus marwicki* Glaessner. Holotype. Waikato Heads (N51/610). Heterian (deposited Auck. University).

2. Otago Museum, Dunedin

C 03 41 *Glypheopsis antipodum* Glaessner. Holotype. Ahuriri Flat, Clutha, (S179/461): ?Ururoan.

3. Auckland War Memorial Museum

Hemiplax hirtipes Heller. 23 specimens, Otago Harbour (S164/484). Post Pleistocene.

4. Canterbury Museum, Christchurch

Tumidocarcinus tumidus (Woodward). Raincliff, South Canterbury, (S101/499). Bortonian-Kaiatan.

5. Victoria University of Wellington, Zoology Dept.

Ctenocheles cf. *maorianus* Powell. Castlecliff (N137). Castlecliffian.
Cancer novaezealandiae (Jacquinot and Lucas). Castlecliff (N137), Castlecliffian.

6. Adelaide University, Department of Geology

Tumidocarcinus dentatus Glaessner. Wharekuri (S117/489). Duntroonian.

7. Dominion Museum, Wellington

Paramithrax minor Filhol. Castlecliff (N137/493). Castlecliffian.
Tumidocarcinus dentatus Glaessner. Wharekuri (S117/489). Duntroonian.

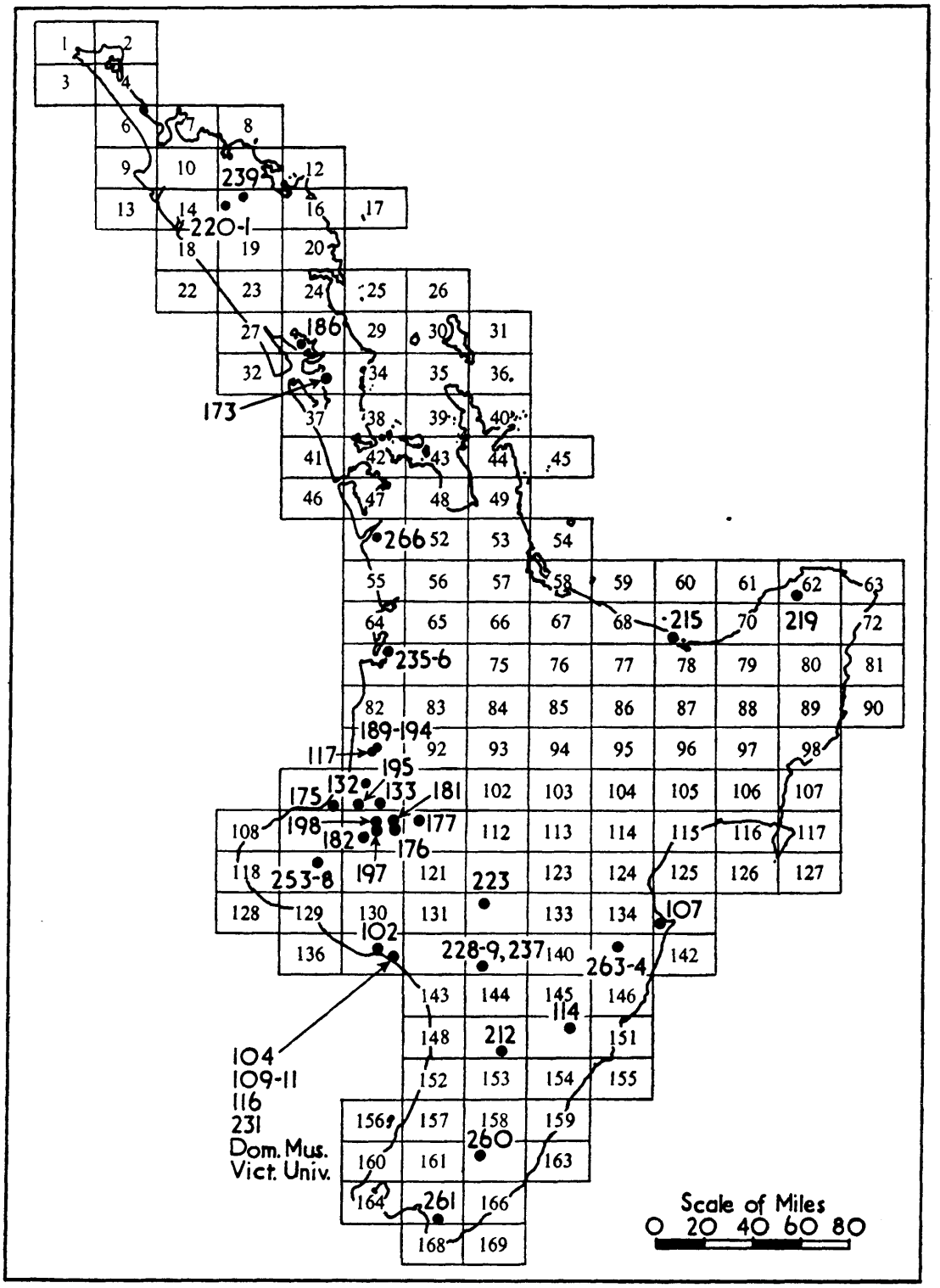


Fig. 23. Geographic distribution of fossil decapod Crustacea in sheet districts of the 1 mile to an inch topographic map series (N.Z.M.S. 1) (North Island). Numbers shown against localities refer to N.Z. Geological Survey register of fossil Crustacea (prefix DC). Other repositories are shown by abbreviations. Dom. Mus., Dominion Museum; Vict. Univ., Victoria University of Wellington.

APPENDIX 2. LOCALITIES OF NEW ZEALAND FOSSIL DECAPODA

The localities are arranged under sheets in the N.Z.M.S. 1 map series (fig. 23–4) Sheet Fossil Numbers are shown thus: N62/531, S18/566. Holotypes are marked (T).

NORTH ISLAND

N15/498 Utakura River, Okaihau. Presumably from boulders. Coll. F. G. Fitzgerald, 1925. Haumurian(?), by local stratigraphy.
Callianassa sp. a. DC 220, 221

N15/499 Waitangi River, 10 chains above Waikuku Stream junction conglomerate boulders (GS 1175). Coll. F. G. Fitzgerald, 1923. Haumurian (associated Mollusca).
Callianassa sp. a. DC 239

N28/687 Komiti (= Pakaurangi) Point, Kaipara Harbour (GS 451), Waitemata Group. Coll. S. H. Cox, 1880. Altonian (associated Mollusca and Foraminifera).
Tumidocarcinus sp. indet. DC 186

N33 Tauhoa S.D. "Found on mantlepiece in Sanderson's vacant house, Mangakura". Coll. H. T. Ferrar, Apr 1924. Probably Holocene concretion from Kaipara Harbour.
Hemiplax hirtipes Heller. DC 173

N51/610 Klondyke Road, Waikato Heads (grid ref. 326979). Coll. B. H. Purser, 1952. Heterian (associated Mollusca).
Mecochirus marwicki Glaessner. DC 266 (T)

N62/531 Waikura Stream, Tapuwaeroa Beds, 1 mile upstream from road, (GS 6561) Coll. H. W. Wellman, Jan 1956. Haumurian (by local stratigraphy).
Callianassa waikurana Glaessner DC 219 (T)

N69/501 Ohope Beach, fossiliferous sandstone in cliff behind west end of beach (GS 3893). Coll. J. Healy, Sep 1946. Putikian Substage, Castlecliffian (associated Mollusca).
Ovalipes cf. *punctatus* (de Haan). DC 215

N73/655 Kawhia-Raglan Road (grid ref. 400178), Puti Siltstone in road cutting (GS 6712). Coll. D. Kear and C. A. Fleming, May 1956.
Mecochirus ? sp. DC 235, 236

N91/517 Awakino-Mahoenui main highway (grid ref. 307473) Mahoenui Formation in road cuttings (GS 5771). Coll. C. A. Fleming, Jan 1945. Otaian (associated Mollusca and nearby microfossil samples).
Callianassa awakina Glaessner DC 189–193, 194 (T)

N91/14 Awakino-Mahoenui main highway (grid ref. ca. 301468), Mahoenui Formation in road cutting near Mangaruka Creek (GS 2592, F 5198). Coll. C. Washbourne and J. Marwick, 1926, 1930. Otaian.
Callianassa awakina Glaessner DC 117

N99/500 Wray's Quarry, Uruti Road, ¼ mile south of Uruti Post Office (grid ref. 080051), Urenui Beds (GS 1139). Coll. L. I. Grange, 1923. Tongaporutuan (associated Mollusca and Foraminifera).
Leptomithrax uruti Glaessner DC 175

N100/16 40 chains from end of Mangaotoro Road. (ca. 250183). Concretion from Mohakatino Beds (GS 4660) Coll. L. I. Grange, 1922. Lower Tongaporutuan ? (associated Foraminifera, Upper Southland to Tongaporutuan).
Tumidocarcinus giganteus Glaessner, DC 132

N100/21 "Tangarakau Gorge" (Locality and origin of specimens obscure). Grange (1927, *N.Z. geol. Surv. Bull. n.s. 31*, Pouatu S.D.) mapped the gorge as in upper Mokau Beds (Southland Series) but the majority of crabs from the district are from the overlying Mohakatino Beds.
Tumidocarcinus giganteus Glaessner, DC 133

N100/222 Upper Waitara S.D. 36 chains west of Rerekino Trig. Station (grid ref. 198000, near boundary with sheet N110). Urenui Beds (GS 2789). Coll. H. J. Evans, N.Z. Petroleum Co., 1940. Tongaporutuan (associated Mollusca).
Leptomithrax uruti Glaessner. DC 195

N110/12 Rail and road cuttings, Mangaone Valley, Pouatu S.D. (GS 1422). Coll. Public Works Department, per P. Marshall. Grange (1927, *N.Z. geol. Surv. Bull. n.s. 31*, Pouatu S.D.) mapped the valley as an inlier of Upper Mokau Beds surrounded by Mohakatino Beds. Lillburnian Foraminifera were identified by Mr N. de B. Hornibrook from the matrix of DC 176.
Tumidocarcinus giganteus Glaessner, DC 176, 187–199, 210

N110/28 Pouatu S.D., Sect. 2B, Block 8. Upper Mokau Beds (GS 7555), perhaps the same locality as N110/12. Coll. L. Bossard. ? Lillburnian.
Tumidocarcinus giganteus Glaessner. DC 181 (holotype)

N110/29 Pouatu S.D., Kohuratahi District, "papa" (GS 7554). Coll. H. A. Ellis, 1920–21. The specimen is referred to the Mokau Beds in *N.Z. geol. Surv. Bull. n.s. 31*, p. 25 but the locality is mapped as Tongaporutu Beds on the accompanying geological map of Pouatu S.D. ? Tongaporutuan.
Tumidocarcinus giganteus Glaessner, DC 182

N110/30 Tahora, Pouatu S.D., on road 6 chains north of Boarding House (GS 7556). Coll. L. I. Grange, 1923. Mohakatino Beds. ? Tongaporutuan.
Tumidocarcinus giganteus Glaessner. DC 197

N110/31 Moki Road, Pouatu S.D. Mohakatino Beds (GS 7557). ? Tongaporutuan.
Tumidocarcinus giganteus Glaessner (DC 198)

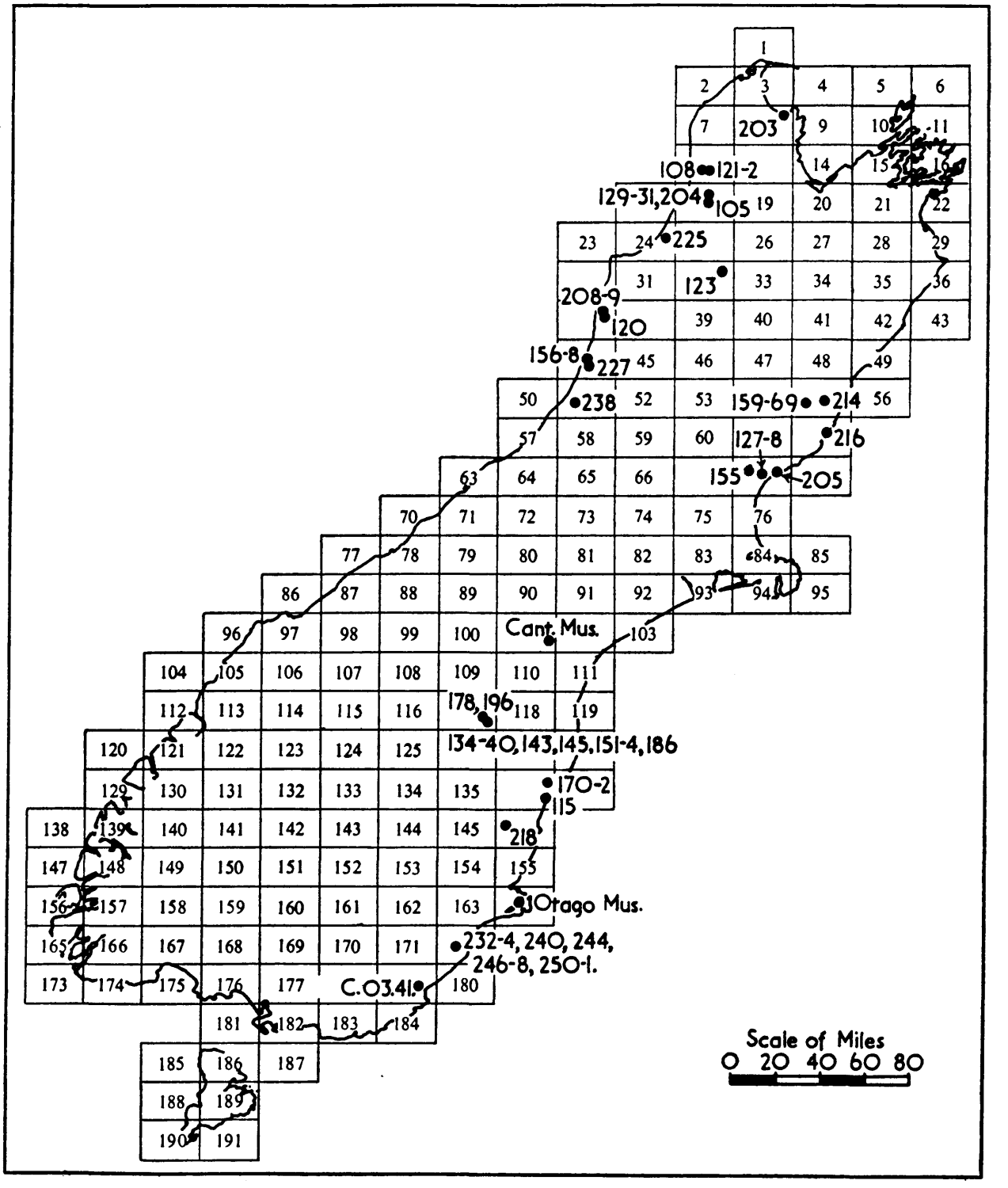


Fig. 24. Geographic distribution of fossil decapod Crustacea in sheet districts of the 1 mile to the inch topographic map series (N.Z.M.S. 1) (South Island). Numbers shown against localities refer to N.Z. Geological Survey register of fossil Crustacea (prefix DC).

NOTE: C. 03.41 refers to collection in Otago Museum; for Otago Mus. read Auckland War Memorial Museum; Cant. Mus. = Canterbury Museum.

N111/498 Wanganui River, east bank, about 12 miles below Taumarunui, near contact between Mokau and Mahoenui beds. Coll. F. D. Gemmell, Mar 1925. ? Altonian (by local stratigraphy).
Tumidocarcinus giganteus Glaessner. DC 177

N119/503 Stanley Road, Huiroa S.D., road cutting 2 chains north of bridge over Makino River (GS 7203). Grid ref. 942684. Coll. Miss D. Rodley, Mar 1958. Kapitean (associated Mollusca).
Leptomithrax atavus Glaessner. DC 253–8 (T255)

N132/501 Taihape-Waiouru main highway, 100 yards north of HMNZS *Irirangi*, Naval Radio Station, from transported shell rock at side of road. Probably from Waiouru Reef-bearing Sandstone. (The District Commissioner of Works, Wanganui, reported in May 1959 that this shell rock probably came from the Ministry of Works pit, one mile south of the Turangi turnoff). Coll. T. Hosking, 1953. ? Opoitian (from local stratigraphy).
Leptomithrax irirangi. DC 223

N135/522 Maraetotara River, Kidnapper S.D. north-west of high terraces (grid ref. 396174), Kidnapper Group (GS 5315). Coll. T. Grant-Taylor, Mar 1951. Castlecliffian, Putikian (associated Mollusca).
Ctenocheles cf. *maorianus* Powell. DC 107

N137/494 Castlecliff-Kai Iwi coast section (grid ref. 485889), Pinnacle Sandstone (GS 4099). Coll. C. A. Fleming and J. Marwick, Feb 1945. Type Castlecliffian, Putikian Substage.
Ovalipes cf. *punctatus* (de Haan). DC 116

N137/495 Castlecliff-Kai Iwi coast section (grid ref. 467903), Gastropod Shell Bed member of Kupe Formation (GS 4042). Coll. C. A. Fleming, Feb 1945. Type Castlecliffian, Putikian Substage.
Ctenocheles cf. *maorianus* Powell. DC 109–11

N137/496 Castlecliff-Kai Iwi coast section (grid ref. 483892). Fallen blocks from Tainui Shell Bed (GS 4101). Coll. C. A. Fleming and J. Marwick, Feb 1945. Type Castlecliffian, Putikian Substage.
Cancer novaezealandiae (Jacquinot and Lucas). DC 104

N137/512 Castlecliff-Kai Iwi coast section (grid ref. 492883). Castlecliffian Shell Bed (GS 4021). Coll. G. J. Lensen, Sept 1956. Type Castlecliffian, Putikian Substage.
Ctenocheles cf. *maorianus* Powell. DC 231

N137/493 Castlecliff-Kai Iwi coast sections, formation uncertain. Castlecliffian.
Ctenocheles cf. *maorianus* Powell. Vict. Univ.
Paramithrax minor Filhol. Dom. Mus.
Cancer novaezelandiae (Jacquinot and Lucas). Vict. Univ.

N137/539 Nukumaru Beach (grid ref. 332956), Nukumaru Brown Sand. (GS 4115). Coll. C. A. Fleming, Feb 1945. Type Nukumaruan (Marahauan Substage).
Cancer novaezealandiae (Jacquinot and Lucas). DC 102

N139/502 Pakihikura Bridge, Rangitikei Valley, boulders from about 80 ft below Pakihikura Pumice. Mangahou Siltstone. Coll. M. T. Te Punga and C. A. Fleming, Dec 1945; Jan 1958. Nukumaruan, Marahauan Substage (by stratigraphic correlation).
Hemiplax major Glaessner. DC 228–9(T), 237

N141/494 Te Aute, Hawke's Bay (GS 833). Te Aute Limestone. Coll. A. Hamilton. Waitotaran (associated Mollusca).
Cancer noveazealandiae (Jacquinot and Lucas). DC 263–4

N149/479 Mangahao S.D. Bridge over Matarua Creek (GS 2811). Coll. J. Marwick, 1932. Waitotaran (associated Mollusca).
Hemiplax sp. DC 212

N150/479 Mangaotoro S.D. Mangahe Stream (grid ref. 745495), Mangatoro Formation (GS 5694). Coll. A. R. Lillie, Mar 1940. Opoitian (by local stratigraphy).
Cancer novaezealandiae Jacquinot and Lucas. DC 114

N162/803 Ruamahanga River, Gladstone, fossiliferous sandstone (GS 3113). Coll. D.A. Cowie, 1958. Nukumaruan (associated Mollusca).
Cancer novaezealandiae Jacquinot and Lucas. DC 260

N165/568 Putangirua Stream, Palliser Bay (= GS 5485). Hurupi Formation. Coll. D. A. Cowie, 1958. Tongaporutuan (associated Mollusca and Foraminifera).
Callianassa sp. b. DC 261

SOUTH ISLAND

S8/498 Tarakohe Marl Pit, Golden Bay, Tarakohe Mudstone (= GS 1286). Coll. Mr Ulrich, Golden Bay Cement Works. Lower Altonian (associated Foraminifera).
Jasus flemingi Glaessner. DC 203(T)

S12/516 Oparara S.D., Postal Creek, 2 chains below junction with Scorpion Creek (grid ref. 639406), GS 4762. Coll. H. W. Wellman and G. W. Grindley. 1948. Altonian (associated Foraminifera).
Lyreidus elegans Glaessner. DC 108

S12/521 Oparara S.D., Postal Creek, 50 chains above junction with Scorpion Creek (grid ref. 644418), GS 4752. Coll. H. W. Wellman and G. W. Grindley, 1948. Clifdenian (associated Mollusca).
Galene proavita Glaessner. DC 121–2

S18/564 Otumahana S.D. Huia Stream, 15 chains up from junction with Bellbird Stream (grid ref. 689285; GS 4771). Coll. H. W. Wellman, G. W. Grindley and E. J. Annear. Altonian (associated Foraminifera).
Tumidocarcinus sp. indet. DC 105

S18/566 Otumahana S.D., Bellbird Stream, 35–45 chains above junction with Huia Stream (grid ref. 692258, GS 4773). Coll. H. W. Wellman and G. W. Grindley, 1948. Clifdenian (associated Mollusca).
Galene proavita Glaessner. DC 129–31, 204 (T129 + 130 + 204)

S24/506 Mokihinui S.D. Patten Creek, coastal strip 2 miles south of Mokihinui River (grid ref. 401966, GS 3642). Coll. H. W. Wellman, May 1946. Lower Tongaporutuan (associated Foraminifera).
Tumidocarcinus giganteus Glaessner. DC 225

S32/594 Tutaki S.D., Earthquake slip west of point where Campbell Creek meets river flats (grid ref. 815645, GS 4719). Coll. R. P. Suggate, Dec 1948. Upper Pareora-Southland Series (associated Foraminifera).
Lyreidus elegans Glaessner. DC 123 (T)

S37/495 Woodpecker Bay near Brighton, "Island Sandstone", GS 31. Coll. A. McKay, 1874. The collection is from a range of beds but Mr N. de B. Hornibrook identified Whaingaroan Foraminifera (F 8265) from DC 120.
Tumidocarcinus tumidus (Woodward). DC 120 (?topotype).

S37/579 Brighton S.D., coast opposite Hunter's (grid ref. 878374), fossiliferous polyzoan band at base of limestone (GS 3676), Coll. H. W. Wellman, 1945. Duntroonian (associated Foraminifera, F 8266–7).
Tumidocarcinus tumidus (Woodward). DC 208–9

S44/465 Cobden Limestone, Greymouth (GS 35). Coll. A. McKay, 1873. Whaingaroan-Duntroonian (by local stratigraphy).
Tumidocarcinus tumidus (Woodward). DC 227

S44/737 Cobden S.D. Port Elizabeth Beach (grid ref. 750966). Coll. H. W. Wellman and M. Gage, May 1949. Type Runangan.
Tumidocarcinus tumidus (Woodward). DC 156–8

S51/583 Waimea S.D. South side of Goldsborough-Kumara Road, one mile west of Goldsborough (grid ref. 670602; GS 4588). Coll. H. W. Wellman and R. P. Suggate, Jul 1948. Kapitean (associated Mollusca).
Pseudocarcinus sp. DC 238

S55 (?) Waiau-ua River, Amuri County (GS 321). Coll. J. Buchanan. 1867. Locality and horizon uncertain. The crustacea are associated with Wanganui Series Mollusca.
? Paguridae, indet. DC 159–69

S55/23 Hawkwood S.D. Rail cutting, 20 chains south of main highway bridge over railway, 2½ miles north of Parnassus (grid ref. 600625; GS 2827). Coll. H. E. Fyfe and J. Marwick, Apr 1934. Nukumaruan (associated Mollusca).
Cancer novaezealandiae (Jacquinot and Lucas). DC 214

S62/98 Cheviot S.D. Coast, 60 chains north of Jed River (grid ref. 627388; GS 2839). Coll. H. E. Fyfe, Jan 1934. Nukumaruan (associated Mollusca).
Cancer novaezealandiae (Jacquinot and Lucas). DC 216

S68/192 Teviotdale S.D. Gully joining Lower Waipara Gorge (grid ref. 128079; GS 4997). Double Corner Formation. Coll. D. R. Gregg, Dec 1949. Waitotaran (associated Mollusca).
Ovalipes sp. a. DC 127–8

S68/251 Mount Brown, Waipara River (GS 66). Coll. A. McKay, 1874. Otaian-Waiauan (by local stratigraphy).
Ommatocarcinus arenicola Glaessner. DC 155 (holotype)

S68/722 Teviotdale S.D. Cliff 200 yards north of mouth of Dovedale stream (grid ref. 237085). Dovedale Siltstone. Coll. G. M. Smart, 1953. Waiauan (associated Foraminifera).
Tumidocarcinus giganteus Glaessner. DC 205

S101/499 Raincliff, South Canterbury. Coll. M. C. Gudex (Presumably from the horizon of the "crab beds and marls" described by Gudex in the nearby Pareora District). Bortonian-Kaiatan (by local stratigraphy).
Tumidocarcinus tumidus (Woodward). Cant. Mus.

S117/489 Kurow S.D., Wharekuri, Waitaki Valley, Wharekuri Greensand. (GS 486). Coll. A. McKay, 1880. Duntroonian (associated Foraminifera and Mollusca).
Tumidocarcinus tumidus (Woodward) DC 134–5, 137–9, 145, 151–2, 154
Tumidocarcinus dentatus Glaessner. DC 136, 140, 143(T), 153, 186; Dominion Museum; Adelaide Univ.

S117/492 Kurow S.D. Fishing Rock, Wharekuri, Waitaki River, Wharekuri Greensand (GS 1341). Coll. P. Marshall, 1927. Duntroonian (associated Mollusca).
Tumidocarcinus tumidus (Woodward). DC 178, 196.

S136/696 Oamaru S.D. Beach at Three Roads (grid ref. 500590). Rifle Butts Formation (GS 5665). Coll. M. Gage, Nov 1947. Awamoan (by local stratigraphy).
Ommatocarcinus sp. DC 115

S136/821 Oamaru S.D. Hutchinson's Quarry (grid ref. 539668) "loose calcareous greensands" (GS 172). (Gee Greensand). Coll. A. McKay, 1876. Type Hutchinsonian.
Menippe sp. DC 170–172

S146/534 Waihemo S.D. Road corner where Palmerston highway meets Green Valley Stream (grid ref. 161425). Concretions in Holocene gravel (GS 2119). Coll. D. A. Brown, Apr 1948. Bortonian (associated Mollusca).
Callianassa sp. DC 218

S164/484 Otago Harbour. Concretions from raised beach. Post-Pleistocene.
Hemiplax hirtipes Heller. Auckland War Memorial Museum.

S172/520 Clarendon S.D. Snowdrift Quarry, Milburn (grid ref. 752460). Bortonian concretions from base of Landon Series Limestone. Coll. H. W. Wellman (1942 (GS 2977)) and N. de B. Hornibrook, Jan 1957 (GS 6793). Bortonian (associated Mollusca).
Laeviranina perarmata Glaessner. DC 233, 246(T), 247, 250
Portunites granulifer Glaessner. DC 232(T), 234, 240, 244, 248, 251.

S179/461 "Ahuriri Flat", Clutha (i.e. 2 miles south-east of Glenomaru). Indurated siltstone. Coll. W. J. Sherry, 1903. Liassic, probably Ururoan Stage (by local stratigraphy).
Glypheopsis antipodum Glaessner. C 03 41, Otago Museum (T).

APPENDIX 3. STRATIGRAPHIC DISTRIBUTION OF DECAPOD COLLECTIONS

The collections listed geographically on pp. 55–8 are classified stratigraphically below.

JURASSIC

Liassic (? Ururoan Stage): S179/461
Kimeridgian (Heterian Stage): N51/610
Tithonian (Puaroan Stage): N73/655

CRETACEOUS

Maestrichtian (Haumurian Stage): N15/498, N15/499, N62/531

EOCENE

Bortonian Stage: S146/534, S172, 520
Bortonian-Kaiatan: S101/499
Runangan Stage: S44/737

OLIGOCENE

Whaingaroan Stage: S37/495
Whaingaroan-Duntroonian: S44/465
Duntroonian Stage: S37/579, S117/489, S117/492
Otaian Stage: N91/14, N91/517
Otaian-Waiauan (Miocene): S68/251

MIOCENE

Hutchinsonian Stage: S136/821
Awamoan Stage: S136/696
Upper Pareora-Southland Series: S32/594
Altonian Stage: N28/545, N111/498 (?), S8/498, S12/516, S18/564
Clifdenian Stage: S12/521, S18/566
Lillburnian Stage: N110/12, N110/28(?)
Lillburnian-Tongaporutuan: N100/16, N100/21
Waiauan Stage: S68/722
Tongaporutuan Stage: N99/500, N100/22, N110/29(?), N110/30(?), N110/31(?), N165/568, S24/506
Kapitean Stage: N119/503, S51/583

PLIOCENE

Lower Pliocene (Opoitian Stage): N132/501(?), N150/479
Upper Pliocene (Waitotaran Stage): N141/494, N149/479, S68/192
Pliocene-Lower Pleistocene: S55(?)

PLEISTOCENE

Lower Pleistocene (Nukumaruan Stage): N137/539, N139/502, N162/803, S55/23, S62/98
Middle Pleistocene (Castlecliffian Stage): N69/501, N135/522, N137/494, N137/495, N137/496, N137/512, N137/493
Post Pleistocene: N33(?), S164/484.

INDEX

(New species, new genera, and systematic references are printed in bold type.)

abdomen, 44, 45.
adaptive radiation, 45.
Adelaide, 24.
adductor lateralis mandibulae, 38, 39.
adductor testis muscle, 39, 43, 44.
Adelaide University, 24, 28.
Ahuriri Flat, 8.
Aldinga, 24.
Altonian, 16, 25.
Anaspididae, 43.
Anomocarida, 42.
Anomura, 48.
antennatus, Archaeopus, 47.
anterior chamber, 38, 39, 42, 43.
anterior gastric muscles, 38.
antipodum, *Glypheopsis*, **8.**
apodemes, 38.
arnesoni, Camarocarcinus, 46.
Archaeopus, 46, 47.
  antennatus, 47.
araucanus, Portunites?, 33.
  Raninoides, 33.
arenicola, *Ommatocarcinus*, **28.**
Astacus fluviatilis, 38.
atavus, *Leptomithrax*, **17,** 32.
Atelecyclidae, 46.
attachment areas of muscles, 38.
attractor epimeralis muscle, 38, 39, 42.
Auckland Harbour, 21.
Auckland Museum, 31.
Aulacosphinctoides Zone, 10.
Australia, 25, 29, 33, 35.
Avitelmessus, 46.
  grapsoideus, 47.
awakina, *Callianassa*, **10.**
Awakino-Mahoenui, 10.
Awamoan, 25, 30.
Axiidae, 48.

Balcombian, 24, 29, 33.
barnacles, 17, 32.
Basal Altonian, 13.
Bellbird Stream, 30.
bispinosa, Galene, 31.
Bortonian, 12, 15, 21, 24, 26, 33.
Bossard, L., 27.
Boreomysis, 43.
Brachyrhyncha, 45, 46, 47.
Brachyura, 38, 42, 45, 48.
branchial chamber, 38, 43.
branchio-cardiac furrow, 38, 39, 42, 43, 44, 46.
branchiostegite, 38.
Brighton, 25, 26.
British Museum, Natural History, 25.
Brown, D. A., 12.
Buchanan, J., 32.

Cainozoic, 33.
Calappa, 34.
Calappidae, 36, 46.
Calappilia, 46.
Callianassa, **10,** 12, 32.
  awakina, 10.
  waikurana, 11, 32.
  sp. a, **12,** 32.
  sp. b, **12.**
Callianassidae, 10.
Camarocarcinus arnesoni, 46.
Campbell Creek, 16.
Cancer, **20,** 32.
  novaezealandiae, **20,** 34.
Cancridae, 20, 46.
Cancriformia, 46.
Canterbury Museum, 26.
carapace, 26, 38, 39, 44.
Carcineretes, 46, 47.
Carcineretidae, 47.
Carcinoplax, 30.
Carcinus, 45.
cardiac ridge, 46.
Castlecliff, 13, 21, 34.
Castlecliffian, 13, 21, 22, 34.
Catometopa, 47.
cephalic region, 44.
cephalothorax, 36, 38.
cervical sulcus (transverse furrow), 39, 42, 44.
chelipeds, 37.
Clifdenian, 25, 30, 34.
Cobden Limestone, 26.
concretions, 32.
Cowie, D., 12, 21.
Cox, S. H., 25.
crabs, origin of, 36.
Crangonoida, 48.
Ctenocheles, **13,** 34.
  cf. *maorianus*, **13.**
  maorianus, 34.
Cymopolia, 46.

Dakoticancridae, 46, 47.
dentatus, *Tumidocarcinus*, **28,** 33.
Dominion Museum, 28, 34.
Doubtless Bay, 22.
Dovedale Stream, 27.
Dromiacea, 45, 46, 47.
Duntroonian, 24, 26, 28, 32.
Dynomenidae, 46.

East Africa, 29.
East Cape Peninsula, 11.
East Wellington, 12.
elegans, *Lyreidus*, **16.**
Ellis, H. A., 27.
endoskeleton, 37.
Eocarcinus, 45.
Eocene, 25, 33, 35.
epigastric regions, 38.
epimeral fold, 38, 39, 43, 45.
epipodite, 38.
Eryma, 42.
Erymaidae, 42, 48.
Eucopia, 43.
Eucyphidea, 48.
Euphausiacea, 43.
Evans, H. J., 18.

facial sutures, 39.
Fiji, 35.
Fishing Rock, 26.
Fitzgerald, F. G., 12.
Fleming, C. A., 8, 10, 19, 21, 31, 32.

flemingi, *Jasus*, **13.**
fluviatilis, *Astacus*, 38.
Fyfe, H. E., 21.

Gage, M., 26, 30.
Galathea strigosa, 45.
Galatheidae, 45.
Galatheidea, 38, 42, 44, 45, 48.
Galene, **30,** 34, 35.
bispinosa, 31.
proavita, 30.
Galenopsis, 30.
Gambier Limestone, 33.
Gastralida, 39, 48.
gastric muscles, 38.
gastricus posterior, 38.
Gemmel, F. D., 27.
Geological Survey of Victoria, 25.
Geryonidae, 46.
giganteus, *Tumidocarcinus*, **27,** 33.
gill chamber, 38, 39, 42.
Gill, E. D., 24.
Gippsland, 33.
Glenoamaru, 8.
Glypheidae, 8.
Glypheocarida, 48.
Glypheopsis, **8.**
antipodum, 8, 32.
Glypheidea, 48.
Glypheocarida, 42.
Golden Bay Cement Works, 13.
Golden Bay, Nelson, 13.
Goldsborough-Kumara Road, 23.
Goneplacidae, 28, 46, 47.
Goneplax, 29.
Goniocypoda, 47.
Grange, L. I., 18, 27.
Grant Taylor, T., 22.
granulifer, *Portunites*, **21,** 33.
Grapsidae, 46.
grapsoideus, *Avitelmessus*, 47.
Green Valley, 12.
Gregg, D. R., 23.
Greymouth, 26.
Grindley, G. W., 16, 30.
Gudex, M. C., 26.
Gymnopleura, 46.

Hamilton, A., 21.
Harpactocarcinus, 25.
"*Harpactocarcinus*" *victoriensis*, 25.
Haumurian Stage, 11, 12, 32.
Hautawan Substage, 21.
Healy, J., 22.
Hemiplax, **31,** 32, 34, 35.
hirtipes, **31.**
Hemiplax? **major, 31.**
Herangi Series, 8.
Herpochelida, 48.
Heterian, 9, 32.
Heterochelida, 48.
Heterura, 49.
Hexapodinae, 47.
Hippidea, 48.
hirtipes, *Hemiplax*, **31.**
Homarus, 38, 42.
Homolidae, 46.
Hornibrook, N. de B., 13, 15, 21, 25.
Hosking, T., 19.
Huia Stream, 25.
Hutchinsonian, 33.
Hutchinson's Quarry, 23.

Indo-Pacific Region, 35.
intestinal region, 38.
irirangi, *Leptomithrax*, **19.**
Irirangi Naval Radio Station, 19.

Jasus, **13,** 14, 34.
flemingi, 13.
Janjukian, 24, 25, 33.
Jed River, Marlborough, 21.

Kaiatan, 24, 26, 33.
Kai Iwi, 13, 21.
Kaipara Harbour, 25, 31.
Kapitean, 17, 24.
Kawhia-Raglan Road, 10.
Kear, D., 10.
Kimmeridgian, 9.
Klondyke, 9.
Komiti, 25.
Kupe Formation, 13.

Laeviranina, **15,** 16, 33.
perarmata, 15, 33.
Lakes Entrance, 25.
Lakes Entrance Formation, 33.
Leptomithrax, **17,** 32, 34, 35.
atavus, 17, 32.
irirangi, 19.
uruti, 18.
Leucosiidae, 46.
Liassic, 8.
Lillburnian, 25, 27.
Lillie, A. R., 21.
Limestone Creek, 26.
linea anomurica, 39.
linea homolica, 39.
linea thalassinica, 39.
lineae, 39.
Lissocardia, 42.
Litogaster, 42, 43, 48.
Longford, 25.
Longford Limestone, 33.
Longford Substage, 25.
Longfordian, 24.
Lophoranina, 35.
Lower Castlecliff Shellbed, 13.
Lower Kimmeridgian, 32.
Lower Miocene, 13, 24, 30.
Lower Oligocene, 26.
Lower Pleistocene, 21, 31, 34.
Lower Pliocene, 19, 21, 24, 33.
Lower Tithonian, 10, 32.
Lower Waipara River, 23.
Lyreidus, **16,** 33, 35.
elegans, 16.

McKay, A., 23, 26, 28.
McNeil, (F.), 17.
Macrophthalmus, 47.
Macrura, 44.
Maestrichtian, 11, 12, 32.
Magila, 48.
Mahoenui Group, 11.
Majidae, 17.
major, *Hemiplax*?, **31.**
Makino River, 17.
Malacostraca, 44.
mandible, 43.
mandibular joint, 39, 42.
mandibular muscles, 38.
mandibular segment, 39, 44.
Mangahou Siltstone, 31.
Mangaone Valley, 27.
Mangaruhia Creek, 10.

maorianus, *Ctenocheles*, 34.
maorianus, *Ctenocheles*, cf., **13.**
Maraekowhai, 27.
Maraetotara River, 22.
Marshall, P., 26, 27.
Marwick, J., 10, 32.
marwicki, *Mecochirus*, **9**, 32.
Marwicki Zone, 13.
Matarua Creek, 32.
maxillipeds, 37, 38.
Mecochiridae, 9.
Mecochirus, **9**, 10, 32.
marwicki, 9. 32.
sp., **10.**
median suture, 39.
Melbourne, Victoria, 24.
Menippe, **23**, 35.
sp., **23.**
mesogastric region, 39.
mesogastric sulcus, 39.
mesogastric-cardiac ridge, 46.
Mesozoic, 35.
Mid-Pleistocene, 21.
Middle Eocene, 12, 15, 21, 24, 26, 33.
Middle Miocene, 27, 29.
Milburn, Otago, 15, 21.
Milne Edwards, H., 13.
minor, *Paramithrax*, 34.
Miocene, 16, 24, 25, 29, 30, 33, 35.
Mokau Group, 11.
Moki Road, 27.
Mokihinui River, 27.
morphogenetic trends, 42.
Mt. Brown, 28.
Mt. Gambier, South Australia, 33.
Mysidacea, 42, 43.

Natantia, 48.
Nebalia, 44.
Necrocarcinus, 46.
Nectochelida, 48.
Nelson, 13.
Nephrops, 42.
Nephropsidea, 42, 48.
North Auckland, 12.
Notopocorystes, 46.
novaezealandiae, *Cancer*, **20**, 34.
Nukumaru Beach, 21.
Nukumaruan, 21, 31, 34.

Ocypodidae, 31, 46, 47.
Ocypodoida, 47.
Ohauan, 32.
Ohope Beach, Bay of Plenty, 22.
Okaihau, 12.
Oligocene, 24, 25, 28, 29, 32, 35.
Ommatocarcinus, **28**, 29, 33, 35.
arenicola, 28.
corioensis, 33.
sp., 29.
Oparara River, 16.
Opthalmoplax, 46, 47.
Opoitian, 19, 21.
Orithopsis, 46.
Otago Harbour, 31.
Otago Museum, 8.
Otaian, 11, 29, 33.
Ototaran Series, 25.
Ovalipes, **22**, 23, 34.
cf. *punctatus*, **22.**
sp. a, **23.**
Oxyrhyncha, 35, 45, 46, 47.
Oxystomata, 36, 46.

Paguridea, 44, 48.
pagurids, 32.
Pakaurangi Point, 25.
Pakihikura Bridge, 31.
Pakihikura Tuff, 31.
Palaemonoida, 48.
Palinura, 42, 48.
Palinuridae, 13.
Palinurus, 38, 43.
Palliser Bay, 12.
Palmerston Road, N. Otago, 12.
Paramithrax minor, 34.
Paranephropsidea, 48.
Parnassus, 21.
Patten Creek, 27.
Pemphicidea, 45, 48.
Pemphix, 39, 42, 43, 48.
Penaeidea, 48.
perarmata, *Laeviranina*, **15**, 33.
pereiopods, 37, 45.
Phyllocarida, 43.
Pinnacle Sand Formation, 13.
Plagiolophus vancouverensis, 47.
Pleistocene, 22, 34, 35.
Pliocene, 21, 24, 34, 35
Port Elizabeth Beach, 26.
Port Vincent, South Australia, 24.
Porcellanidae, 45.
Portunidae, 21, 45, 46, 47.
Portunites, **21**, 32.
Portunites ? *araucanus*, 33.
Portunites **granulifer, 21**, 33.
Postal Creek, 16.
post-cervical furrow, 32, 42, 43, 44.
Post-Pleistocene, 31.
Post-Tertiary, 21.
Powell, (A. W. B.), 17.
proavita, *Galene*, **30.**
Prosoponidae, 45.
Pseudocarcinus, **23**, 33.
sp., **23.**
Pseudoglyphea, 42, 43, 48.
Pseudopemphix, 42, 43, 48.
pseudo-rostrum, 46.
pterygostomal suture, 39.
Puaroan Stage, 10.
punctatus, *Ovalipes*, cf., **22.**
Purser, B. H., 9.
Putangirua Creek, 12.
Pygocephalomorpha, 43.

Queensland, 29.

Raincliff, South Canterbury, 26.
Rangitikei River, 31.
Raninidae, 15, 36, 46.
Raninoides, 16, 32, 33.
Raninoides ? *araucanus*, 33.
regions, 38.
Reptantia, 48.
Rerekino Trig., 18.
Retroplumidae, 47.
Rodley, D., 17.
rostral spines, 46.
Ruamahanga R., Gladstone, 21.
Runangan, 24, 25, 26, 33.

Sakai, [T.], 17.
scaphognathite, 38.
Schluteria tetracheles, 48.
Scyllaridea, 42.
Seal Rock, 25.
segmental boundaries, 44.
Sherry, W. J., 8.

sillon inférieur, 38.
Smart, G. M., 27.
Snowdrift Quarry, Clarendon, Otago, 15, 21, 32.
Southland Series, 16.
Stanley Road, 17.
Stenopodidea, 48.
subsidiary furrows, 39.
Suggate, R. P., 16, 23.
Surveyor's Point, 24.
Syncarida, 43.

Tahora, 27.
Tainui Shellbed, 21.
Tangarakau River, 27.
Tarakohe Marl Pit, 13.
Taumarunui, 27.
Te Aute, Hawke's Bay, 21.
telson, 44.
Te Punga, M. T., 31.
Thalassinidea, 44, 48.
thoraco-abdominal muscles, 38.
thoracopods, 37.
thorax, 36, 38.
Three Roads, 30.
Tongaporutuan, 12, 24, 25, 27.
transverse furrows, 39, 42.
Trichelida, 48.
Tumidocarcinus, 24, 25, 32, 33, 25.
  dentatus, 28, 33.
  giganteus, 27, 33.
  tumidus, **25,** 33.
tumidus, **Tumidocarcinus, 25,** 33.

Ulrich, 13.
University of Auckland, 9.
Upper Castlecliff Shellbed, 13.
Upper Eocene, 24, 26, 33.
Upper Jurassic, 10.
Upper Miocene, 12, 17, 18, 24, 27, 35.
Upper Oligocene, 11.
Upper Pareora Series, 16.
Upper Piripauan, 11.
Upper Pleistocene, 13.
Upper Pliocene, 23.
Upper Tongaporutuan, 18.
Utakura River, 12.
Urenui beds, 18.
Ururoan, 8.
uruti, *Leptomithrax*, **18.**
Uruti, P. O., 18.

Victoria University of Wellington, 13, 21.

Waiauan, 29, 33.
Waiau-ua River, 32.
Waikato Heads, 9.
Waikura Stream, 11.
waikurana, *Callianassa*, **11,** 32.
Waiouru Reef-bearing Sandstone, 19.
Waipara River, 28.
Waitaki River, 24, 26, 28.
Waitakian, 25.
Waitangi River, 12.
Waitotaran, 21, 23, 32.
Wanganui River, 27.
Washburne, C. W., 10.
Wellman, H. W., 11, 15, 16, 21, 23, 25, 26, 27, 30, 32.
Whaingaroan, 25, 26, 33.
Wharekuri, 26, 28.
Wharekuri Greensand, 24, 28.
Withers, T. H., 25.
Woodpecker Bay, 25, 26.
Wray's Quarry, 18.

Xanthidae, 23, 46.
Xanthopsis, 32, 33, 35.

Yaldwyn, J. C., 22, 34.

PLATES

PLATE 1

Jasus flemingi Glaessner, n. sp. (page 13)

Holotype × $\frac{3}{5}$ (DC 203). Tarakohe Marl Pit, Lower Altonian.

0 1 2 3 4 5

PLATE 2

Glypheopsis antipodum Glaessner, n. sp. (page 8)

Fig. 1. Holotype. Dorsal view of carapace, first abdominal segments and fragments of pereiopods, × 1. (Otago Museum, C.03,41) "Ahuriri Flat, Clutha", ?Ururoan.

Mecochirus marwicki Glaessner, n. sp. (page 9)

Fig. 2. Holotype. Contours outlined in ink, ×1·3. (DC 266).
a – anterior portion, before preparation, seen from ventral side.
b – posterior portion, counterpart (dorsal view) photographically reversed and placed relative to anterior portion as preserved in the rock. Waikato Heads, Heterian.
Fig. 3. Paratype. Dorsal view of anterior portion of carapace and posterior portion of abdomen. From the rock specimen containing the holotype.

Callianassa awakina Glaessner, n. sp. (page 10)

Fig. 4. Holotype. External view of propodus of left chela, × 1. (DC 194a) Awakino Valley, Otaian (GS 5771).
Fig. 5. Paratype. Internal view of propodus of left chela, × 1. (DC 117) Awakino Valley, Otaian (GS 2592).

Callianassa waikurana Glaessner, n. sp. (page 11)

Fig. 6. Holotype. External view of right chela, × 1. (DC 219) Waikura Stream, Haumurian (GS 6561).

Callianassa sp. a (page 12)

Fig. 7. External view of propodus of left chela, × 1. (DC 220) Utakura R., Haumurian.

Callianassa sp. b (page 12)

Fig. 8. External view of left chela, × 1. (DC 261) Putangirua Creek, Tongaporutuan (GS 5485).

Ctenocheles cf. **maorianus** Powell (page 13)

Fig. 9. Finger of right smaller chela, × 1·5. (DC 110) Castlecliff, Castlecliffian (GS 4099).
Fig. 10. Finger of right larger chela, × 1·5. (DC 107) Kai Iwi, Castlecliffian (GS 4042).
Fig. 11. Finger of left smaller chela, × 1·5. (DC 111) Castlecliff, Castlecliffian (GS 4099).
Fig. 12. Fragmentary propodus of right smaller chela, × 1·5. (DC 231) Castlecliff, Castlecliffian.

Laeviranina perarmata Glaessner, n. sp. (page 15)

Fig. 13. Carapace of holotype. Left margin damaged, right antero-lateral tooth represented by an impression which was whitened in the photograph, × 1. (DC 246) Snowdrift Quarry, Bortonian (GS 2977).
Fig. 14. Right chela, × 1, Paratype (DC 233) Snowdrift Quarry, Bortonian (GS 2977).

Lyreidus elegans Glaessner, n. sp. (page 16)

Fig. 15. Carapace, frontal portion missing, × 1·5, Paratype (DC 108) Postal Creek, Altonian (GS 4099).
Fig. 16. Carapace, frontal portion missing, and with transverse and longitudinal fractures, × 1, Holotype (DC 123) Campbell Creek, Upper Pareora or Southland Series (GS 4719).

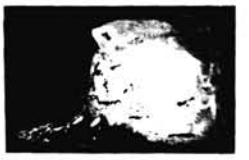
Leptomithrax uruti Glaessner, n. sp. (page 18)

Fig. 17. Carapace of holotype, × 1. (DC 175) Uruti, Tongaporutuan (GS 1139).

1

2a

2b

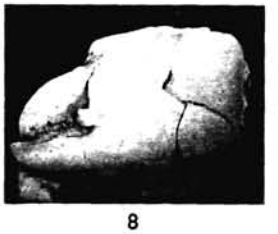


4

5

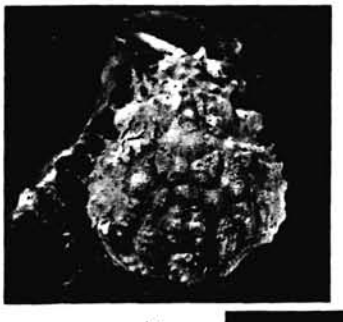
6

7



8

3



17

13

9
10
11

14

15

16

12

PLATE 3

Leptomithrax atavus Glaessner, n. sp. (page 17)

Fig. 1. Dorsal view of holotype, × 1. (DC 255) Makino River, Kapitean (GS 7203).

Leptomithrax uruti Glaessner, n. sp. (page 18)

Fig. 2. Dorsal view of holotype, × 2·4. (DC 175) Uruti, Tongaporutuan (GS 1139).

Leptomithrax ririangi Glaessner, n. sp. (page 19)

Fig. 3. Dorsal view, × 1. (DC 223) Ririangi, Opoitian.
Fig. 4. Anterior portion of ventral side, × 1. (DC 223) Ririangi, Opoitian.

Cancer novaezealandiae (Jacquinot and Lucas) (page 20)

Fig. 5. Part of ventral side showing left chela and abdomen, × 1. (DC 114) Mangaotoro S.D., Opoitian (GS 5694).
Fig. 6. Dactylus of left chela, × 1. (DC 104) Castlecliff, Castlecliffian (GS 4101).

Portunites granulifer Glaessner, n. sp. (page 21)

Fig. 7. Dorsal view of holotype showing the carapace and the ridged upper surface of the carpus of the right cheliped, × 1. (DC 232) Snowdrift Quarry, Bortonian (GS 2977).

Ovalipes cf. **punctatus** (de Haan) (page 22)

Fig. 8. External surface of dactylus of right chela, × 1. (DC 215) Ohope, Castlecliffian (GS 3893).

Ovalipes sp. a (page 23)

Fig. 9. External surface of finger of right chela showing elongate projections on granulated ridges, × 1. (DC 128) Lower Waipara, Waitotaran (GS 4997).

Menippe sp. (page 23)

Fig. 10. External surface of right immovable finger, × 1. (DC 170) Hutchinson's Quarry, Hutchinsonian (GS 172).

Pseudocarcinus sp. (page 23)

Fig. 11. External view of dactylus of right (larger) claw, tip restored, × 1. (DC 238) Goldsborough, Kapitean (GS 4588).

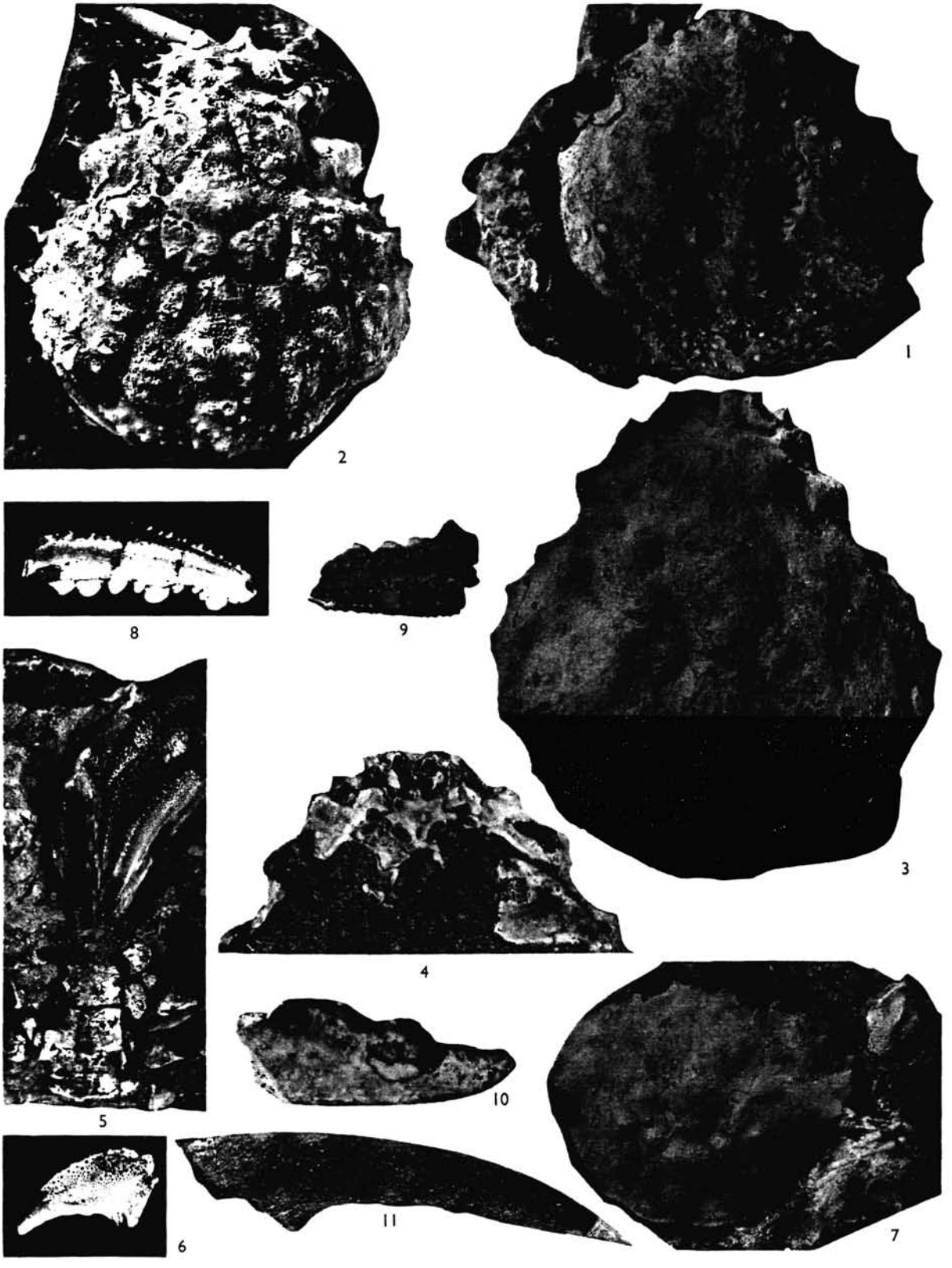

1
2
3
4
5
6
7
8
9
10
11

PLATE 4

Tumidocarcinus tumidus (H. B. Woodward) (page 25)

Fig. 1. Plaster cast of holotype, dorsal side, × 1. (DC 211) Woodpecker Bay, Brighton, Whaingaroan-Duntroonian.

Fig. 2. Plaster cast of holotype, ventral side, × 1. (DC 211) Woodpecker Bay, Brighton, Whaingaroan-Duntroonian.

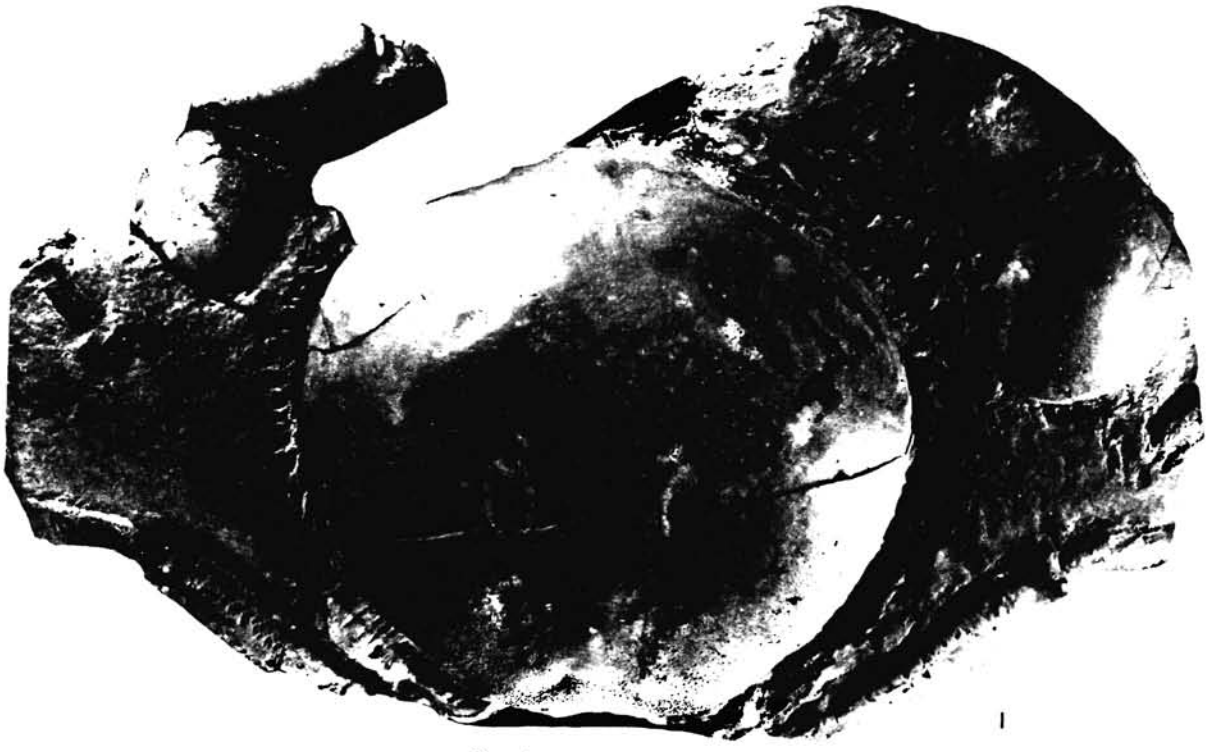
1

2

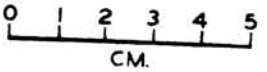
PLATE 5

Tumidocarcinus giganteus Glaessner, n. sp. (page 27)

Fig. 1. Holotype, dorsal side, × ⅔ (approx.) (DC 181) Pouatu S.D., ?Lillburnian (GS 7555).
Fig. 2. Holotype, ventral side, × ⅔ (approx.) (DC 181) Pouatu S.D., ?Lillburnian (GS 7555).



1



2

PLATE 6

Tumidocarcinus giganteus Glaessner, n. sp. (page 27)

Fig. 1. Dorsal side of paratype, × 1. (DC 205) Dovedale, Waiauan.
Fig. 2. Ventral view of paratype, showing male abdomen, × 1. (DC 205) Dovedale, Waiauan.
Fig. 3. Right (larger) chela and fingers of left chela of female paratype, × 1. (DC 225) Patten Creek, Tongaporutuan (GS 3642).
Fig. 4. Anterior view of paratype showing dorsal curvature and steep sides of carapace, × 1. (DC 176) Mangaone, Lillburnian (GS 1422).

Tumidocarcinus tumidus (H. B. Woodward) (page 25)

Fig. 5. Anterior view, × 1. (DC 156) for comparison with fig. 4. Point Elizabeth, Runangan (GS 4873).
Fig. 6. Dorsal view of anterior portion of carapace, shell (dark) partly preserved, × 1. (DC 156) Point Elizabeth, Runangan (GS 4873).

Tumidocarcinus dentatus Glaessner, n. sp. (page 28)

Fig. 7. Dorsal view of holotype. Internal mould, × 1. (DC 143) Wharekuri, Duntroonian (GS 486).
Fig. 8. Ventral view of holotype showing sternum and male abdomen, × 1. (DC 143) Wharekuri, Duntroonian (GS 486).

1

5

4

2

8

3

7

6

PLATE 7

Tumidocarcinus giganteus Glaessner, n. sp. (page 27)

Fig. 1. External view of large claw, fingers reconstructed, × 1. (DC 180) Mangaone Valley, Lillburnian (?) (GS 1422).

Fig. 2. Ventral view of paratype showing female abdomen, × 1. (DC 225) Patten Creek, Tongaporutuan (GS 3642).

Ommatocarcinus arenicola Glaessner, n. sp. (page 28)

Fig. 3. Dorsal view of holotype, × 1. (DC 155) Mount Brown, Otaian-Waiauan (GS 66).

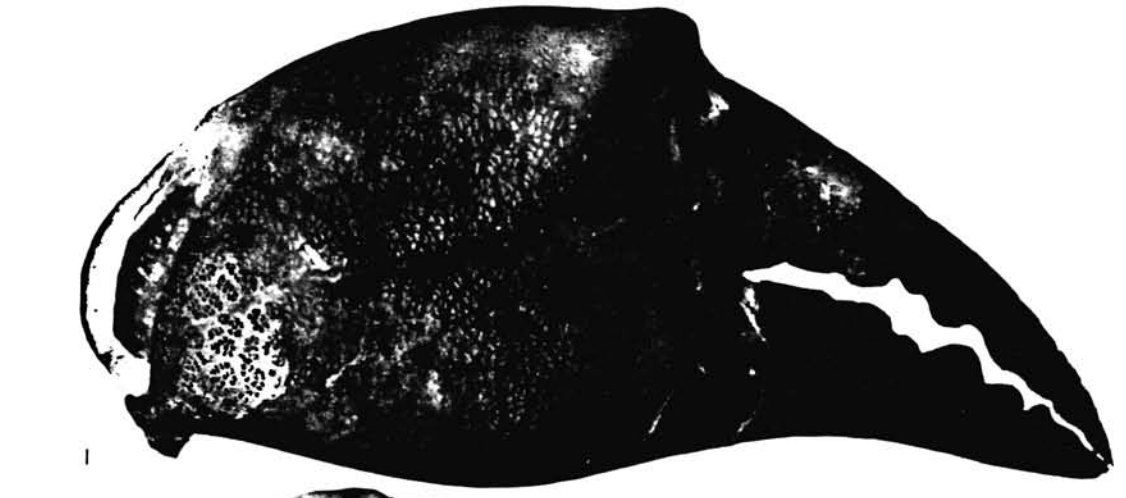
Galene proavita Glaessner, n. sp. (page 30)

Fig. 4. Dorsal view of holotype. The left antero-lateral portion is restored. The claw is crushed against the cephalothorax, × 1. (DC 129–130–204) Bellbird Stream, Clifdenian (GS 4773).

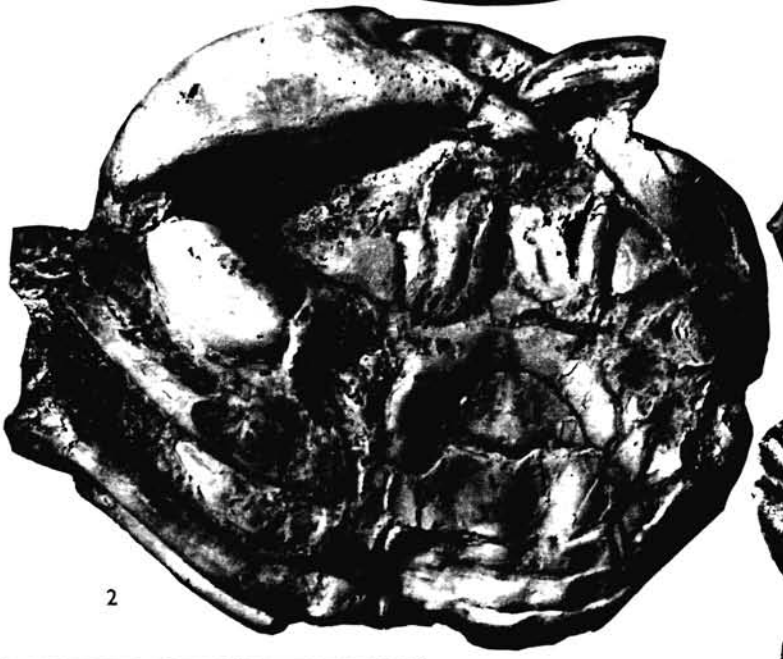
Fig. 5. Ventral view of holotype showing male abdomen, sternum and claw (open), × 1. (DC 129–130–204) Bellbird Stream, Clifdenian (GS 4773).

Hemiplax ? major Glaessner, n. sp. (page 31)

Fig. 6. Dorsal view of holotype, anterior portion damaged, × 1. (DC 229) Pakihikura Bridge, Nukumaruan (GS 4191).

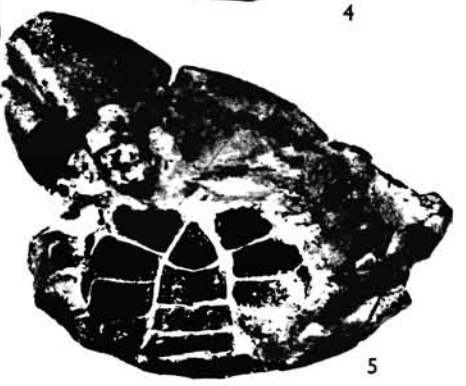


1



2

4



5

6

3

R. E OWEN, GOVERNMENT PRINTER, WELLINGTON, NEW ZEALAND—1960

1,100/11/59—15633 A