Jenkins, R. 1972

Compliments from Richard J.

METANEPHROPS, A NEW GENUS OF LATE PLIOCENE TO RECENT LOBSTERS (DECAPODA, NEPHROPIDAE)

BY

RICHARD J. F. JENKINS

Department of Geology and Mineralogy, University of Adelaide, Adelaide, South Australia 5001, Australia

Reprinted from: CRUSTACEANA, Vol. 22, Part 2, 1972

LEIDEN
E. J. BRILL

METANEPHROPS, A NEW GENUS OF LATE PLIOCENE TO RECENT LOBSTERS (DECAPODA, NEPHROPIDAE)

BY

RICHARD J. F. JENKINS

Department of Geology and Mineralogy, University of Adelaide, Adelaide, South Australia 5001, Australia

INTRODUCTION

In 1966 the carapace of a fossil lobster was discovered by Mr. and Mrs. W. Elliot in a loose cobble on Motunau Beach, about 39 miles N.N.E. of Christchurch, South Island of New Zealand. Subsequently six more specimens of the lobster, also in loose cobbles, were collected at the same locality by Miss H. D. Adams, Mrs. J. R. Taggart, and Messrs. J. Cairney, S. A. Chidgey and L. Tregoning. Dr. D. R. Gregg, Keeper of Geology, Canterbury Museum, Christchurch, sent this material to Professor M. F. Glaessner, of the University of Adelaide, South Australia, who suggested the present study.

The fossil is a new species but is clearly related to extant lobsters which occur in the Indo-West-Pacific region, the West Indies, and off the southeast coast of South America. Previously these Recent species were referred to the genus *Nephrops* Leach, 1814. They and the new species are here accommodated in a new genus, *Metanephrops*, while *Nephrops* is restricted to contain only the extant *N. norvegicus* (Linnaeus) and one certain fossil species.

The cobbles enclosing the specimens of the present fossil were probably derived from concretions in the Greta Siltstone which forms the coastal cliffs at Motunau Beach (Dr. D. R. Gregg, pers. comm.). Fleming (1963) considered the faunule from Motunau to be Waitotaran and suggested it was no younger than the middle of this stage. D. G. Jenkins (1967) places the Waitotaran in the late Pliocene.

The specimens studied are deposited in the Canterbury Museum, Christchurch, New Zealand (indicated (C.M.) in the rest of this paper), and are catalogued in the 'Canterbury Museum register of fossil Arthropoda'.

Terminology

The terminology used for the carapace grooves in the descriptive parts of this paper follows the notation for *Nephrops norvegicus* given by Glaessner (1960, text-fig. 18, drawing 10). This notation differs radically from that traditionally used by zoologists in descriptions of '*Nephrops*' species; in particular the hepatic and cervical grooves are now considered the cervical and postcervical grooves respectively.

The term margin in this work is used to mean a free edge of the exoskeleton or a hypothetical line marking the outline of a particular region or area of the exoskeleton. The term border is restricted to a peripheral ridge or a line of thickening at a free edge of the exoskeleton.

SUBFAMILY NEPHROPINAE DANA, 1852

Metanephrops gen. nov.

Designated type species. — *Nephrops japonicus* Tapparone Canefri, 1873.

Diagnosis. — Carapace slightly compressed laterally; rostrum elongate with a single pair of lateral spines; dorsolateral margins of rostrum continued back onto carapace as more or less parallel ridges bearing 3 to 5 pairs of prominent spines; antennal spine greatly expanded, lamellate; usually 7 longitudinal ridges on carapace posterior to postcervical groove. Scaphocerite broad, often circular in shape. First pair of pereiopods almost symmetrical.

Remarks. — It has long been recognized that extant Indo-West-Pacific and American nephropsids assigned to *Nephrops* Leach differ in several important features from the European type species *Cancer norvegicus* Linnaeus, 1758 (see De Man, 1916: 98; Yaldwyn, 1954: 730). This problem is resolved by the removal of the Indo-West-Pacific and American forms to *Metanephrops* gen. nov., and restriction of *Nephrops* to the extant type species and the Pliocene fossil *N. reedi* Carter, 1898, from Suffolk, England. Other fragmentary fossils referred to *Nephrops* either cannot be identified from literature, or belong to different genera (see p. 163).

Nephrops differs from *Metanephrops* in the following features: the rostrum has three pairs of lateral spines instead of one and the dorsolateral margins of the rostrum are not continued back onto the carapace as more or less parallel ridges, the antennal spine is small, only five longitudinal ridges are present on the carapace posterior to the postcervical groove, the scaphocerite is narrow and lanceolate, and the first pair of pereiopods are distinctly heterochelous.

The previously described extant forms listed below are here referred to *Metanephrops*. These forms are each distinguished by combinations of differences and thus seem valid species.

Nephrops japonicus Tapparone Canefri, 1873
Japan: Market, Mitani, Aiti-ken; east of Owase, 180-379 m; off Lake Hamana-ko, 100-189 m; Suruga Bay; Sagami Bay; Tokyo Bay.

Nephrops thomsoni Spence Bate, 1888
Between Samboangan and Manila, Philippine Islands; Formosa; northern part of South China Sea; southern part of South China Sea off Sarawak and North Borneo; 159-314 m.

Nephrops andamanicus Wood-Mason, 1892
S.E. Africa; Andaman Sea; north of Bali I., Indonesia; 186-840 m. The specimen from north of Bali Island was taken on a bottom of mud and broken shells (De Man, 1916). The material mentioned by Holthuis (1964: 71) from off Eucla, Western Australia at 219-820 m is a new

species according to Dr. A. J. Bruce (pers. comm.). Dr. Bruce reached this conclusion after comparing additional material of the Australian form with specimens of *N. andamanicus* from South Africa and the Bay of Bengal.

Nephrops rubellus Moreira, 1903
S.E. coast of South America, roughly between 23° and 38°S; 50-150 m.

Nephrops arafurensis De Man, 1905
Kei Islands, Moluccas, 560 m. Taken from a bottom of liquid brown mud above solid bluish grey mud (De Man, 1916).

Nephrops challengeri Balss, 1914
New Zealand, Tasman Sea off Cook Strait, E. coast of North Island north to Hawke Bay; Chatham Is.; 146-503 m.

Nephrops sibogae De Man, 1916
Off Kei Islands, 310 m. Taken from a bottom of fine grey mud (De Man, 1916).

Nephrops sagamiensis Parisi, 1917
(= *N. japonicus* sensu Balss, 1914 = *N. intermedius* Balss, 1921) Sagami Bay, Japan, 250 m; northern part of South China Sea.

Nephrops binghami Boone, 1927
British Honduras; north coast of Cuba; Bahama Is.; 438-885 m. Bahama Is. specimens from a bottom of grey sand (Holthuis, 1964).

Nephrops boschmai Holthuis, 1964
Off Eucla, Western Australia, 220-823 m.

Nephrops neptunus Bruce, 1965
Northern part of South China Sea, 731-795 m.

Nephrops sinensis Bruce, 1966a
Northern part of South China Sea, 205-391 m. Mud was brought up on the sole of the trawls used to take the species (Bruce, 1966a).

Nephrops australiensis Bruce, 1966b
N.E. of Port Hedland. Western Australia, 434 m. Greenish brown *Globigerina* ooze was sampled near where the species was taken (Bruce, 1966b).

None of the several fossil species referred to *Nephrops* appear to belong to *Metanephrops*. *N. reedi* Carter from the Pliocene (probably Boytonian), at Boyton, Suffolk, England, is known from incomplete chelae; it is allied to *N. norvegicus* (cf. Woods, 1931). The Pleistocene forms *N. costatus* Rathbun, 1918, and *N.* sp. Rathbun, 1918, from the Panama Canal Zone and the Oligocene or Miocene species *N. maoensis* Rathbun, 1920, and *N. aequus* Rathbun, 1920, from the Dominican Republic, all described from more or less fragmentary fingers or chelae, show only a casual resemblance to either *N. reedi* or *N. norvegicus*, and hence are of questionable identity. *N. shastensis* Rathbun, 1929, from the Cretaceous of California appears referable to the genus *Hoploparia* McCoy. The short, stout fingers of *N. americanus* Rathbun, 1935, from the Cretaceous of Texas, are quite unlike those of *N. norvegicus* or any of the known members of *Metanephrops* (the fingers of *Nephrops reedi* are imperfect).

Metanephrops motunauensis sp. nov. (text-fig. 1A-E; pls. 1, 2)

Material. — Seven specimens, six with all or part of the abdomen visible. Five specimens have the abdomen similarly sculptured and are thought to be female; one has the abdomen more complexly sculptured and is probably a male. Bruce (1965) described a comparable sexual dimorphism in *M. neptunus*.

The holotype (♀, zfc 201 (C.M.)) and one paratype (♀, zfc 170 (C.M.)) show most of the body and fragments of the pereiopods. The allotype (♂, zfc 202 (C.M.)) has several abdominal segments, a portion of one uropod and most of the right first pereiopod visible. One paratype (♀, zfc 193 (C.M.)) has the carapace, the anterior portion of the abdomen and the left and a fragment of the right first pereiopod exposed, and is associated with the fragmentary remains of a crab. One paratype (zfc 40 (C.M.)) is a carapace with the tip of the rostrum and the ventral and posterior margins damaged. Two paratypes (♀, zfc 134; ♀, zfc 183. (C.M.)) show the abdomen with the first segment and portions of the telson and uropods eroded.

The matrix of all specimens is a grey calcareous siltstone. The exoskeleton is usually replaced by a brown phosphatic mineral, and occasionally by pyrite which also forms small crystalline aggregates and films adjacent to the fossil. In one instance (zfc 202) areas of the natural skeletal material showing traces of coloration are preserved. One specimen (zfc 40) is slightly compressed dorsoventrally while the others are all compressed laterally and are asymmetrically distorted or fractured.

The positioning of one of the more complete remains (zfc 170; pl. 2 fig. 1a) resembles that of the partly completed reptantian macruran moults illustrated by Hale (1927, fig. 11) and Thomas (1966, pl. 1 fig. 2). Thomas indicated that moulting occurred while the animal lay on its side. In the fossil exuviae the carapace has moved back towards the abdomen. Specimens zfc 40, zfc 134, zfc 183, and zfc 202 may also be parts of moults. The holotype (zfc 201) and specimen zfc 193 show little displacement of the different parts of the body and are probably remains of dead animals.

Occurrence. — Motunau Beach. Probably derived from the Greta Siltstone.

Age. — Waitotaran, late Pliocene.

Diagnosis. — Anterior two-thirds and lateral aspects of posterior third of carapace spinulose; dorsal aspect of posterior third smooth or finely granulate with a few scattered larger granules and spinules. Tergum of 6th somite of female abdomen with 5 spinules on each lateral aspect and 3 pairs of sub-median spinules. Palms of first pair of pereiopods with a broad dorsal ridge ornamented by a dense band of spinules.

Description. — The rostrum is incompletely known. Its anterior portion apparently consisted of a strong forwardly directed spine with the base wedge-shaped in section, formed into a deep keel below. The proximal portion of the rostrum, equal to about one third the length of the carapace, is directed forwards and slightly upwards relative to the dorsal surface of the gastric regions and has the

dorsolateral margins developed into strong, outwardly produced carinae which have a fine, marginal border and a rounded, longitudinal ridge above; the region between these ridges is depressed. Anteriorly each carina apparently terminated in a forwardly and slightly upwardly directed spine lateral to the base of the main anterior rostral spine.

The dorsal ridges on the rostral carinae are continued onto the carapace as two postrostral ridges. The postrostral ridges are progressively less accentuated rearwards; they are sub-parallel for the first half of their length, and then converge slightly rearwards before abruptly curving inwards to the mid-line of the carapace a short distance in advance of the postcervical groove. The postrostral ridges are armed with four pairs of fairly evenly spaced, laterally compressed teeth of which only the bases are known. The teeth were apparently forwardly directed; the bases of the first pair, positioned directly above the supraorbital margins, are very large; those of the following pair are markedly smaller. The bases of the third and fourth pairs show a progressive decrease in size from the second pair. The area between the postrostral ridges is depressed and nearly smooth except for an occasional spinule and a slight, median longitudinal ridge which bears a few small granules. In the mid-line of the carapace is a suture which extends forwards to the base of the rostrum. Lateral to the postrostral ridges the dorsal surface of the carapace is ornamented by scattered spinules. The supraorbital margins are deeply concave and have a distinct border continuous with that on the postrostral carinae. A brief distance behind each supraorbital margin is a short ridge bearing a small spine. Further rearwards another small spine is situated on a longitudinal gastric carina. The antennal spine is very large; its lateral margin is sub-parallel relative to that of its opposite and its apparently acute tip is directed forwards and slightly outwards. The cervical groove is deeply impressed; the ridge forming the hind margin of the groove bears a line of spinules, the uppermost of which, level with the rear of the gastric carina, is slightly more prominent. The gastroorbital groove is expressed by a broad longitudinal depression below the gastric carina. The narrow, distinct antennal groove is directed forwards and then upwards; the area of the carapace between it and the antennal carina is spinulose. The antennal region is gently expanded and bears only a few scattered granules. The anterior branchial region is expanded and densely spinulose. Above the anterior branchial region is a small, indistinct, triangular region. The postcervical groove is strongly impressed across the dorsal aspect of the carapace; laterally it joins the deeply impressed lateral portions of the branchiocardiac groove. Between the ventral portions of the cervical and branchiocardiac grooves is an expanded oval area bearing a short, weak, longitudinal ridge which apparently terminated anteriorly in a small spine. Above this oval area a narrow groove branches from the branchiocardiac groove. The area between the upper portion of the cervical groove and the branchiocardiac groove is ornamented by scattered spinules. Behind the postcervical and branchiocardiac grooves the carapace is abruptly inflated and bears a line of spinules. The cardiac region has a broad, low sagittal ridge which

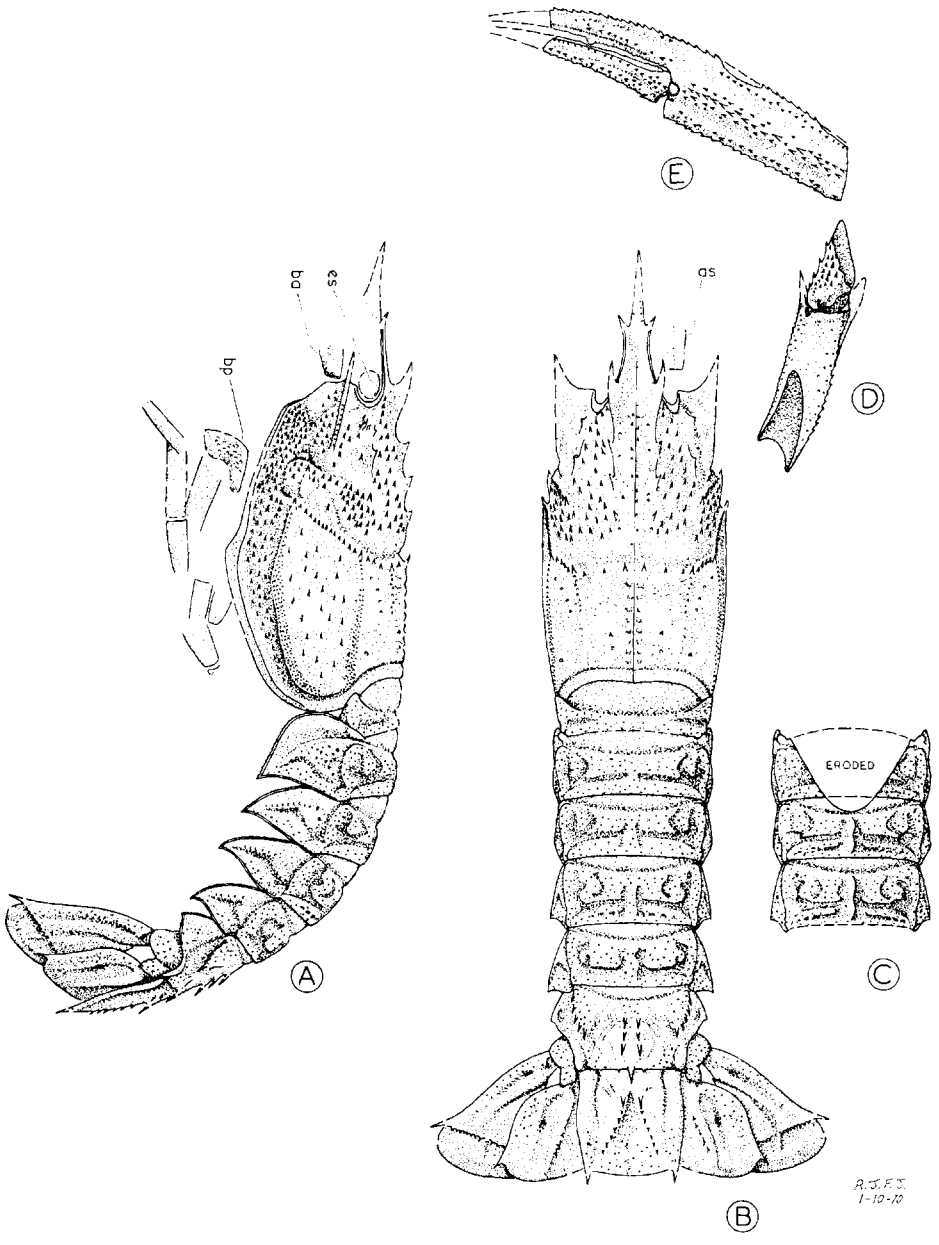


Fig. 1. Reconstruction of *Metanephrops motunauensis* gen. nov., sp. nov. Areas with large stipple are coarsely pitted. All drawings to same scale, approximately 2/3 times natural size. A, ♀, lateral view: upper distal portion of eyestalk (es), basal joint of left antennal peduncle (ba), basis of left first pereiropod (bp); B, ♀, dorsal view: right antennal scale (as); C, ♂, allotype, zfc 202 (C.M.), dorsal view of second, third and fourth abdominal segments; D, ♂, allotype, dorsal view of merus and carpus of right first pereiopod; E, ♂ allotype, dorsal view of chela of right first pereiopod.

apparently bore a pair of spines just behind the postcervical groove and seven or eight pairs of tubercles or spinules along its length. Otherwise the surface of the region is smooth except for one or two spinules and granules on the posterolateral portions. Lateral to the cardiac region broad longitudinal depressions with a transversely wrinkled surface represent the inner portions of the branchiocardiac groove. Each branchiostegite has three longitudinal ridges. The narrow uppermost ridge is moderately convergent rearwards relative to its opposite and bears an irregular line of sub-spiniform granules. The second ridge is gently arched upwards or nearly straight, with the anterior portion narrow and bearing a few large granules, and the posterior part wider and more finely granulated. The fairly broad lower ridge curves upwards posteriorly and is closely covered by small, anteriorly directed squamose granules for the greater part of its length; its extreme posterior portion extends upwards and slightly forwards to meet the posterior end of the second ridge and is smooth. All three ridges apparently terminated anteriorly in a small spine. Between the first and second ridges the carapace is finely granulate with a few larger granules. Between the second and third ridges the carapace is fairly smooth with widely spaced fine spinules; below the third ridge the surface is granulate and spinulose. The ventral and posterior margins of the carapace have a well defined border. The border is narrow below the anterior branchial region, but is gently recurved and dilates to double its initial width below the anterior quarter of the branchiostegite. Below the posterior part of the branchiostegite the border forms an angular carina. Across the posterior margin of the carapace the border is smooth.

The dorsal part of the eyestalks is broadly rounded so that the corneae must have been large and nearly spherical.

The basal joint of the antenna is sub-quadrate. The antennal scale is imperfectly known; it is large and plate-like with a longitudinal ridge on the dorsal surface. Short sub-cylindrical elements represent the antennal peduncle.

The mandibular gnathobases have the anterior margin rounded, the ventral surface convex and smooth, and the inner margin produced to an obtuse angle and finely denticulate. The left gnathobase has a short groove extending outwards and forwards from the obtuse angle of the inner margin.

The terga of the first to fifth somites of the female abdomen have a large, lunate, smooth articulating facet anterior to a strong transverse groove. The non-articular portion of the first tergum is constricted medially and has a deep transverse groove on either side. The non-articular portions of the second to fifth terga have a low median ridge and a distinctive sculpture formed by several deep grooves. A deep transverse groove narrowly interrupted medially is situated on the posterior part of these terga and two grooves are positioned laterally. On the second to fourth terga the inner lateral groove is strongly arched upwards with a slender anterior extension joining the anterior transverse groove. The inner lateral groove joins the posterior transverse groove on the second and third terga, but usually is just separated from the posterior groove on the fourth tergum. The outer lateral

groove extends forwards from the outer part of the posterior groove and has either a short upwardly or downwardly produced branch on the second to fourth terga. On the fifth tergum the inner lateral groove curves downwards to meet the outer lateral groove. The third to fifth terga have a submedian pair of short, longitudinal grooves at the median interruption of the posterior transverse groove. The fourth tergum has a transverse row of six to eight depressions on the raised area between the posterior groove and the posterior margin. The lateral aspects of the first to fifth terga are broadly lobate. Raised areas on these terga are coarsely pitted; the grooves are closely and finely pitted. The sixth tergum has a raised axial region and two raised anterolateral lobes. The axial region bears three pairs of posteriorly directed spinules, the first and third pairs notably larger. A row of five posteriorly directed spinules, the most posterior largest, is situated on each anterolateral lobe. A pair of spinules and a central spine are situated on the posterior margin of the segment. The pleura of the abdominal somites are demarcated from their respective terga by a deep depression. Those of the first somite are much reduced and are apparently obtusely triangular in shape. Those of the second to fifth somites are petal-shaped with the hind margin gently recurved, mainly straight, and the tip acute and directed downwards and more or less rearwards; the margins have a finely serrate narrow border and there is a deep, kinked pleural groove. The second pair of pleura, far the broadest, have the anterior margin rounded and are unique in having a small, prominent, upper-anterior expansion behind which the anterior transverse groove of the tergum extends directly onto each pleuron as an arcuate depression. The anterior portions of the third and fourth pairs of pleura are depressed; the fourth and fifth have a small rounded expansion adjacent to the posterior corner of the tergum. Raised areas on the second to fifth pairs of pleura are pitted and granulate. The sixth pair of pleura have a nearly right-angular tip, a very narrow marginal border, and only a slight depression representing the pleural groove; the surface is nearly smooth and finely pitted. The telson is sub-rectangular with the lateral margin gently recurved and the posterior margin slightly convex; at each of the postero-lateral corners is a rearwardly directed spine. A large delta-shaped depression with a weak median groove lies on the posterior four-fifths of the segment. The apex of this depression was apparently straddled by a pair of spines. A line of six spinules is situated on each of the ridges lateral to the delta-shaped depression; otherwise the telson is smooth. The uropods are similar to those of extant members of the genus. The large segment of the exopodite has the outer margin finely granulate and bears a series of spinules on the posterior margin. The endopodite has an inner longitudinal ridge bearing several spinules near the distal end and the outer margin of the segment terminates posteriorly in a spine.

The sculpture of the terga and pleura of the second to fourth somites of the male abdomen is not greatly dissimilar from that in the female. However, the third and fourth terga have a more prominent, distinctively waisted median crest isolated by elongate submedian grooves. The fourth tergum has an additional

transverse groove behind the equivalent of the posterior transverse groove in the female. The second and third male terga have a transverse line of more or less coalescent depressions in the same position as the extra transverse groove on the fourth tergum.

The extended length of the first pair of pereiopods of both the male and female is between 2 and 2½ times the length of the carapace. In the male the merus is about two-thirds the length of the carapace and is markedly compressed dorsoventrally. The inner margin of the merus is rounded and terminates distally in a large spine; the outer margin is rounded proximally, but bifurcates distally to form a strong upper crest terminating in a small blunt projection and a rounded lower crest produced to a large distal process. An elongate V-shaped suture is situated on the basal two-thirds of the inner face of the merus; lines of small spinules and granules extend along the margins of the joint towards the distal spine and processes; the faces are mainly smooth. The carpus is imperfectly known; its surface bears longitudinal rows of spinules and the inner margin apparently bore a row of spines. The palm is about three-quarters the length of the carapace; it is compressed dorsoventrally and gradually widens distally; the outer margin is carinate and bears a line of spinules continuous onto the margin of the fixed finger; the inner margin is more rounded and is ornamented by three rather irregular rows of large spinules; the ventral face is angled to form two longitudinal ridges, the inner at a quarter the width of the palm and densely spinulose, and the outer near the outer margin of the palm and with a line of prominent spinules; the dorsal face is broadly ridged, the ridge terminating at the articulation of the moveable finger and with a dense band of spinules; between the ridges the palm is fluted and nearly smooth. The fingers are apparently only slightly shorter than the palm and are strong, gently curved, and prominently ridged. The fixed finger has the outer margin angled to form a strong carina ornamented by a line of denticules; the ventral face of the finger has two weak ridges, each with a row of small spinules; the dorsal face has a single fairly prominent ridge, also with a row of small spinules; the prehensile margin bears a line of close-set, small, bluntly conical teeth, every second or third of which is slightly larger, and one large tooth below a gap in the small teeth at about half the length of the finger; two finely perforate areas which probably bore brushes of hair in life are situated on the basal quarter of the finger on either side of the prehensile margin. The moveable finger has one weak ventral ridge with a row of small spinules, and two fairly prominent dorsal ridges ornamented by rows of moderate-sized spinules; the inner margin is rounded; a spine is situated at the base of the innerdorsal ridge; the prehensile margin bears small, close-set teeth. Traces of coloration are present on the hand; the fingers and the ridges on the palm are cream or pale orange; the fluted areas of the palm are pale grey speckled with darker grey.

The first pair of pereiopods of the female are imperfectly known, but seem similar to those of the male. The ischium is a short segment compressed dorso-

ventrally and with the lower proximal margin apparently deeply concave and the lower surface sparsely granulate.

The second to fifth pereiopods of the female are known only from fragments. They are formed of relatively slender elongate, sub-cylindrical segments which have a smooth, finely pitted surface.

Measurements. — The measurements of the 7 available specimens are contained in table I.

TABLE I

Measurements (mm)

	Holotype ♀ zfc 201	Allotype ♂ zfc 202	Paratype ♀ zfc 170	Paratype zfc 40	Paratype ♀ zfc 193	Paratype ♀ zfc 183	Paratype ♀ zfc 134
Carapace, length in dorsal midline	(52)	—	(47)	(52)	(42)	—	—
Carapace, length in lateral aspect	60	—	—	(67)	—	—	—
Carapace, width	—	—	—	40	(26)	—	—
Carapace, depth	33	—	(33)	(35)	31	—	—
Abdomen, length	98	—	(84)	—	—	(71)	(68)
3rd abdominal tergum, length	(9)	9.3	(8)	—	(8)	8.6	7.9
4th abdominal tergum, length	(11)	(10)	11	—	(10)	(10)	10.1
Telson, length	20	—	20	—	—	—	—
Telson, breadth	—	—	18	—	—	—	—

1st pereiopod

	Lt.	Rt.	Lt.
Ischium	(11)	—	—
Merus	—	(40)	(48)
Carpus	—	(20)	
Palm	—	(44)	(41)
Fixed finger	—	(73)	(73)

EXPLANATION OF TABLE I

Carapace length in dorsal midline is from the rearmost part of the supraorbital margin to the posterior margin of the carapace. Carapace length in lateral aspect is from the rearmost part of the supraorbital margin to the rearmost part of the posterior margin of the branchiostegite. Carapace width and depth are maximal measurements taken near postcervical groove. Abdomen length is the overall length of the abdomen reconstructed to the extended or "straightened" position. The length of abdominal terga is measured in the dorsal midline from the posterior lip of the transverse groove immediately behind the articulating facet to the posterior margin of the segment. Measurements of broken or imperfect items are bracketed.

Remarks. — The extant species here assigned to *Metanephrops* can be divided into four main groups (De Man, 1916; Yaldwyn, 1954; and later authors). These groups are characterized as follows:

Carapace smooth or finely granulate. Terga of second to fifth abdominal somites conspicuously furrowed with arched or oblique lateral grooves and a submedian pair of longitudinal grooves. Palms of chelae of first pair of pereiopods with prominent spinulose ridges; fingers slender, gently curved or nearly straight, carinate basally. *M. japonicus*; *M. andamanicus* (Wood-Mason, 1892); *M. sagamiensis*; *M. andamanicus* (sensu Holthuis, 1964).

Carapace finely granulate. Terga of abdominal somites not conspicuously furrowed. Palms of chelae of first pair of pereiopods with prominent spinulose ridges; fingers strong, with spinulose carinae. *M. rubellus, M. binghami.*

Carapace spinulose. Terga of second to fifth abdominal somites conspicuously furrowed, but without prominent submedian longitudinal grooves. Palms of chelae of first pair of pereiopods angulated or ridged dorsally, convex ventrally, and coarsely or finely granulate; fingers either strong, curved and feebly carinate, or slender, straight and rounded in section. *M. arafurensis, M. neptunus, M. australiensis.* The single known specimen of *M. arafurensis* is mutilated and lacks the posterior portion of the abdomen, the first pair of pereiopods and the antennal flagella.

Carapace smooth or finely granulate. Terga of second to fifth abdominal somites smooth or punctate, with or without a single transverse furrow interrupted medially. Palms of chelae of first pair of pereiopods weakly ridged, finely granulate; fingers slender, straight, rounded in section. *M. thomsoni, M. challengeri, M. sibogae, M. boschmai, M. sinensis.*

M. motunauensis resembles members of both the "*japonicus*" and "*arafurensis*" groups. *M. motunauensis* resembles *M. japonicus* and *M. andamanicus* in the form of the abdominal sculpture and in having prominent spinose ridges on the chelae of the first pair of pereiopods. The fossil resembles *M. arafurensis* and *M. neptunus* in the general form of the abdominal sculpture and in having the carapace spinulose. The spinulation of the sixth abdominal tergum of *M. motunauensis* somewhat resembles that in *M. neptunus*, as illustrated on pl. XV of Bruce (1965), while the fingers of the first pair of pereiopods are quite similar.

M. motunauensis is readily distinguished from *M. japonicus* by the following characters:

a. The anterior two-thirds and the lateral aspects of the posterior portion of the carapace of *M. motunauensis* are spinulose. The carapace of *M. japonicus* is not spinulose.

b. The fossil has four pairs of teeth on the postrostral ridges while *M. japonicus* has five.

c. The submedian raised areas on the second to fifth abdominal terga of *M. motunauensis* are not further subdivided as in *M. japonicus.*

d. Five spinules are situated on the lateral aspects of the sixth abdominal tergum in the fossil. Only a single spinule is situated in this position in *M. japonicus.*

e. In *M. motunauensis* the median dorsal ridge on the palms of the first pair of pereiopods is ornamented by a dense band of spinules. The equivalent ridge

on the chelae of *M. japonicus* bears a single row of spinules except near the distal end.

Clear differences between *M. motunauensis* and *M. andamanicus* are:

a. The carapace of *M. andamanicus* is not spinulose.

b. *M. andamanicus* has only 3 pairs of teeth on the postrostral ridges.

c. The sixth abdominal tergum of the fossil has 5 spinules situated on the lateral aspects and 3 pairs of spinules positioned submedially. The same abdominal tergum in *M. andamanicus* has one spinule near the middle of the lateral margin and lacks paired submedial spinules.

d. The median dorsal ridge on the palms of the first pair of pereiopods of *M. andamanicus* bears one or two rows of spinules, not a dense band of spinules as in the fossil.

The principal differences between *M. motunauensis* and *M. arafurensis* are:

a. The dorsal aspect of the posterior two-thirds of the carapace of *M. neptunus* is smooth or finely granulate with only a few scattered larger granules and occasional spinules. The same region in *M. arafurensis* is strongly spinulose.

b. *M. arafurensis* has five pairs of spines on the postrostral ridges, not four as in the fossil.

c. The inner lateral grooves on the second and third abdominal terga of *M. arafurensis* are directed obliquely downwards and forwards. The equivalent grooves on the same somites of *M. motunauensis* are arched upwards.

d. On the third abdominal tergum of *M. arafurensis* no longitudinal submedian grooves are present as in the fossil.

The following main differences between *M. motunauensis* and *M. neptunus* may be noted:

a. The dorsal aspect of the posterior two thirds of the carapace of *M. neptunus* is densely spinulose.

b. The postrostral ridges bear only three pairs of teeth in *M. neptunus* and are divergent rearwards for most of their length, not slightly convergent as in the fossil.

c. *M. neptunus* lacks the uppermost branchiostegal ridge present in the fossil.

d. The second to fifth abdominal terga of *M. neptunus* have an additional pair of transverse grooves not present in *M. motunauensis*. Short submedian longitudinal grooves are developed only on the second and third abdominal terga of males of *M. neptunus*.

e. The sixth abdominal tergum of *M. neptunus* apparently has a series of five or six submedian pairs of spinules, not three pairs as in *M. motunauensis*.

f. The palms of the first pair of pereiopods of the fossil are elongate and have prominent spinulose ridges on the dorsal and ventral surfaces. In *M. neptunus* the palms are relatively short, convex ventrally and coarsely granulate.

M. motunauensis is clearly intermediate between the modern "*japonicus*" and "*arafurensis*" species groups, suggesting that these two sections had a common ancestry. Studies I have made of other fossil Decapoda suggest that new species

evolve from a single lineage at intervals of the order of 5-15 $\times$ 10^6 years. The relatively youthful geologic age of *M. motunauensis* (about 3 $\times$ 10^6 years) precludes it being directly ancestral to the "*japonicus*" and "*arafurensis*" groups as these each contain several quite distinct species. Rather the fossil is considered to have retained many of the characters of an earlier form near the ancestry of these two groups. Somewhat closer affinity between *M. motunauensis* and the "*arafurensis*" group is inferred from the incompletely spinulose carapace of the fossil.

DISTRIBUTION AND EVOLUTION OF METANEPHROPS

The geographic distribution of species of *Metanephrops* is summarized in fig. 2. The modern species have been taken at depths between 50 and 885 metres, the majority of records being deeper than about 150 metres (fig. 3). Typically the modern species are found on soft muds, and rarely sand, on the outer edge of the continental shelf and the upper part of the continental slope (see also Bruce, 1966). The matrix of the specimens of *M. motunauensis* also indicates a fine-grained substrate. The relatively limited occurrence, in the geological record, of

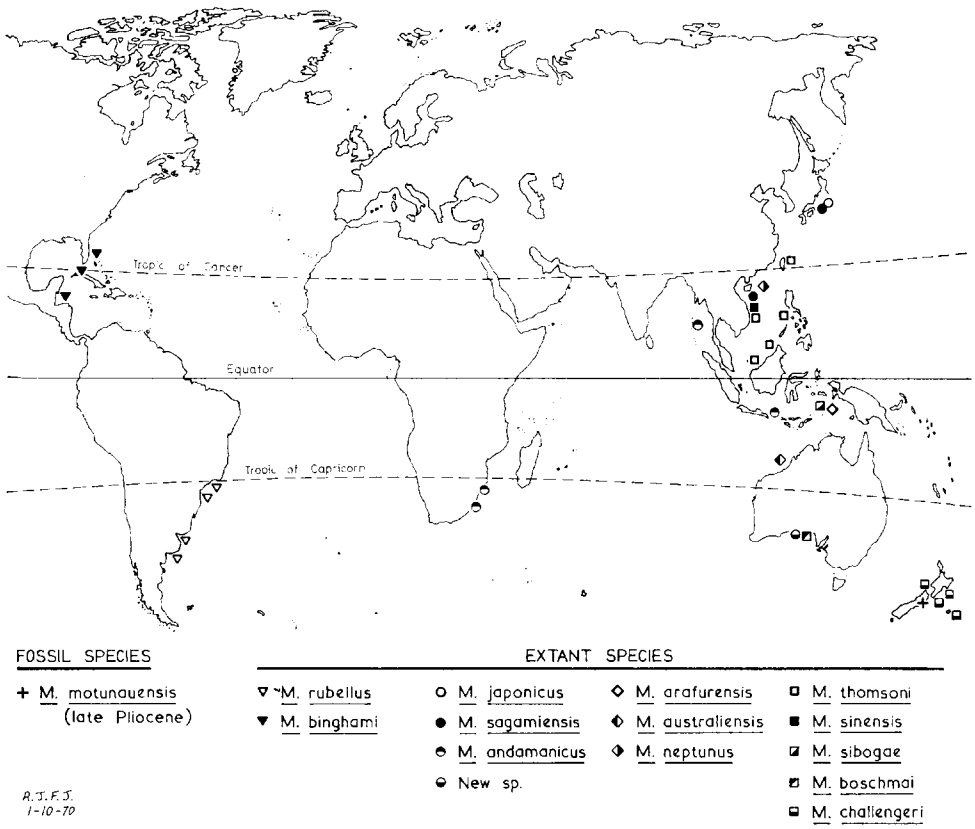


Fig. 2. Geographic distribution of species of *Metanephrops* gen. nov.

exposed sediments deposited on the margin of the continental shelf and the upper part of the continental slope is the probable reason why only one fossil member of the genus is yet known.

Geographic records of several extant species and each of the four main species groups are widely scattered. However, recent systematic surveys in the South China Sea and investigations off New Zealand and Australia suggest species may be more widespread and abundant than indicated by the older records, and show that the distribution of single species is probably fairly continuous (Bruce, 1966).

The "*japonicus*" group seems the most widely distributed of the extant species groups. The distributions of the "*japonicus*" and "*thomsoni*" groups are apparently largely exclusive. Members of these two groups inhabiting the same or adjacent regions are found at similar depths; for example off the east coast of Asia and Japan *M. japonicus, M. sagamiensis, M. thomsoni* and *M. sinensis* are all known at depths within the range 100 to about 400 metres. Three of these species, *M. sagamiensis, M. thomsoni* and *M. sinensis* occur in the northern part of the South China Sea (Bruce, 1966, 1966a, 1966b). *M. thomsoni* is the most numerous species in this area. *M. sinensis* is almost equally abundant, but tends to be taken at greater depths than *M. thomsoni*, although both have been taken in the same trawl. It is suggested that a northwards invasion of species of the "*thomsoni*" group into the South China Sea may be actively displacing members of the "*japonicus*" group from the area. Similarly the ancestor of *M. challengeri* probably reached New Zealand in the late Tertiary and replaced the Pliocene *M. motunauensis*.

Members of the "*arafurensis*" group occupy part of the same region as the

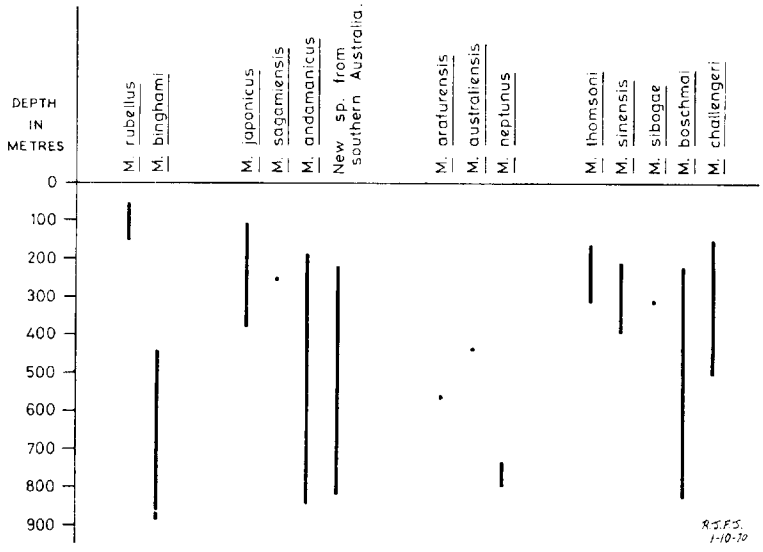


Fig. 3. Known depth range of extant species of *Metanephrops* gen. nov.

"thomsoni" group. The species of the *"arafurensis"* group are known at depths within the range 434-795 metres; *M. thomsoni, M. sinensis* and *M. sibogae* are not known deeper than 310-391 metres.

The American species occupy ranges fairly symmetrically positioned on either side of the equator. It seems possible that this resulted from splitting of a single species formerly occupying an equatorial range.

The inferred phylogenetic relationships of the different members of the genus are indicated in fig. 4. No direct ancestor to the genus is known. It is inferred from the large number of Indo-West-Pacific species that the genus originated in this province. The *"japonicus"* and *"arafurensis"* sections are suggested to be the oldest of the modern species groups as they include the most diverse species. *M. neptunus* is the most aberrant member of the *"arafurensis"* group. The American species seem most closely allied to the *"japonicus"* group (see also De Man, 1916: 97); the carapace and first pair of legs are quite similar in these forms. *Metanephrops* possibly reached the Atlantic around southern Africa, but more probably migrated through Tethys prior to or during the Lower Miocene. The sea connection between the Indian and Atlantic Oceans through Tethys was lost in the late Lower Miocene (Ruggieri, 1967). The *"thomsoni"* group appears more closely allied to the *"arafurensis"* group and probably evolved from near the ancestor of *M. australiensis*, off northern Australia or in the Indonesian region, central to the

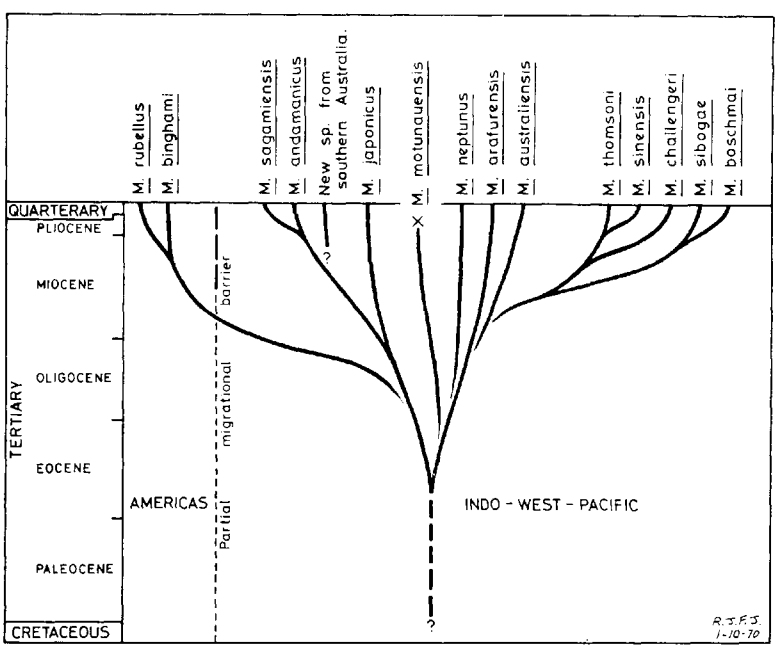


Fig. 4. Inferred phylogenetic relationships of species of *Metanephrops* gen. nov. Except for the fossil *M. motunauensis* sp. nov., the geological time scale is arbitrary with respect to the phylogenetic scheme.

present distribution of these two groups. Members of the *"thomsoni"* group and *M. australiensis* have the abdomen comparably furrowed and the first pair of legs extremely similar.

ACKNOWLEDGEMENTS

Grateful acknowledgement is extended to Professor M. F. Glaessner for suggesting this work and for his advice and constructive criticism at all stages. I sincerely thank Dr. D. R. Gregg of the Canterbury Museum, New Zealand, for the loan of specimens and for providing information on stratigraphy; Dr. A. J. Bruce, East African Fisheries Research Organization, Mombasa, Kenya, for his helpful correspondence on several matters and for kindly allowing me to comment on his recognition of a new species; Dr. Mary Wade, Queensland Museum, Brisbane, Queensland, for reading and criticizing sections of the manuscript; and Mrs. B. McGowran, University of Adelaide, for help with linguistics and preparation of the typescript.

ZUSAMMENFASSUNG

Metanephrops gen. nov. (Typusart *Nephrops japonicus* Tapparone Canefri, 1873) wird für elf rezente Indo-West-pazifische und zwei amerikanische Hummerarten, sowie für die neue fossile Art *Metanephrops motunauensis* aus dem oberen Pliozän Neuseelands errichtet. Die rezenten Arten wurden früher zu *Nephrops* Leach, 1814 (Typusart *Cancer norvegicus* Linnaeus, 1758) gestellt. Sie unterscheiden sich aber wesentlich von dieser Gattung durch die reduzierte Zahl der Dornen des Rostrums, die Anwesenheit kräftig bedornter subparalleler, postrostraler Furchen, den stark vergrösserten antennalen Dorn, die Entwicklung eines zusätzlichen Paares von Längsfurchen am hinteren Teil des Karapax, die breitere Antennenschuppe und die Abwesenheit von ausgesprochener Heterochelie. *M. motunauensis* steht zwischen den *"japonicus"* und *"arafurensis"* Gruppen von De Man (1916) und späteren Autoren. Die Verbreitung und vermutliche stammesgeschichtliche Verwandtschaft der Arten von *Metanephrops* wird besprochen.

REFERENCES

BRUCE, A. J., 1965. On a new species of Nephrops (Decapoda, Reptantia) from the South China Sea. Crustaceana, **9**: 274-284, pls. 13-15.

——, 1966. Distribution of the genus Nephrops (Crustacea Decapoda Macrura) in the Indo-Pacific region. Nature, London, **209** (5022): 535.

——, 1966a. Nephrops sinensis sp. nov., a new species of lobster from the South China Sea. Crustaceana, **10**: 155-166, pls. 10-12.

——, 1966b. Nephrops australiensis sp. nov., a new species of lobster from northern Australia (Decapoda Reptantia). Crustaceana, **10**: 245-258, pls. 25-27.

FLEMING, C. A., 1963. Macrofossils. In: D. D. WILSON, Geology of Waipara Subdivision (Amberley and Motunau Sheets S68 and S69). Bull. geol. Surv. New Zealand, (n. ser.) **64**: 60-63.

GLAESSNER, M. F., 1960. The fossil decapod Crustacea of New Zealand and the evolution of the order Decapoda. Palaeont. Bull., Wellington, **31**: 1-63, text-figs. 1-22, pls. 1-7.

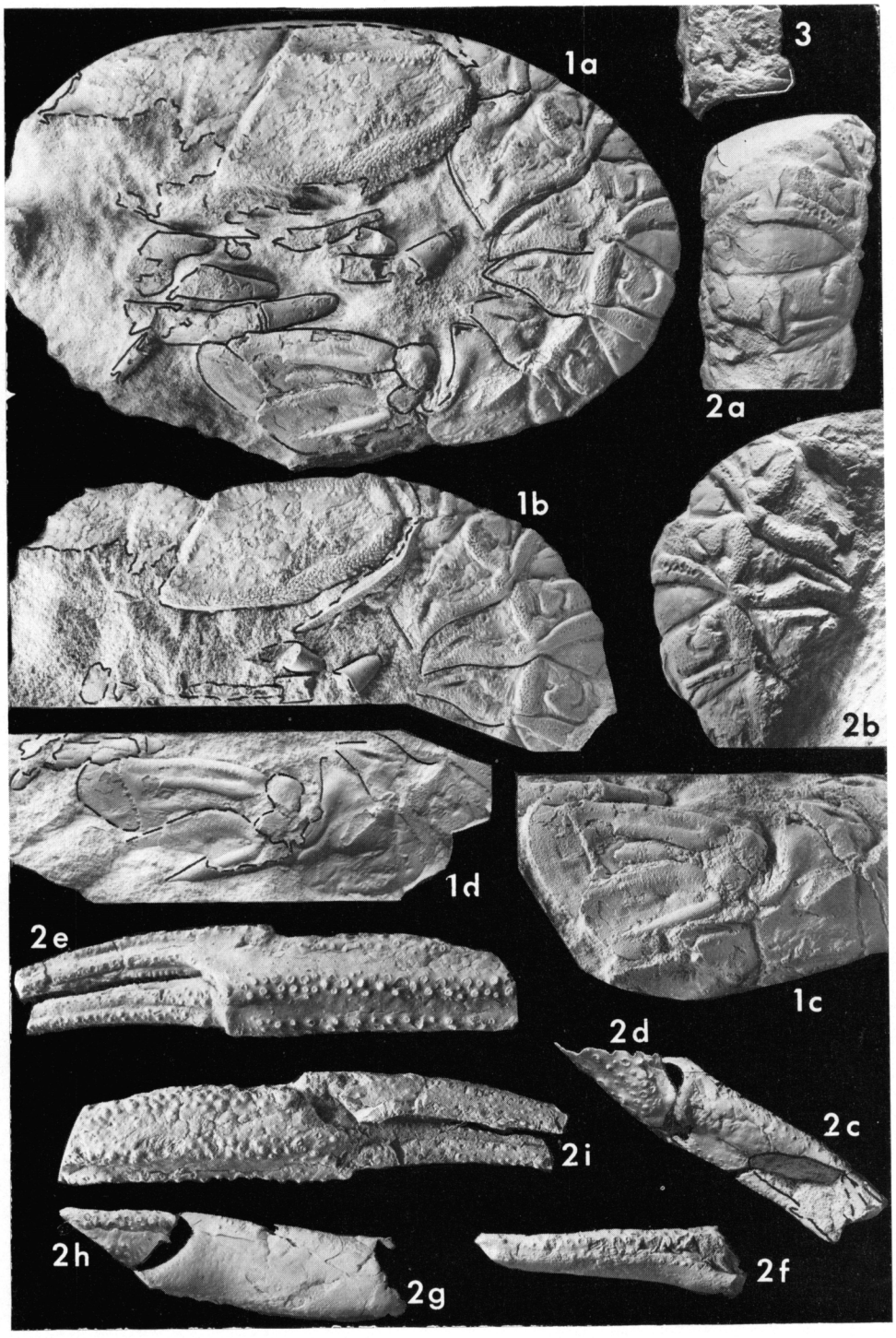
HALE, H. M., 1927. The crustaceans of South Australia. Handbook of the flora and fauna of South Australia, **1**: 1-201, figs. 1-202 (Government Printer, Adelaide).

HOLTHUIS, L. B., 1964. On some species of the genus Nephrops (Crustacea Decapoda). Zool. Meded. Leiden, **39**: 71-78, fig. 1.

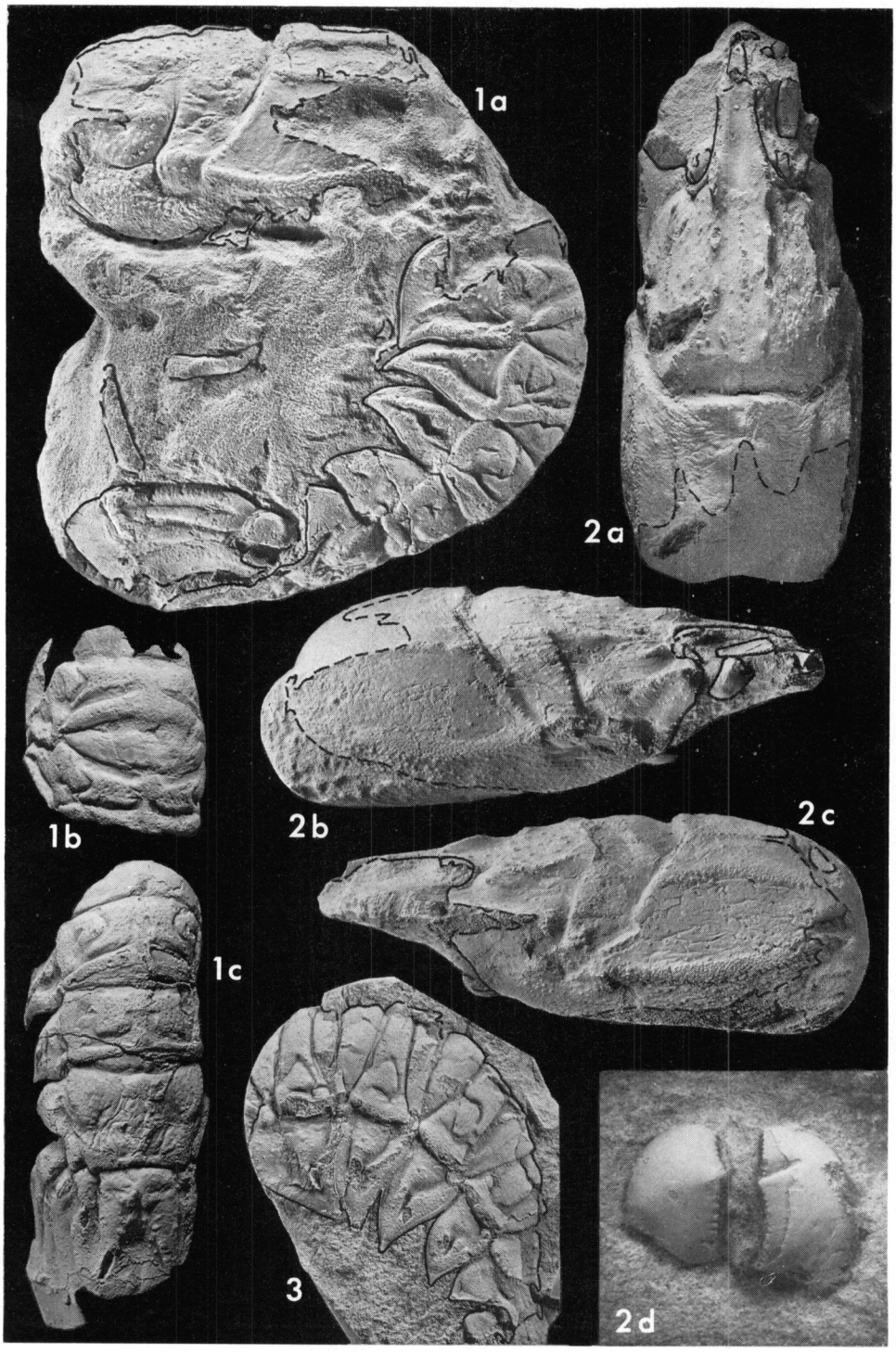
JENKINS, D. G., 1967. Planktonic foraminiferal zones and new taxa from the Lower Miocene to Pleistocene of New Zealand. New Zealand Journ. Geol. Geophys., **10** (4): 1064-1078, figs. 1-4.

MAN, J. G. DE, 1916. The Decapoda of the Siboga Expedition, 3. Families Eryonidae, Palinuridae, Scyllaridae and Nephropsidae. Siboga Exepd. Monogr., **39** (a) (2): 1-222, pls. 1-4.

RUGGIERI, G., 1967. The Miocene and later evolution of the Mediterranean Sea. In: C. G. ADAMS & D. V. AGER, eds., Aspects of tethyan biogeography. Publ. Syst. Assoc., **7**: 281-290, figs. 1-2.



Metanephrops motunauensis gen. nov., sp. nov. Ink lines outlining structures are drawn contiguous with the outer perimeter of the structure. Solid lines mark real margins, dashed lines accidental fractures. Figures all natural size. Explanation see p. 177.



Metanephrops motunauensis gen. nov., sp. nov. Masking and outlining of structures contiguous with the outer perimeter of the structure. Dashed lines indicate accidental fractures. Explanation see p. 177.

THOMAS, L. R., 1966. Moulting behaviour of the Western Australian Crayfish Palinurus cygnus George (Decapoda Reptantia). Crustaceana, **11**: 111-112, pl. 1.

WOODS, H., 1931. A monograph of the fossil macrurous Crustacea of England. Monogr. palaeontograph. Soc. London, **76** (7): 89-122, pls. 25-27.

YALDWYN, J. C., 1954. Nephrops challengeri Balss, 1914, (Crustacea, Decapoda, Reptantia) from New Zealand and Chatham Island waters. Trans. roy. Soc. New Zealand, **82** (3): 721-732, figs. 1, 2.

PL. II

Fig. 1. Paratype ♀, zfc 170 (C.M.): (a) lateral view, × 1; (b) second and third segments of abdomen, dorsal view, × 1; (c) posterior portion of abdomen, dorsal view, × 1.

Fig. 2. Paratype, zfc 40 (C.M.): (a) carapace, portions of eyestalks, right antennal scale, basis of antenna, and antennal peduncle visible, dorsal view, × 7/8; (b) same, mandibular gnathobases also shown, right lateral view, × 7/8; (c) carapace, left lateral view, × 7/8; (d) mandibular gnathobases, ventral view, × 2½.

Fig. 3. Paratype ♀, zfc 134 (C.M.): second to sixth segments of abdomen, lateral view, × 1.

PL. I

Fig. 1. Holotype ♀, zfc 201 (C.M.): (a) lateral view; (b) latex cast of counterpart, hind portion of lower marginal border of carapace showing; (c) uropod and hind portion of abdomen; (d) latex cast of counterpart of uropod and hind portion of abdomen, spinulation of hind margin of large segment of exopodite visible.

Fig. 2. Allotype ♂, zfc 202 (C.M.): (a) second to fifth segments of abdomen, dorsal view; (b) second to fifth segments of abdomen, lateral view; (c) merus of first pereiopod, dorsal view; (d) carpus of first pereiopod, dorsal view; (e) propodus and dactylus of first pereiopod, dorsal view; (f) merus of first pereiopod, outer lateral view; (g) merus of first pereiopod, ventral view; (h) carpus of first pereiopod, ventral view; (i) propodus and dactylus of first pereiopod, ventral view.

Fig. 3. Paratype ♀, zfc 193 (C.M.): hind portion of left half of carapace showing posterior marginal border, dorsal view.

Received for publication 17 November 1970.