

**Crustacea Decapoda: *Diacanthurus* gen. nov.,
a new genus of hermit crabs (Paguridae)
with both Recent and fossil representation,
and the descriptions of two new species**

Patsy A. McLAUGHLIN

Shannon Point Marine Center, Western Washington University
1900 Shannon Point Road, Anacortes, WA 98221-4042, U.S.A.

&

Jacques FOREST

Muséum national d'Histoire naturelle
Laboratoire de Zoologie (Arthropodes)
61 rue Buffon, 75005 Paris

ABSTRACT

The new genus, *Diacanthurus*, is proposed for a group of three Recent and one fossil species formerly assigned to the heterogeneous genus *Pagurus* Fabricius. In addition to the transfer of *Pagurus clifdenensis* Hyden & Forest (fossil), *P. spinulimanus* (Miers), *P. rubricatus* (Henderson), and *P. ophthalmicus* (Ortmann), two new species, *Diacanthurus ephyra* sp. nov. from New Caledonia and Western Australia, and *D. richeri* sp. nov. from New Caledonia are assigned to this new genus. Expanded diagnoses or descriptions and illustrations of all Recent species are provided.

RÉSUMÉ

Crustacea Decapoda : *Diacanthurus* gen. nov., nouveau genre de Paguridae représenté par des formes actuelles et une forme fossile. Description de deux espèces nouvelles.

Le nouveau genre *Diacanthurus* est proposé pour un groupe comprenant trois espèces actuelles et une espèce fossile précédemment attribuées au genre hétérogène *Pagurus* Fabricius. En plus de *Pagurus clifdenensis* Hyden & Forest (fossile), *P. spinulimanus* (Miers), *P. rubricatus* (Henderson) et *P. ophthalmicus* (Ortmann), transférés au genre *Diacanthurus*,

McLAUGHLIN, P.A. & FOREST, J., 1997. — Crustacea Decapoda: *Diacanthurus* gen. nov., a new genus of hermit crabs (Paguridae) with both Recent and fossil representation, and the descriptions of two new species. In: A. CROSNIER (ed.), Résultats des Campagnes MUSORSTOM, Volume 18. *Mém. Mus. nat. Hist. nat.*, **176**: 235-259. Paris ISBN: 2-85653-511-9.

deux espèces nouvelles sont décrites: *D. ephyma* sp. nov., de Nouvelle-Calédonie, des îles Chesterfield et d'Australie occidentale, et *D. richeri*, de Nouvelle-Calédonie. Des diagnoses développées ou des descriptions, ainsi que des illustrations, sont fournies pour toutes les espèces actuelles.

Diacanthurus gen. nov. se distingue des autres genres de Paguridae par la structure particulière du telson : les deux lobes postérieurs sont symétriques ou presque, en forme de croissants, avec un sommet aigu, et séparés par une profonde incision médiane dont les bords internes portent chacun une forte épine. D'autres traits morphologiques caractérisent encore le genre, comme le grand développement de l'article basilaire des pédoncules oculaires.

Les différences entre les espèces portent notamment sur la forme et l'ornementation des chélicèdes qui présentent un remarquable gradient évolutif suivant la séquence *D. richeri*, *D. ophthalmicus*, *D. clifdenensis*, *D. spinulimanus*, *D. ephyma* et *D. rubricatus*. Ce gradient porte sur la largeur relative et l'asymétrie des mains, qui s'accroissent, alors que les tubercules et dents de la face dorsale sont de plus en plus développés.

En dehors des deux espèces nouvelles, à distribution néo-calédonienne, le nouveau genre est représenté dans plusieurs régions de l'Indo-Ouest Pacifique : Nouvelle-Zélande (*D. spinulimanus* et *D. rubricatus*), Japon (*D. ophthalmicus*) et aussi Australie occidentale (*D. ephyma*).

Les distributions bathymétriques diffèrent suivant les espèces. Celles-ci sont surtout représentées entre 200 et 400 mètres, à l'exception de *D. ophthalmicus*, capturé entre 100 et 200 mètres, et de *D. spinulimanus*, le plus souvent recueilli par moins de 100 mètres de profondeur.

INTRODUCTION

HYDEN and FOREST (1980) described a new species of pagurid, *Pagurus clifdenensis* Hyden & Forest, from the early Miocene of southern New Zealand. At the time, the authors noted the similarities between their fossil species and two Recent New Zealand species, *Pagurus spinulimanus* (Miers, 1876) and *Pagurus rubricatus* (Henderson, 1888). Recognizing the distinctiveness of all three taxa, HYDEN and FOREST (1980) indicated that these species would be transferred to a new genus when revisionary studies of the New Zealand pagurid fauna were completed.

Certain characters, not available in the fossil species, clearly set the two Recent species apart from other *Pagurus* species, particularly the structure of the telson. It is, as the generic name *Diacanthurus* implies, composed of two very prominent spines (Fig. 1a). This unique telson structure was also depicted by MIYAKE (1978) for the Japanese species, *Pagurus ophthalmicus* (Ortmann, 1892). An examination of ORTMANN's holotype by one of us (PMcL) confirmed similarities indicative of a close phylogenetic relationship among the three Recent taxa. During studies of the MUSORSTOM collections from New Caledonia, two additional and undescribed species have been recognized that share all of the morphological characteristics of *Diacanthurus* as defined herein.

MATERIALS AND METHODS

The holotypes of *Pagurus rubricatus* and *P. spinulimanus* were borrowed from The Natural History Museum, London (NHM); the holotype of *P. ophthalmicus* was borrowed from the Musée Zoologique, Université Louis Pasteur, Strasbourg (MZUS). The MUSORSTOM collections are the property of the Muséum national d'Histoire naturelle, Paris (MNHN); the specimen from Western Australia is the property of the Western Australian Museum, Perth (WAM). Supplemental materials of *P. rubricatus* and *P. spinulimanus* have come from the collections of the New Zealand Oceanographic Institute (NZOI); National Museum of New Zealand, Wellington, (NMNZ), now the Museum of New Zealand Te Papa Tongarewa (MoNZ), and include collections originally belonging to the Zoology Department, Victoria University of Wellington (VUZ); Portobello Marine Laboratory, University of Otago (PMLUO); and the personal collection of one of the authors (PMcL). Supplemental specimens of *P. ophthalmicus* from the R/V *Albatross* Northwest Pacific Expedition are the property of the National Museum of Natural History, Smithsonian Institution (USNM); additional specimens from Japan are from the collections of Zoology, Crustacea, Natural History Museum and Institute, Chiba (CBM-ZC), and PMcL's personal collection. Specimens have, for the most part, been returned to their institutions of origin; however, some paratypes of the new species have been deposited in the USNM. Most station data for the French bathyal faunal expeditions in New Caledonia are documented in RICHER DE FORGES (1990, 1993) and RICHER DE FORGES and CHEVILLON (1996). The abbreviations BS, DW, and CP refer to bottom station, Waren dredge and beam trawl, respectively. The

measurement of shield length, given in parentheses (), and measured from the midpoint of the anterior margin of the shield (broadly rounded rostral projection) to the midpoint of the posterior margin of the shield, provides an indication of animal size. Measurements of the ocular peduncle refer exclusively to the length of the distal segment, and are measured from the base to the distal margin (or apex) of the cornea along the lateral face; corneal diameter represents maximum width of the cornea. Lengths of the dactyls and propodi of the ambulatory legs were measured on the lateral faces from the dorsodistal margin (excluding the claw of the dactyl) to the dorsoproximal margin. Terminology for the diagnoses and descriptions follows that of MCLAUGHLIN (1974, 1997). Two keys to the species are presented. The first is based principally on characters of the chelipeds and ambulatory legs, which may be lost in preserved specimens, thus rendering the key useless. The second, which is based essentially on characters of the ocular peduncles and telson is less subject to the drawbacks than the first, is highly reliable for large specimens, but may not be as applicable to small specimens. It is hoped that between the two, accurate identifications of these generally quite similar species can be made.

Genus *DIACANTHURUS* nov.

Pagurus Fabricius, 1775: 410 (in part).
Eupagurus Brandt, 1851: 105 (in part).

TYPE SPECIES. — *Eupagurus spinulimanus* Miers, 1876. Gender masculine.

DIAGNOSIS. — Eleven pairs of phyllobranchiate gills. Rostrum obsolete to broadly rounded. Ocular peduncles well developed, intersegmental articulating membrane very prominent; ocular acicles widely separated, dorsal surface flattened or slightly convex, very broadly triangular, produced distally and with strong terminal, marginal or submarginal spine or spines. Antennal peduncles with supernumerary segmentation. Mandible with deeply concave inner surface; ultimate segment of 3-segmented palp with 2 or 3 rows of short stiff bristles in distal half and 1 row of finer setae proximally. Maxillule (Fig. 1b) with internal endopodal lobe well developed, external lobe obsolete. Maxilla (Fig. 1c) with moderately broad, proximally subrectangular scaphognathite. First maxilliped (Fig. 1d) with basal portion of exopod somewhat bulbous. Third maxilliped (Fig. 1e) with crista dentata well developed and 1 accessory tooth.

Chelipeds unequal. Left cheliped with some degree of clockwise rotation of propodal-carpal articulation; dorsolateral margin of chela weakly to strongly inflated proximally. Ambulatory legs with dactyls and propodi of second and third pereopods similar. Fourth pereopods semichelate; propodal rasp consisting of several rows of small corneous scales.

Males with paired gonopores, almost completely masked by ventral fringe of long stiff setae, no sexual tubes; no paired pleopods, 3 unpaired, uniramous or very unequally biramous left pleopods (pl₃-pl₅). Females with paired gonopores; no paired pleopods, 4 biramous left pleopods (pl₂-pl₅), first 3 egg-carrying, last as in males.

Abdomen with somites delimited by strong transverse fibrils. Tergite of sixth abdominal segment with deep median transverse groove. Uropods strongly asymmetrical. Telson (Fig. 1a) with an indentation on the lateral margins; posterior lobes generally symmetrical, each with primarily "half-moon" contour, blade-like lateral margin and acute terminal angle, usually broadly separated and with distinct median cleft, inner margins each with 1 prominent spine in basal half.

ETYMOLOGY. — From the Greek *di* meaning two, *acantha* meaning spine, and *oura* meaning tail, referring to the distinctive telson characteristic of this genus.

Keys to the Recent species of *Diacanthurus*

1. Carpi of third pereopods each with row of spines on dorsal margin 2
- Carpi of third pereopods with only spine at dorsodistal angle (sometimes 1 additional spinule proximally) 4

2. Ocular peduncles short (Fig. 2d), stout, corneas noticeably dilated. Maximum width of palm of right chela at least 1.25 (usually 1.5) times length of dorsomesial margin *D. rubricatus*
 — Ocular peduncles moderately long, not particularly stout, corneas not noticeably dilated. Maximum width of palm of right chela only slightly greater than length of dorsomesial margin 3
3. Dactyl of right chela with row of short spines or spinulose tubercles on dorsomesial surface; usually with 2 or 3 longitudinal rows of nearly coalesced, often blunt tubercles on dorsal surface. Spines on carpi of third pereopods weakly developed *D. ophthalmicus*
 — Dactyl of right chela with row of long spines on dorsomesial surface; 2 or 3 longitudinal rows of well-spaced, often acute tubercles on dorsal surface. Spines of carpi of third pereopods strongly developed *D. ecphyma* sp. nov.
4. Ocular peduncles short (Fig. 2c), moderately stout; antennal peduncles reaching beyond bases of corneas. Dorsal surfaces of palms of both chelas with numerous moderately closely-spaced quite small tubercles or spinules *D. richeri* sp. nov.
 — Ocular peduncles long (Fig. 2e), moderately slender; antennal peduncles not usually reaching to bases of corneas. Dorsal surfaces of palms of both chelae with relatively few, widely-spaced irregular longitudinal rows of moderately large tubercles *D. spinulimanus*

1. Corneas slightly dilated. Ratio of peduncular length to corneal diameter between 3.5 and 4:1 *D. spinulimanus*
 — Corneas moderately or strongly dilated. Ratio of peduncular length to corneal diameter less than 3:1 2
2. Ratio of peduncular length to corneal diameter between 2:1 and 2.5:1 3
 — Ratio of peduncular length to corneal diameter less than 2:1 4
3. Telson longer than broad. Palm of right chela strongly asymmetrical; strong spines on mesial margin and on distal half of lateral margin *D. ecphyma* sp. nov.
 — Telson as long as broad. Palm of right chela almost symmetrical; both margins with regular spines of moderate size *D. ophthalmicus*
4. Ocular acicles unidentate. Telson longer than broad. Maximum width of palm of right chela more than 1.25 times length of dorsomesial margin. Antennal peduncles equal to or slightly longer than ocular peduncles *D. rubricatus*
 — Ocular acicles usually bidentate (at least on 1 side). Telson as long as broad. Maximum width of palm of right chela only slightly greater than length of dorsomesial margin. Antennal peduncles shorter than ocular peduncles *D. richeri* sp. nov.

Diacanthurus ecphyma sp. nov.

Figs 2a, 3a-i

MATERIAL EXAMINED. — **New Caledonia**. CHALCAL: stn D 65, 22°11.50'S, 159°15.40'E, 305 m, 27.07.1984: 1 ♂ (4.4 mm) (MNHN Pg 5479).

SMIB 4: stn DW 43, 24°46.6'S, 168°08.8'E, 245 m, 08.03.1989: 2 ♂, 1 ♀ (3.6-5.6 mm) (USNM 276062).

BERYX 11: stn 18, 24°48'S, 168°09'E, 250-270 m, 16.10.1992: 1 ♀ (4.2 mm) (MNHN Pg 5478).

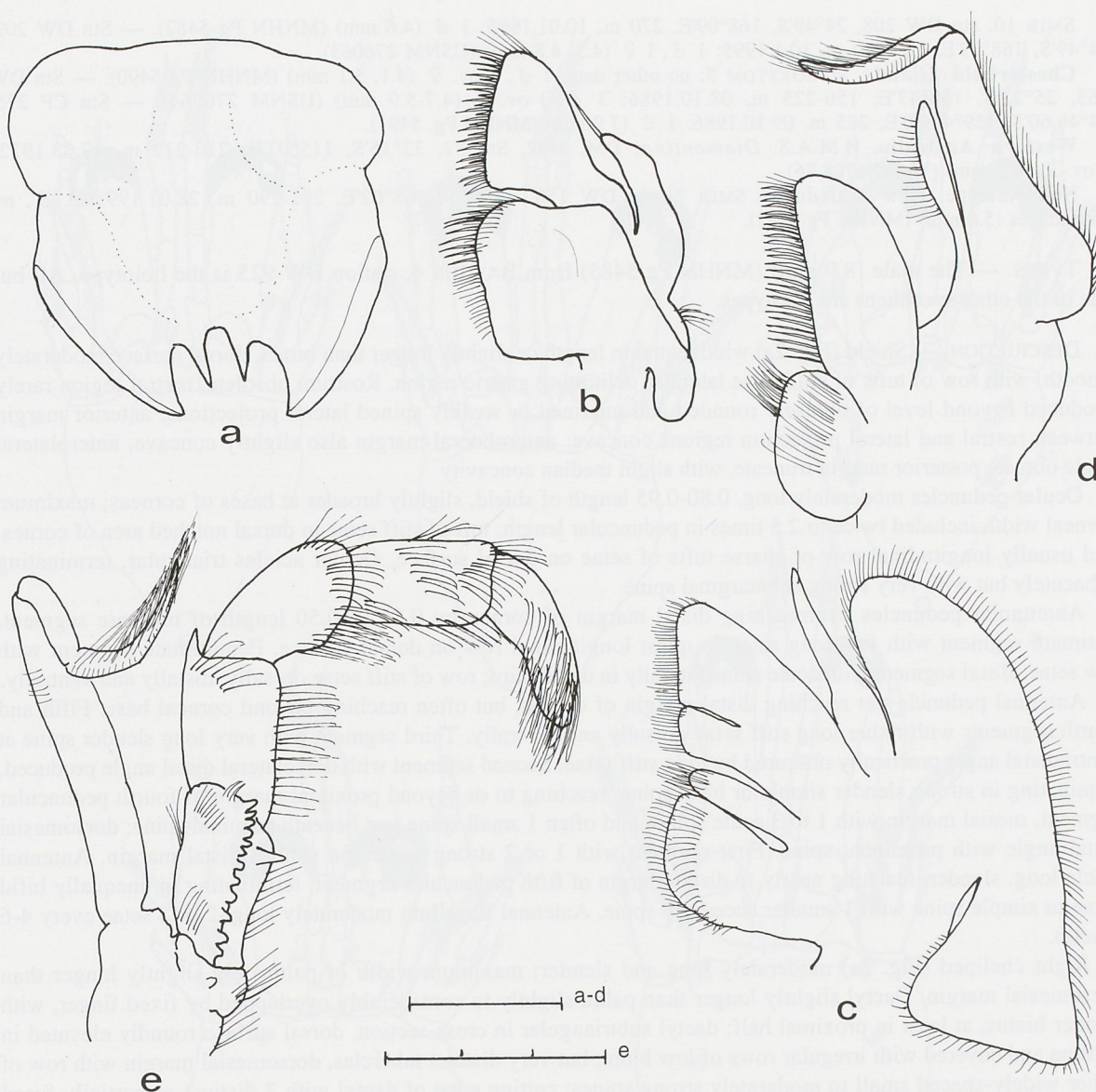


FIG. 1. — **a**, *Diacanthurus ophthalmicus* (Ortmann, 1892), ♀ holotype (6.2 mm) from Sagami Bay, Japan: telson. — **b-e**, *Diacanthurus spinulimanus* (Miers, 1876), ♂ (8.7 mm) from Paria Rock, Hawks Bay, New Zealand: **b**, maxillule (external view); **c**, maxilla (external view); **d** first maxilliped (external view); **e**, third maxilliped (internal view). Scales equal 1.0 mm (a-d) and 3.0 mm (e).

SMIB 8: stn DW 155, 24°45'S, 168°08'E, 257-262 m, 28.01.1993: 1 ♂ (5.4 mm) (MNHN Pg 5480). — Stn DW 159, 24°46'S, 168°08'E, 241-245 m, 28.01.1993: 1 ♂ (2.8 mm). — Stn DW 170, 23°41'S, 168°01'E, 241-244 m, 29.01.1993: 1 ov. ♀ (5.8 mm) (MNHN Pg 5481).

BATHUS 4: stn DW 904, 18°59'S, 163°11'E, 461 m, 04.08.1994: 1 ov. ♀ (8.9 mm) (MNHN Pg 5483). — Stn DW 924, 18°54'S, 163°24'E, 344-360 m, 07.08.1994: 2 ov. ♀ (7.6, 7.9 mm) (MNHN Pg 5484). — Stn DW 925, 18°54'S, 163°23'E, 370-405 m, 07.08.1994: 1 ♂, 2 ♀ (4.6-8.9 mm) (MNHN Pg 5485). — Stn DW 926, 18°56'S, 163°25'E, 325-330 m, 07.08.1994: 1 ♀ (4.0 mm) (MNHN Pg 5486). — Stn CP 936, 19°03'S, 163°28'E, 258-252 m, 08.08.1994: 2 ♂ (8.3, 8.5 mm) (MNHN Pg 5487). — Stn CP 939, 18°58'S, 163°25'E, 304-320 m, 08.08.1994: 1 ♂ (9.2 mm) (MNHN Pg 5488). — DW 942, 19°04'S, 163°28'E, 270-264 m, 08.08.1994: 1 ♂ (4.9 mm) (MNHN Pg 5489).

HALICAL 1: stn DW 01, 18°56'S, 163°24'E, 380-400 m, 23.11.1994: 2 ♀ (6.8, 8.7 mm) (MNHN Pg 5477).

SMIB 10: stn DW 208, 24°49'S, 168°09'E, 270 m, 10.01.1995: 1 ♂ (4.6 mm) (MNHN Pg 5482). — Stn DW 209, 24°49'S, 168°09'E, 329-560 m, 10.1.1995: 1 ♂, 1 ♀ (4.5, 4.8 mm) (USNM 276063).

Chesterfield Islands. MUSORSTOM 5: no other data: 1 ♂, 1 ov. ♀ (4.1, 5.1 mm) (MNHN Pg 5490). — Stn DW 263, 25°22'S, 159°47'E, 150-225 m, 08.10.1986: 3 ♂, 1 ov. ♀ (4.7-5.9 mm) (USNM 276064). — Stn CP 275, 24°46.60'S, 159°40.30'E, 285 m, 09.10.1986: 1 ♂ (7.9 mm) (MNHN Pg. 5491).

Western Australia. H.M.A.S. *Diamantina*: DM. 1/72, Stn 32, 32°15'S, 115°07'E, 210-212 m, 17.03.1972: 1 ov. ♀ (6.3 mm) (WAM 1708.86).

Non paratype. **New Caledonia.** SMIB 8: stn DW 158, 24°46'S, 168°02'E, 262-290 m, 28.01.1993: 1 ♂, no appendages (5.0 mm) (MNHN Pg 5492).

TYPES. — The male (8.9 mm) (MNHN Pg 5485) from BATHUS 4, station DW 925 is the holotype. All but one of the other specimens are paratypes.

DESCRIPTION. — Shield (Fig. 2a) width equal to length or slightly longer than broad, dorsal surface moderately smooth, with row of tufts of stiff setae laterally delimiting gastric region. Rostrum obsolete, rostral region rarely produced beyond level of obtusely rounded and unarmed or weakly spined lateral projections; anterior margin between rostral and lateral projection regions concave; anterolateral margin also slightly concave, anterolateral angle obtuse; posterior margin truncate, with slight median concavity.

Ocular peduncles moderately long, 0.80-0.95 length of shield, slightly broader at bases of corneas; maximum corneal width included twice to 2.5 times in peduncular length; tuft of stiff setae in dorsal notched area of cornea, and usually longitudinal row of sparse tufts of setae on dorsal surface. Ocular acicles triangular, terminating subacutely but with very strong submarginal spine.

Antennular peduncles overreaching distal margin of cornea by 0.15 to 0.50 length of ultimate segment. Ultimate segment with few long setae in quasi longitudinal row on dorsal surface. Penultimate segment with few setae. Basal segment with acute spine laterally in distal third; row of stiff setae dorsally, distally and ventrally.

Antennal peduncle not reaching distal margin of cornea, but often reaching beyond corneal base. Fifth and fourth segments with rather long stiff setae dorsally and ventrally. Third segment with very long slender spine at ventrodiscal angle practically obscured by long stiff setae. Second segment with dorsolateral distal angle produced, terminating in strong slender simple or bifid spine, reaching to or beyond proximal margin of fourth peduncular segment, mesial margin with 1 to 3 acute spines and often 1 small spine just beneath terminal spine; dorsomesial distal angle with prominent spine. First segment with 1 or 2 strong spines on ventral distal margin. Antennal acicle long, slender, reaching nearly to distal margin of fifth peduncular segment, terminating in unequally bifid spine or simple spine with 1 smaller accessory spine. Antennal flagellum moderately long; 2 or 3 setae every 4-6 articles.

Right cheliped (Fig. 3a) moderately long and slender; maximum width of palm only slightly longer than dorsomesial margin. Dactyl slightly longer than palm, slightly to considerably overlapped by fixed finger, with slender hiatus, at least in proximal half; dactyl subtriangular in cross-section, dorsal surface roundly elevated in midline and covered with irregular rows of low blunt, but very distinct tubercles, dorsomesial margin with row of rather widely-spaced small to moderately strong spines; cutting edge of dactyl with 3 distinct or partially fused calcareous teeth proximally and several small to moderately large more distinct molar-like teeth in distal half, terminating in calcareous claw; mesial face rounding into ventral surface and provided with tufts of long stiff setae. Palm equal to or shorter than carpus; dorsomesial margin with row of small to large, often slender acute or subacute spines, dorsomesial distal angle with cluster of low but distinct tubercles; dorsal surface of palm and fixed finger covered, but not densely, with small conical spinules or subacute tubercles, usually not obscured by mat of very short fine setae (Fig. 3b), frequently 1 sparse row of slightly stronger conical tubercles in midline of palm, dorsoproximal margin sometimes with 1 or 2 moderate to very prominent spines medially; dorsolateral margin with row of usually very much smaller spines on palm becoming considerably stronger on fixed finger; cutting edge of fixed finger with row of distinct or somewhat fused calcareous teeth proximally, several more distinct teeth distally, terminating in calcareous claw; inner faces of dactyl and fixed finger each often with several additional calcareous teeth; mesial face of palm relatively smooth or with low protuberances and moderately long and stiff setae, ventral surface and lateral face both with rows of tufts of setae. Carpus about as long as merus; dorsomesial margin with row of long, slender, very acute spines and adjacent second smaller and somewhat irregular row;

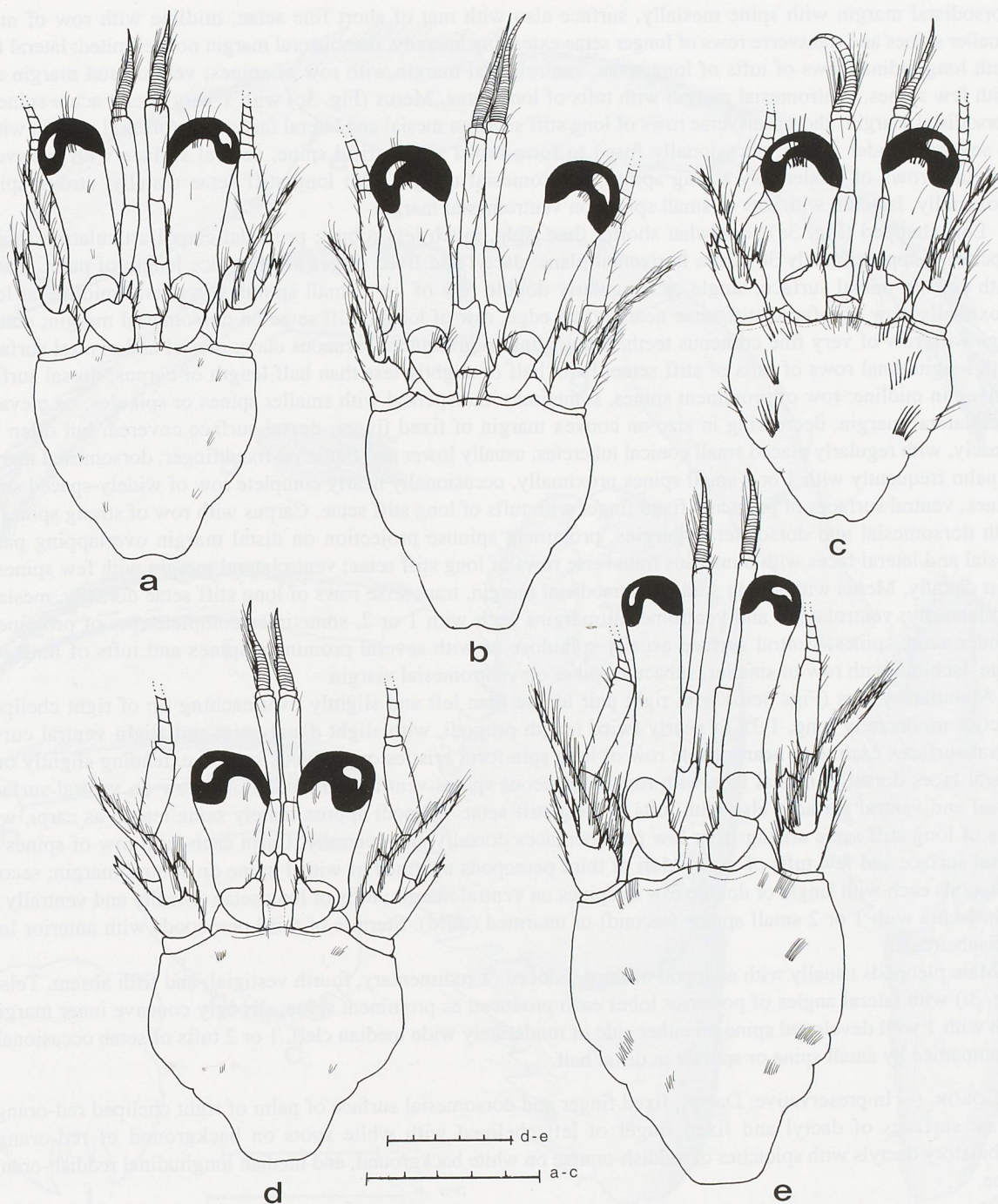


FIG. 2. — Shield and cephalic appendages.

a, *Diacanthurus ephyma* sp. nov., ♂ (5.9 mm) from MUSORSTOM 5 Stn DW 263. — **b**, *Diacanthurus ophthalmicus* (Ortmann, 1892), ov. ♀ (6.4 mm) from Minabe, Wakayama, Japan. — **c**, *Diacanthurus richeri* sp. nov., ♂ (5.9 mm) SMIB 8 Stn DW 190. — **d**, *Diacanthurus rubricatus* (Henderson, 1888), ♀ (8.4 mm) from NZOI Stn D 121. — **e**, *Diacanthurus spinulimanus* (Miers, 1876), ♀ (12.0 mm) from Paria Rock, Hawks Bay, New Zealand.

Scales equal 5.0 mm.

dorsodistal margin with spine mesially, surface also with mat of short fine setae, midline with row of much smaller spines and transverse rows of longer setae extending laterally, dorsolateral margin not delimited; lateral face with longitudinal rows of tufts of long setae, ventrolateral margin with row of spines; ventrodistal margin also with few spines, ventromesial margin with tufts of long setae. Merus (Fig. 3c) with 1 very strong acute spine on dorsodistal margin; short transverse rows of long stiff setae on mesial and lateral faces; ventrolateral margin with 3 to several slender spines, occasionally fused to form broad single trifold spine, ventral surface with transverse irregular rows of moderately strong spines, ventromesial margin with long stiff setae distally, strong spines proximally. Ischium with row of small spines on ventromesial margin.

Left cheliped (Fig. 3d) somewhat shorter than right, much less robust; propodal-carpal articulation rotated clockwise approximately 30° from horizontal plane; dactyl and fixed finger nearly twice length of palm. Dactyl with convex dorsal surface, single or irregularly double row of very small spinules in dorsal midline at least proximally, row of tufts of stiff setae near cutting edge, row of longer stiff setae on dorsomesial margin; cutting edge with row of very fine corneous teeth, terminating in prominent corneous claw; mesial and ventral surfaces with longitudinal rows of tufts of stiff setae. Palm half or slightly less than half length of carpus; dorsal surface convex in midline; row of prominent spines, sometimes interspersed with smaller spines or spinules, on elevated dorsolateral margin, decreasing in size on convex margin of fixed finger; dorsal surface covered, but often not densely, with regularly placed small conical tubercles, usually lower and flatter on fixed finger; dorsomesial margin of palm frequently with 1 or 2 small spines proximally, occasionally nearly complete row of widely-spaced small spines; ventral surfaces of palm and fixed finger with tufts of long stiff setae. Carpus with row of strong spines on both dorsomesial and dorsolateral margins, prominent spinose projection on distal margin overlapping palm; mesial and lateral faces with numerous transverse rows of long stiff setae; ventrolateral margin with few spines at least distally. Merus with strong spine at dorsodistal margin, transverse rows of long stiff setae dorsally, mesially and laterally; ventrolateral and ventromesial margins each with 1 or 2, sometimes complete row of prominent, slender acute spines; ventral surface usually spinulose or with several prominent spines and tufts of long stiff setae. Ischium with row of smaller, subacute spines on ventromesial margin.

Ambulatory legs (Figs 3e-h) with right pair longer than left and slightly overreaching tip of right cheliped. Dactyls moderately long, 1.35 to nearly twice length propodi, with slight distal twist and slight ventral curve; dorsal surfaces each with nearly triple row of long spiniform bristles or corneous spines, extending slightly onto mesial faces dorsally; mesial face with row of corneous spines ventrally and additional row on ventral surface; dorsal and ventral surfaces also with tufts of long stiff setae. Propodi approximately same length as carpi, with tufts of long stiff setae arising from low protuberances dorsally and ventrally. Carpi each with row of spines on dorsal surface and few tufts of setae. Meri of third pereopods unarmed or with 1 spine on ventral margin; second pereopods each with single or double row of spines on ventral margin; tufts of long setae dorsally and ventrally on both. Ischia with 1 or 2 small spines (second) or unarmed (third). Sternite of third pereopods with anterior lobe semisubcircular.

Male pleopods usually with endopod of third reduced or rudimentary, fourth vestigial, and fifth absent. Telson (Fig. 3i) with lateral angles of posterior lobes each produced as prominent spine; strongly concave inner margins each with 1 well developed spine on either side of moderately wide median cleft, 1 or 2 tufts of setae occasionally accompanied by small spine or spinule in distal half.

COLOR. — In preservative: Dactyl, fixed finger and dorsomesial surface of palm of right cheliped red-orange. Dorsal surfaces of dactyl and fixed finger of left cheliped with white spots on background of red-orange. Ambulatory dactyls with splotches of reddish-orange on white background, and median longitudinal reddish-orange stripe.

ETYMOLOGY. — A noun in apposition, from the Greek, *ekphyma*, meaning an eruption of pimples, and referring to the pimple-like appearance of the left chela.

DISTRIBUTION. — New Caledonia and Chesterfield Islands; Western Australia; 212-461 m (at least).

REMARKS. — *Diacanthurus ephyma* bears a strong resemblance to *D. ophthalmicus*, but is easily distinguished from the latter species by: 1) the clearly distinct rows of subacute to blunt tubercles on the dorsal

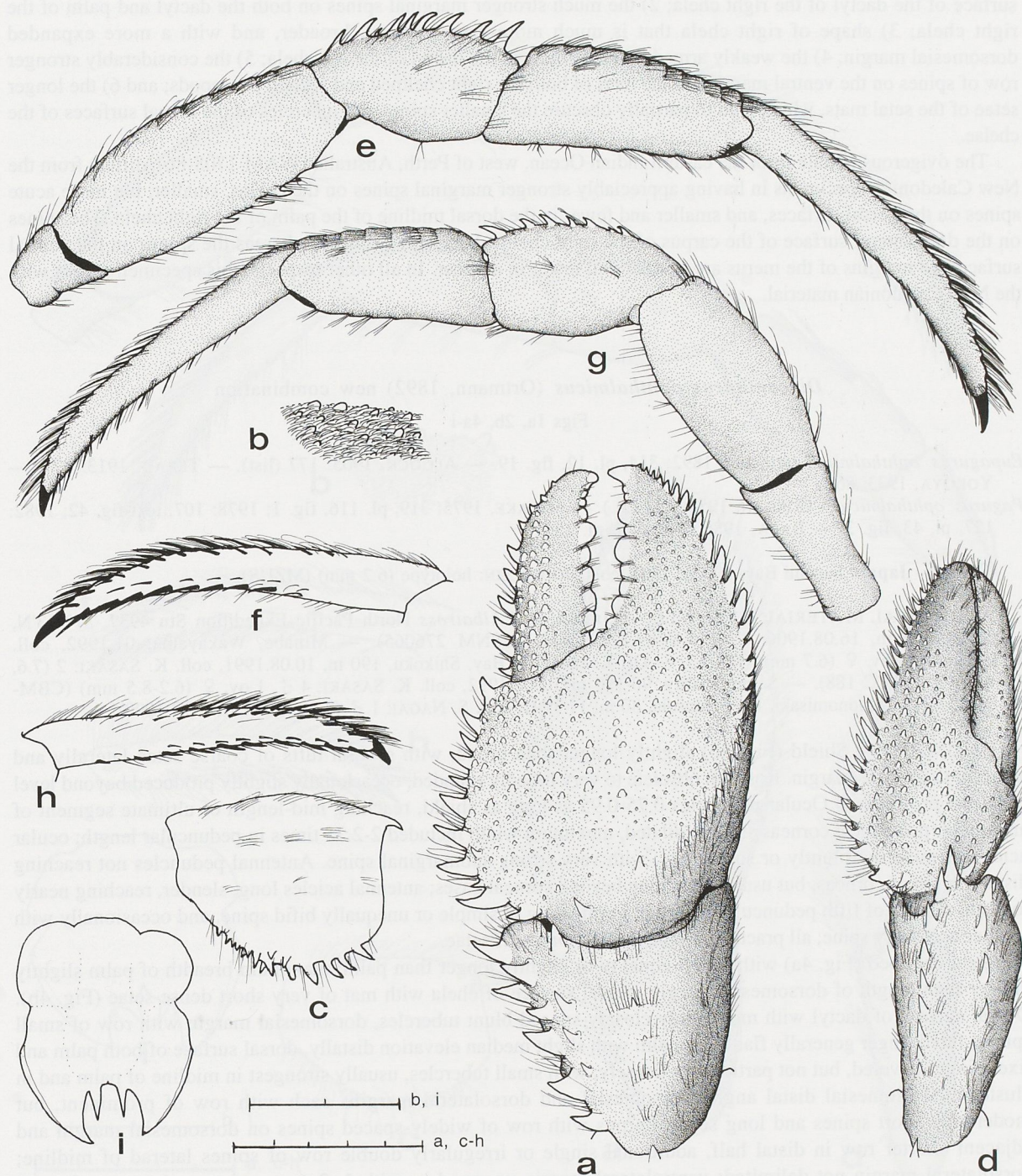


FIG. 3. — *Diacanthurus ephyma* sp. nov., ♂ (5.9 mm) from MUSORSTOM 5 Stn DW 263: **a**, chela and carpus of right cheliped (surface setal mat not shown); **b**, enlarged area of dorsal surface of palm of right chela showing setal mat; **c**, merus of right cheliped (lateral view); **d**, chela and carpus of left cheliped (surface setal mat not shown); **e**, right second pereopod (lateral view); **f**, dactyl of right second pereopod (mesial view); **g**, left third pereopod (lateral view); **h**, dactyl of left third pereopod (mesial view); **i**, telson.

Scales equal 2.0 mm (b, i) and 5.0 mm (a, c-h).

surface of the dactyl of the right chela; 2) the much stronger marginal spines on both the dactyl and palm of the right chela; 3) shape of right chela that is much more asymmetrical, broader, and with a more expanded dorsomesial margin; 4) the weakly armed dorsal surface of the dactyl of the left chela; 5) the considerably stronger row of spines on the ventral margins of the meri of both the right cheliped and second pereopods; and 6) the longer setae of the setal mats, which tend to partially obscure the smaller spines and tubercles of the dorsal surfaces of the chelae.

The ovigerous female from the eastern Indian Ocean, west of Perth, Australia (WAM 1708-86), differs from the New Caledonian specimens in having appreciably stronger marginal spines on the chelas, smaller, but more acute spines on the dorsal surfaces, and smaller and fewer in the dorsal midline of the palm of the right chela. The spines on the dorsolateral surface of the carpus of the right cheliped are also stronger, whereas the spines on the ventral surface and margins of the merus are smaller and fewer in number. In all other respects, this specimen agrees with the New Caledonian material.

Diacanthurus ophthalmicus (Ortmann, 1892) new combination

Figs 1a, 2b, 4a-i

Eupagurus ophthalmicus Ortmann, 1892: 314, pl. 12, fig. 19. — ALCOCK, 1905: 177 (list). — TERAO, 1913: 371. — YOKOYA, 1933: 86.

Pagurus ophthalmicus - GORDAN, 1956: 333 (lit.). — MIYAKE, 1975: 319, pl. 116, fig. 1; 1978: 107, text-fig. 42; 1982: 127, pl. 43, fig. 3. — BABA, 1986: 209, 305, pl. 153.

TYPE. — **Japan**. Sagami Bay, 100 m, 1881, coll. DÖDERLEIN: holotype (6.2 mm) (MZUS).

ADDITIONAL MATERIAL EXAMINED. — **Japan**. R/V *Albatross* North Pacific Expedition Stn 4937, 31° 13'N, 130°43'E, 106 m, 16.08.1906: 1 ♂, 4 ♀ (4.8-6.2 mm) (USNM 276065). — Minabe, Wakayama, 01.1992, coll. M. IMAFUKU: 1 ov. ♀ (6.7 mm) (PMcL). — Off Kochi, Tosa Bay, Shikoku, 190 m, 10.08.1991, coll. K. SASAKI: 2 (7.6, 7.7 mm) (CBM-ZC 188). — Same locality, 90-190 m, 07.07.1992, coll. K. SASAKI: 4 ♂, 1 ov. ♀ (6.2-8.5 mm) (CBM-ZC 192). — Off Shionomisaki, Kii Peninsula, 80 m, 11.1991, coll. S. NAGAI: 1 ♂ (7.6 mm) (CBM-ZC 1099).

DIAGNOSIS. — Shield (Fig. 2b) slightly longer than broad, with several tufts of coarse setae laterally and adjacent to anterior margin. Rostrum obsolete to very broadly rounded, occasionally slightly produced beyond level of lateral projections. Ocular peduncles 0.75-0.95 as long as shield, reaching mid-length of ultimate segment of antennular peduncles; corneas slightly dilated, maximum width included 2-2.35 times in peduncular length; ocular acicles terminating bluntly or subacutely, with very strong submarginal spine. Antennal peduncles not reaching distal margin or corneas, but usually reaching beyond corneal bases; antennal acicles long, slender, reaching nearly to distal margin of fifth peduncular segment, terminating in simple or unequally bifid spine, and occasionally with smaller accessory spine, all practically obscured by long stiff setae.

Right cheliped (Fig. 4a) with dactyl equal to or slightly longer than palm; maximum breadth of palm slightly greater than length of dorsomesial margin; dorsal surface of chela with mat of very short dense setae (Fig. 4b). Dorsal surface of dactyl with moderately closely-spaced blunt tubercles, dorsomesial margin with row of small spines; fixed finger generally flattened, palm with slight median elevation distally, dorsal surface of both palm and fixed finger covered, but not particularly densely, with small tubercles, usually strongest in midline of palm and in cluster at dorsomesial distal angle; dorsomesial and dorsolateral margins each with row of prominent, but moderately short spines and long setae. Carpus with row of widely-spaced spines on dorsomesial margin and adjacent shorter row in distal half, additional single or irregularly double row of spines laterad of midline; dorsolateral margin not delimited; ventrolateral margin unarmed or with 1, 2 or more, to entire row of small spines. Merus (Fig. 4c) with 1 very strong spine on dorsodistal margin; ventromesial and ventrolateral margins each with acute spines and long setae, at least distally, ventral surface with few spines.

Left cheliped (Fig. 4d) with covering of short dense setae on chela; longitudinal row of small tubercles on dorsal midline of dactyl; dorsal surface of palm and fixed finger with spinules or tubercles, dorsolateral margin with row of prominent spines. Carpus with 2 longitudinal rows of spines on dorsal surface and prominent dorsodistal

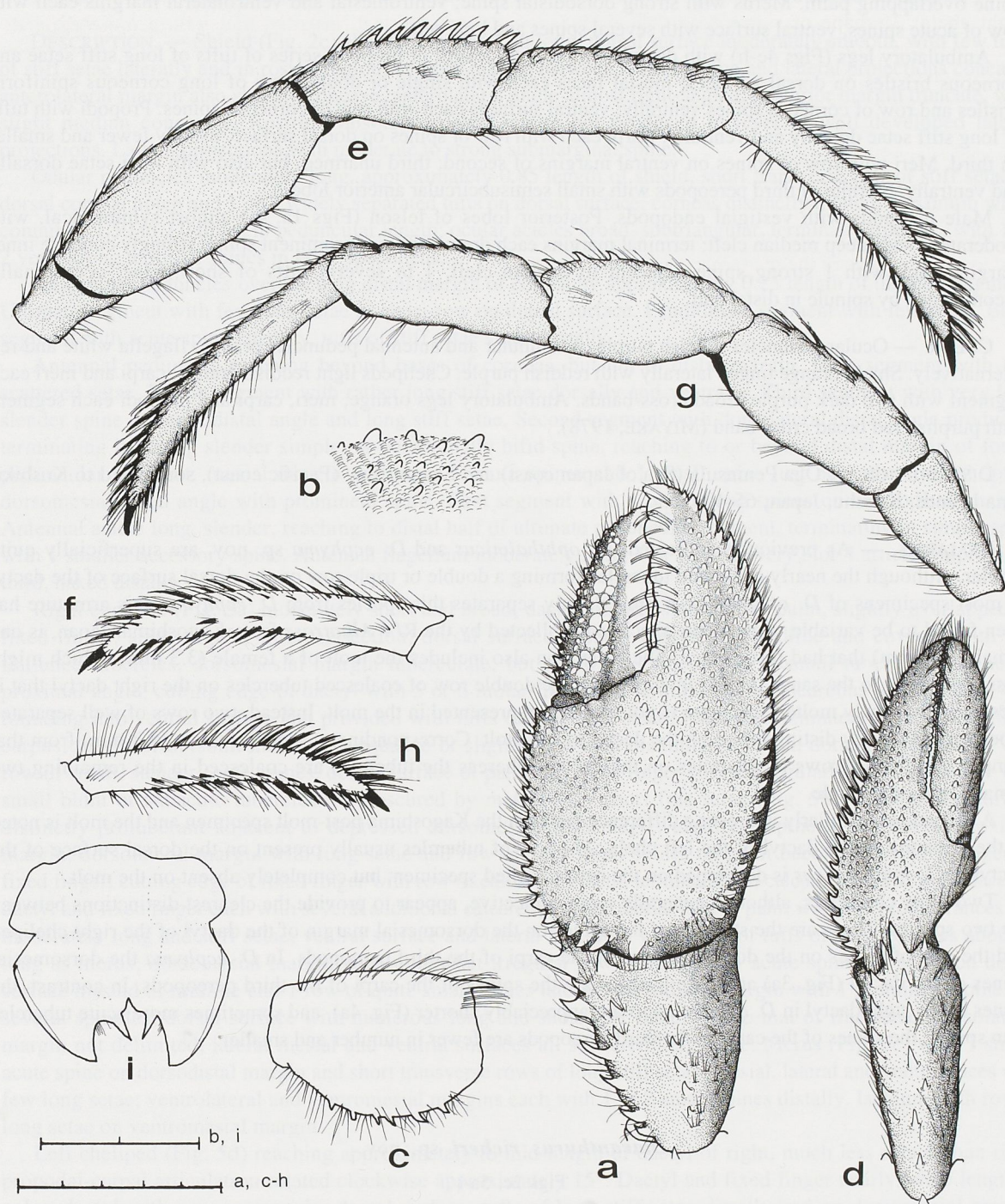


FIG. 4. — *Diacanthurus ophthalmicus* (Ortmann, 1892), ov. ♀ (6.4 mm) from Minabe, Wakayama, Japan: **a**, chela and carpus of right cheliped (surface setal mat not shown); **b**, enlarged area of dorsal surface of palm of right chela showing setal mat; **c**, merus of right cheliped (lateral view); **d**, chela and carpus of left cheliped (surface setal mat not shown); **e**, right second pereopod (lateral view); **f**, dactyl of right second pereopod (mesial view); **g**, left third pereopod (lateral view); **h**, dactyl of left third pereopod (mesial view); **i**, telson.

Scales equal 2.0 mm (b, i) and 5.0 mm (a, c-h).

spine overlapping palm. Merus with strong dorsodistal spine; ventromesial and ventrolateral margins each with row of acute spines, ventral surface with several spines and long setae.

Ambulatory legs (Figs 4e-h) with dactyls 1.35 to 1.50 length of propodi, series of tufts of long stiff setae and corneous bristles on dorsal surfaces; mesial faces each with single or double row of long corneous spiniform bristles and row of corneous spines ventrally; ventral surfaces each with row of corneous spines. Propodi with tufts of long stiff setae dorsally and ventrally. Carpi each with row of spines on dorsal surface, usually fewer and smaller on third. Meri with row of spines on ventral margins of second; third unarmed, but also with long setae dorsally and ventrally. Sternite of third pereopods with small semisubcircular anterior lobe.

Male pleopods with vestigial endopods. Posterior lobes of telson (Figs 1a, 4i) almost symmetrical, with moderately wide deep median cleft; terminal margins each drawn out into prominent spine; strongly concave inner margins each with 1 strong spine adjacent to median cleft, 1 to several tufts of short setae, occasionally accompanied by spinule in distal half.

COLOR. — Ocular peduncles reddish purple. Antennular and antennal peduncles orange; flagella white and red alternatively. Shield orange tinged laterally with reddish purple. Chelipeds light reddish orange; carpi and meri each segment with two dark purple broad cross-bands. Ambulatory legs orange; meri, carpi and propodi each segment with purplish red broad cross-band (MIYAKE, 1978).

DISTRIBUTION. — Oga Peninsula (Sea of Japan coast) and Sagami Bay (Pacific coast), southward to Koshikijima Islands, Kyushu, Japan; 65-400 m.

REMARKS. — As previously indicated, *D. ophthalmicus* and *D. ecphyma* sp. nov. are superficially quite similar. Although the nearly coalesced tubercles forming a double or triple row on the dorsal surface of the dactyl in most specimens of *D. ophthalmicus* immediately separates this species from *D. ecphyma*, this armature has been found to be variable. Among the specimens collected by the R/V *Albatross* from Kagoshima, Japan, is one female (5.3 mm) that had just molted. The collection also includes the molt of a female (3.3 mm), which might possibly belong to the same animal. Interestingly, the double row of coalesced tubercles on the right dactyl that is present in the newly molted specimen is not similarly represented in the molt. Instead, two rows of well separated tubercles are clearly distinguished on the dactyl of the molt. Corresponding, a second female (5.8 mm) from that sample has distinct rows of tubercles on the dactyl, whereas the tubercles are coalesced in the remaining two females and single male.

A second, and similarly interesting difference between the Kagoshima post-molt specimen and the molt is noted in the armature of the dactyl of the left chela. The row of tubercles usually present on the dorsal surface of the dactyl in *D. ophthalmicus* is developed on the newly molted specimen, but completely absent on the molt.

Two other characters, although generally more subjective, appear to provide the clearest distinctions between the two species. These are the strength of the spines on the dorsomesial margin of the dactyl of the right cheliped and the row of spines on the dorsal surfaces of the carpi of the third pereopods. In *D. ecphyma* the dorsomesial spines of the dactyl (Fig. 3a) are quite long, as are the spines of the carpi of the third pereopods. In contrast, the spines of the right dactyl in *D. ophthalmicus* are appreciably shorter (Fig. 4a), and sometimes more acute tubercles than spines; the spines of the carpi of the third pereopods are fewer in number and smaller.

Diacanthurus richeri sp. nov.

Figs 2c, 5a-i

MATERIAL EXAMINED. — **New Caledonia.** SMIB 8: stn DW 187, 23°18'S, 168°06'E, 390-540 m, 31.01.1993: 1 ♀ (3.6 mm) (USNM 276065). — Stn DW 190, 23°18'S, 168°05'E, 305-310 m, 31.01.1993: 1 ♂, 1 ♀ (5.7, 5.8 mm) (MNHN Pg 5493).

BATHUS 2: stn DW 729, 22°52'S, 167°11'E, 400 m, 12.05.1993: 1 ♂ (3.5 mm) (MNHN Pg 5494).

BATHUS 3: stn DW 830, 23°19'S, 168°01'E, 361-365 m, 29.11.1993: 1 ♂, 1 ♀ (3.5, 6.2 mm) (MNHN Pg 5495).

TYPES. — The female (6.2 mm) from BATHUS 3 Stn DW 830 is the holotype. The others are paratypes.

DESCRIPTION. — Shield (Fig. 2c) slightly broader than long, dorsal surface moderately smooth, with few tufts of stiff setae laterally and in rostral region; anterior margin between rostral region and lateral projections concave; anterolateral margin also slightly concave, anterolateral angle almost right-angled; posterior margin truncate, with slight median concavity. Rostrum obsolete; rostral region not produced to level of well developed lateral projections. Lateral projections with moderate to strong submarginal spine.

Ocular peduncles moderately long, approximately 0.85 length of shield, short transverse row of stiff setae in dorsal corneal notch and 1 or 2 widely separated tufts on dorsal surface; corneas distinctly dilated, maximum width contained 1.50 to 2.0 times in peduncular length; ocular acicles broad, subtriangular, terminally truncate, with 1 or 2 very strong terminal spines in large specimens.

Antennular peduncles overreaching distal margin of cornea by approximately 0.25 length of ultimate segment. Ultimate segment with few long setae in quasi-row on dorsal surface. Penultimate segment with few setae. Basal segment with acute spine laterally, tufts of stiff setae ventrodistally.

Antennal peduncles reaching beyond bases of corneas, but not to distal margin. Fifth segment with few scattered setae. Fourth segment with rather long stiff setae dorsally and ventrally. Third segment with very long slender spine at ventrodiscal angle and long stiff setae. Second segment with dorsolateral distal angle produced, terminating in strong slender simple, or occasionally bifid spine, reaching to or beyond distal margin of fourth peduncular segment; mesial margin with 2 or 3 acute spines and 1 small spine just beneath terminal spine; dorsomesial distal angle with prominent spine. First segment with 1 or 2 strong spines on ventrodiscal margin. Antennal acicle long, slender, reaching to distal half of ultimate peduncular segment, terminating in simple spine with 1 smaller accessory spine. Antennal flagellum moderately long; 1 or 2 setae every 3 or 4 articles in proximal third, naked distally.

Right cheliped (Fig. 5a) moderately short and broad; dactyl slightly shorter than palm, slightly overlapped by fixed finger; subtriangular in cross-section; dorsal surface roundly elevated in midline and covered with low flattened tubercles, dorsomesial margin tuberculate, but not well defined, 1 or 2 small tuberculate spines at proximal angle; cutting edge of dactyl with 5 or 6 molar-like teeth, terminating in calcareous tooth; mesial face rounding into ventral surface and provided with tufts of long stiff setae. Palm approximately equal to length of carpus; length of dorsomesial margin equal to or slightly less than maximum breadth; dorsomesial margin with row of small, slender acute spines, dorsal surface of palm and fixed finger covered regularly but not densely with small blunt or subacute tubercles not obscured by mat of very short fine setae (Fig. 5b); dorsomesial surface distinctly protuberant adjacent to depressed dorsomesial distal angle; usually 1 spine in midline at proximal margin, dorsolateral margin with long setae and row of very small spines on palm becoming much stronger on fixed finger; cutting edge of fixed finger with row of calcareous teeth, terminating in calcareous claw; inner faces of dactyl and fixed finger each with several additional calcareous teeth; mesial face of palm with low protuberances and moderately long and stiff setae; ventral surface and lateral face both with rows of tufts of setae. Carpus about as long as merus; dorsomesial margin with somewhat irregular row of long, very acute spines, 1 spine on dorsal surface mesiad of midline and 1 row of quite small spines laterad; dorsodistal margin with 1 prominent spine and several spinules; dorsal surface with numerous long and short stiff setae, but no mat of fine setae; dorsolateral margin not delimited, lateral mesial and ventral surfaces all scattered long setae. Merus (Fig. 5c) with 1 strong acute spine on dorsodistal margin and short transverse rows of long stiff setae; mesial, lateral and ventral faces with few long setae; ventrolateral and ventromesial margins each with 1 or 2 small spines distally. Ischium with row of long setae on ventromesial margin.

Left cheliped (Fig. 5d) reaching approximately to mid-length of dactyl of right, much less robust than right; propodal-carpal articulation rotated clockwise approximately 15°. Dactyl and fixed finger nearly twice length of palm; dactyl with convex granular dorsal surface, tufts of long stiff setae distally and on dorsomesial margin; cutting edge with row of very fine corneous teeth, terminating in prominent corneous claw; mesial and ventral surfaces with tufts of stiff setae. Palm half or slightly less than half length of carpus; dorsal surface roundly elevated in midline, row of slender spines on dorsolateral margin, decreasing in size on fixed finger; dorsal surface covered with mat of short fine setae and uniform but not densely packed small tubercles; dorsomesial margin with

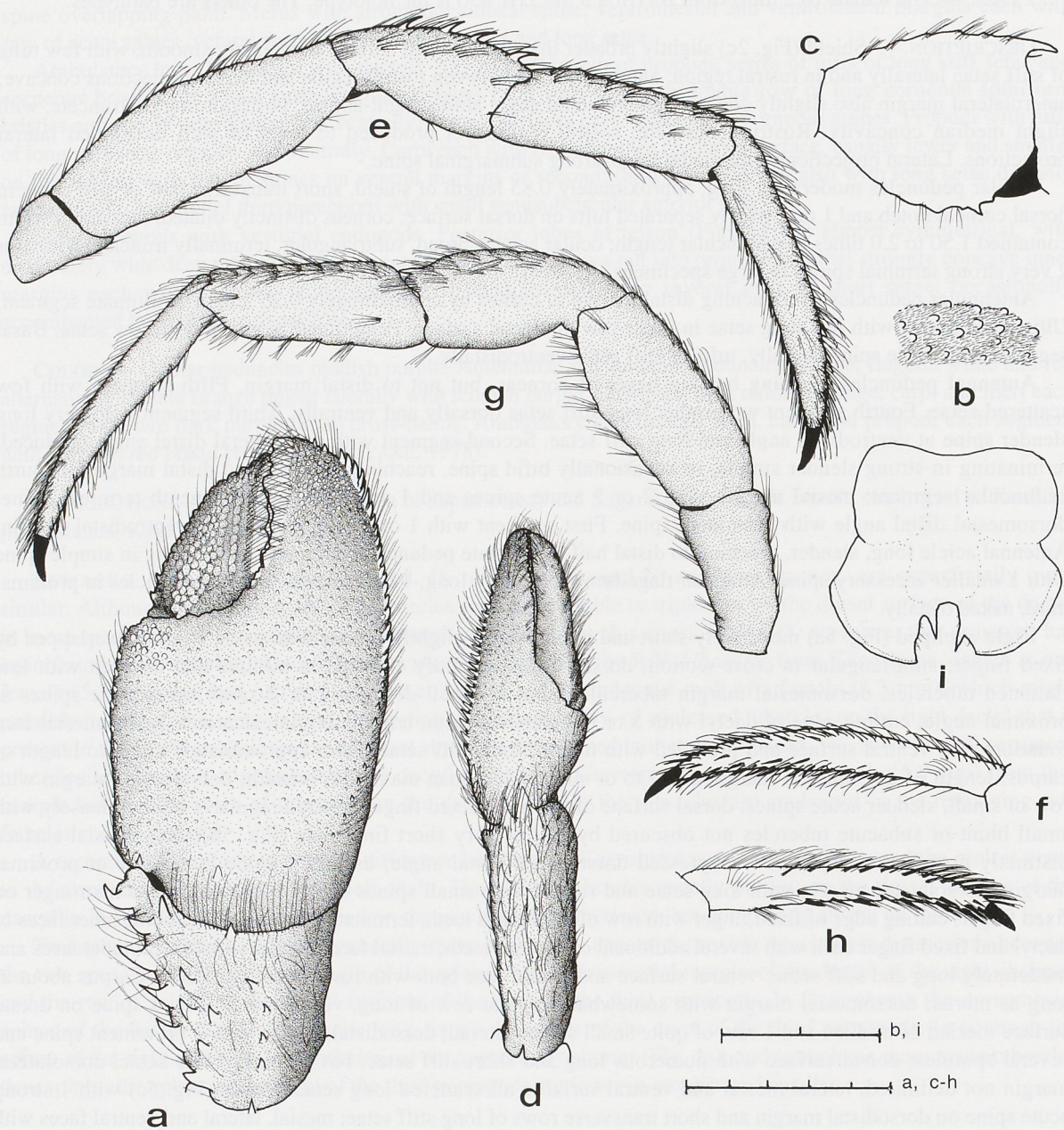


FIG. 5. — *Diacanthurus richeri* sp. nov., ♂ (5.9 mm) SMIB 8 Stn DW 190: **a**, chela and carpus of right cheliped (surface setal mat not shown); **b**, enlarged area of dorsal surface of palm of right chela showing setal mat; **c**, merus of right cheliped (lateral view); **d**, chela and carpus of left cheliped (surface setal mat not shown); **e**, right second pereopod (lateral view); **f**, dactyl of right second pereopod (mesial view); **g**, left third pereopod (lateral view); **h**, dactyl of left third pereopod (mesial view); **i**, telson.

Scales equal 2.0 mm (b, i) and 5.0 mm (a, c-h).

1 or 2 small spines in proximal third; ventral surfaces of palm and fixed finger with tufts of long stiff setae. Carpus with row of strong spines on both dorsomesial and dorsolateral margins, prominent spine on distal margin overlapping palm; mesial and lateral faces with numerous transverse rows of long stiff setae. Merus with small

spine at dorsodistal margin, transverse rows of long stiff setae dorsally, mesially and laterally; ventrolateral and ventromesial margins each with row of small spines, ventral surface with tufts of long stiff setae. Ischium with row of very small spines on ventromesial margin.

Ambulatory legs (Figs 5e-h) generally similar. Dactyls approximately 1.25 length propodi; with slight distal twist and slight ventral curve; dorsal surfaces each with transverse rows of long corneous spines-like bristles; mesial faces each with row of corneous spines ventrally and frequently also dorsally; ventral surfaces each with row of corneous spines, dorsal and ventral surfaces also with tufts of long stiff setae. Propodi same length as carpi or slightly longer, with tufts of long stiff setae arising from low protuberances dorsally and ventrally. Carpi of second each with 3 or 4 widely-spaced strong spines on dorsal surface; third with 1 spine at dorsodistal angle and few tufts of setae. Meri with low protuberances and tufts of long setae dorsally and ventrally. Ischia unarmed. Sternite of third pereopods with anterior lobe semisubcircular, slightly skewed.

Males pleopods with endopods usually absent. Telson (Fig. 5i) with lateral angles of posterior lobes not strongly produced, terminally subacute; inner margins nearly perpendicular, each usually with 1 spine on either side of moderately wide median cleft (only 1 in holotype), often extending more than 0.50 length of margin.

COLOR. — In preservative: Only faint tinge of reddish-yellow remaining on chelae.

ETYMOLOGY. — This species is named in honor of Bertrand RICHER DE FORGES, of ORSTOM, a principal collector for the MUSORSTOM campaigns.

HABITAT. — Not known.

DISTRIBUTION. — New Caledonia; 305-400 m (at least).

REMARKS. — In lacking a row of spines on the dorsal margins of the carpi of the third pereopods, *D. richeri* appears most closely allied to *D. spinulimanus*. However, the two species are easily separated by the differences in armature of the dorsal surfaces of the chelae. Additionally, *D. richeri* frequently has a pair of strong spines on each ocular acicle in large specimens. Of the six specimens available, the three largest specimens all have a pair of spines on each acicle. In the three smaller specimens, the terminal acicular margin is straight, with a strong spine developed mesially, and in one of the three a second small spine is present laterally on one acicle. The terminal margins of the acicles in *D. spinulimanus* are triangular and only a single spine has been observed in all of the specimens examined.

One small, questionably female specimen (3.5 mm) (MNHN Pg 5494) possessed both female gonopores and what appeared to be a small right male gonopore. Unpaired pleopods three to five had moderately well developed exopods, but very rudimentary endopods were present only on the third and fourth. The second pleopod was uniramous and rudimentary; however, in small female specimens of all species of *Diacanthurus*, the second pleopod is appreciably less developed than either the third or fourth.

Diacanthurus rubricatus (Henderson, 1888) new combination

Figs 2d, 6a-j

Eupagurus rubricatus Henderson, 1888: 69, pl. 7, fig. 4. — G.M. THOMSON, 1899: 180. — ALCOCK, 1905: 176 (list). — CHILTON, 1911: 297. — E.F. THOMPSON, 1930: 272.

Eupagurus intermedius - CHILTON, 1911: 297; not *Eupagurus intermedius* Lenz, 1901.

Pagurus rubricatus - GORDAN, 1956: 335 (lit). — HAND, 1975: 510. — PROBERT *et al.*, 1979: 381 (list). — HYDEN & FOREST, 1980: 473. — SCHEMBRI, 1982a: 101, figs 1-12. — SCHUCHERT, 1996: 48.

"*Pagurus*" *rubricatus* - SCHEMBRI, 1982b: 868; 1988: 93. — SCHEMBRI & MCLAY, 1983: 34, figs 21, 24.

TYPE. — **New Zealand**. Holotype (6.6 mm; abdomen missing) (NHM 1888.33).

ADDITIONAL MATERIAL EXAMINED. — **New Zealand**. Off Napier: 37 m, 11.1923: coll. W.J. PHILLIPPS: 1 ♂, 1 ♀ (11.2, 14.9 mm) (NMNZ). — Off Banks Peninsula, Trawler *Phyllis*, 36-18 m, 21.08.1929: 1 ♂ (15.5 mm) (MNHN-Pg

5496). — Portobello Marine Laboratory: stn MU 66-75, East of Taiaroa Head, 51-55 m, 09.12.1966: 1 ♂ (16.6 mm) (PMLUO).

R.V. *Kaharoa* (coll. M. MORRISON): stn 10, 36°55'S, 176°17'E, 348-352 m, 09.04.1996: 1 ♂ (10.0 mm) (PMcL). — Stn 26, 37°05'S, 176°15'E, 395-399 m, 13.04.1996: 1 ♀ (9.7 mm) (PMcL). — Stn 55, 36°54'S, 176°18'E, 442-445 m, 22.04.1996: 1 ♂ (9.9 mm) (PMcL).

NZOI: stn A 901, 43°17'S, 177°04'E, 251 m, 08.09.1963: 1 ov. ♀ (11.9 mm) (NZOI). — Stn C 753, 35°20'S, 172°52'E, 190 m, 17.03.1962: 1 ♀ (7.7 mm) (NZOI). — Stn F 739, 37°36'S, 179°06'E, 529-459 m, 27.03.1967: 2 ♂ (3.9, 5.2 mm) (NZOI). — Stn D 121, 43°16'S, 177°10'E, 210 m, 11.10.1963: 1 ♂, 2 ♀, 2 ov. ♀ (6.8-16.4 mm) (NZOI). — Stn D 267, 40°50'S, 173°43'E, 60 m, 06.10.1964: 1 ♀ (3.9 mm) (NZOI). — Stn E 106, 43°55'S, 177°10'W, 180 m, 11.10.1964: 2 ♂, 5 ♀ (7.6-15.5 mm) (NZOI). — Stn E 114, 43°35'S, 176°15'W, 135 m, 13.10.1964: 2 ♂, 2 ♀ (3.3-7.3 mm) (NZOI). — Stn E 727, 37°40'S, 177°12'E, 300-278 m, 25.03.1967: 1 ♀ (8.5 mm) (NZOI). — Stn E 759, 43°45'S, 173°40'E, (?)1951-2134 m, 31.03.1967: 1 ♀ (5.0 mm) (NZOI). — Stn E 785, 44°00'S, 168°18'E, 282 m, 17.10.1967: 1 ov. ♀ (11.9 mm) (NZOI). — Stn F 741, 40°30'S, 174°30'E, 117 m, 02.04.1967: 1 ♂, 1 ♀ (5.2, 8.3 mm) (NZOI).

DIAGNOSIS. — Shield (Fig. 2d) subquadrate, slightly broader than long, moderately flat, with lateral tufts of setae. Rostrum virtually obsolete to obtusely rounded, sometimes produced slightly beyond level of weakly developed lateral projections, large specimens occasionally with small rostral protuberance. Ocular peduncles moderately stout, 0.50-0.90 length of shield (0.50-0.75 in large specimens); corneas somewhat dilated, corneal diameter included 1.25 to 1.80 in peduncular length; ocular acicles broad basally, slender and acuminate distally, with usually strong submarginal spine. Antennular and antennal peduncles overreaching distal margin of corneas. Antennal acicle long, slender, reaching distal half or nearly to distal margin of fifth peduncular segment, mesial margin setose.

Chelipeds with distal segments usually covered with short matted setae (Fig. 6b); dactyl of right cheliped (Fig. 6a) with several rows of rounded tubercles on dorsal surface; palm with dorsomesial margin commonly inflated, maximum breadth of palm usually at least 1.50 times length of dorsomesial margin, or often in very large specimens only 1.25 times; dorsal surface elevated in midline, frequently more prominently produced distally, and with inverted, quasi V-shaped series of large blunt tubercles; remainder of dorsal surface with scattered rounded tubercles at least partially obscured by setae, dorsomesial and dorsolateral margins each with row of spines. Carpus with strong row of spines on dorsomesial margin, dorsal surface with conical spines, strongest and most numerous mesial of midline, partially obscured by setae; distal margin with 1 or 2 prominent spines. Merus (Fig. 6c) with strong spine at dorsodistal margin; ventrolateral margin with row of small spines or spinules and prominent spinose protuberance proximally.

Left cheliped (Fig. 6d) with propodal-carpal articulation rotated clockwise 45-60° from horizontal plane. Dorsal surface of dactyl with dense mat of setae usually obscuring several irregular rows of small spines or spinulose tubercles; dorsolateral margin of palm strongly convex, somewhat elevated proximally and armed with blunt spines, dorsal surface covered by short dense setae, often completely obscuring irregular rows of small spines or spinulose tubercles. Dorsal surface of carpus with 2 rows of spines. Merus with strong spine on dorsodistal margin; ventromesial and ventrolateral margins each with row of slender spines.

Ambulatory legs (Figs 6e-h) usually slightly overreaching tip of right cheliped; dactyls considerably longer than propodi, slightly twisted; dorsal margins each with row of long corneous spiniform bristles, but few additional setae; mesial faces each with dorsal and ventral row of small corneous spinules; ventral margins each with row of long corneous spines interspersed with shorter corneous spines or spiniform bristles. Propodi with transverse setose ridges dorsally and fewer similar ridges ventrally. Carpi of both second and third with spinose dorsal margins. Meri of second each with row of widely-spaced low, sometimes spinulose protuberances or small spines on ventral margins; third unarmed. Sternite of third pereopods with subquadrate to subrectangular anterior lobe.

Male pleopods usually uniramous; third occasionally with vestige of endopod. Telson (Figs 6i, j) with posterior lobes laterally convex or nearly straight, mesially concave and drawn out into strong terminally blunt or acute "half-moon"; 1 strong, but usually quite short spine basally on either side of broad, often moderately deep median cleft, occasionally 1 or 2 spinules on inner margin.

COLOR. — Ocular peduncle white with red longitudinal stripe ventrally; antennules white; antennae uniformly reddish-brown; chelipeds and ambulatory legs yellow-brown ground color tending to white ventrally, with bright

red bands on distal ends of meri and patch of same color on mesial faces at proximal ends of carpi; carpi also with light purple longitudinal stripe on dorsal margins (SCHEMBRI & MCLAY, 1983).

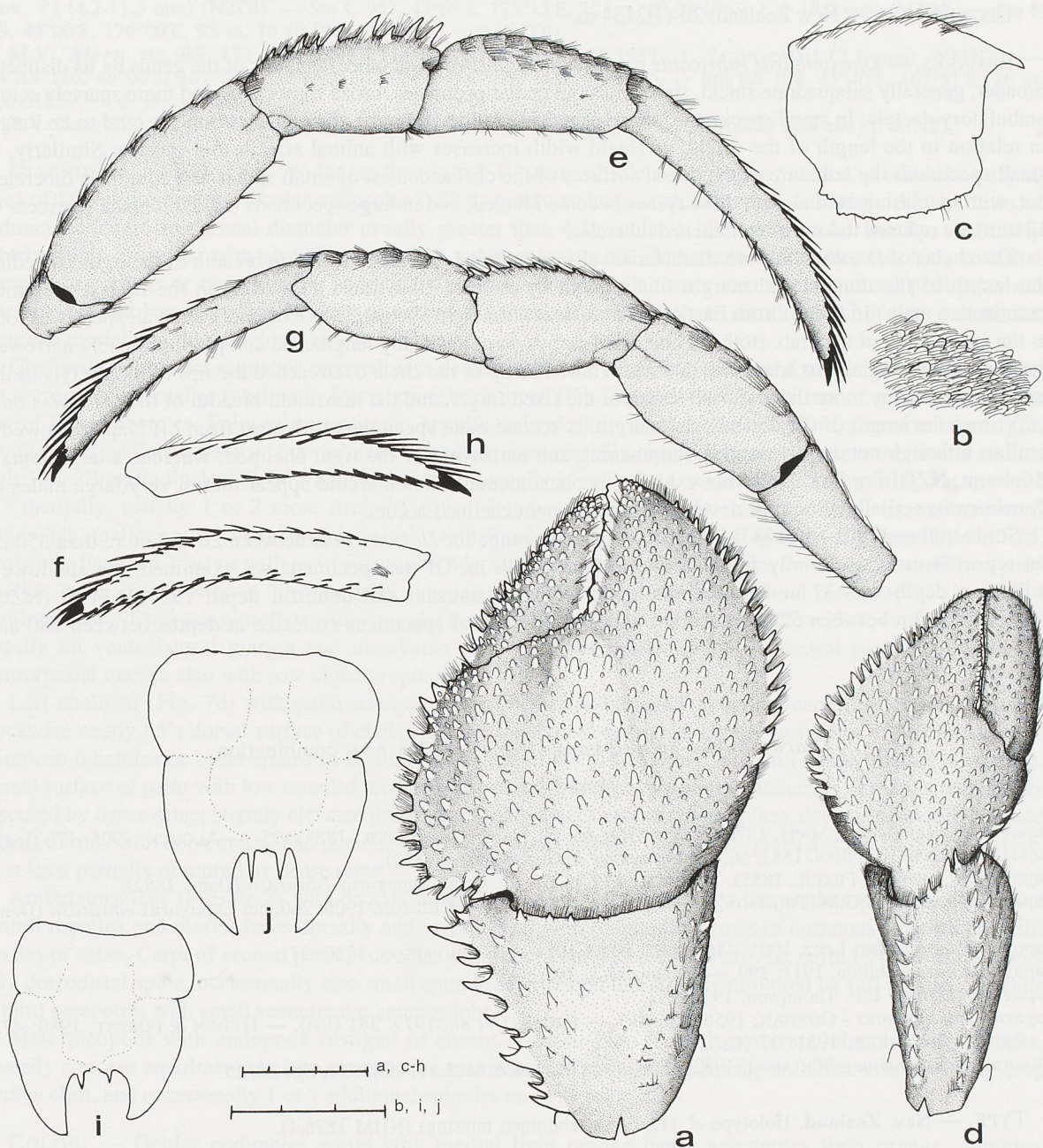


FIG. 6. — *Diacanthurus rubricatus* (Henderson, 1888), a-i, ♀ (8.4 mm) from NZOI Stn D 121; j, ♀ (9.6 mm) from Bay of Plenty, New Zealand: a, chela and carpus of right cheliped (surface setal mat not shown); b, enlarged area of dorsal surface of palm of right chela showing setal mat; c, merus of right cheliped (lateral view); d, chela and carpus of left cheliped (surface setal mat not shown); e, right second pereopod (lateral view); f, dactyl of right second pereopod (mesial view); g, left third pereopod (lateral view); h, dactyl of left third pereopod (mesial view); i-j, telson.

Scales equal 3.0 mm (b, i, j) and 5.0 mm (a, c-h).

HABITAT. — Found occupying variety of gastropod shells, which may be covered with the hydrozoan *Hydractinia rubricata* Schuchert, or may carry the anemones *Paracalliactis rosea* Hand and *Calliactis conchicola* Parry.

DISTRIBUTION. — New Zealand; 20-(?)2134 m.

REMARKS. — *Diacanthurus rubricatus* is easily distinguished from other members of the genus by its distinctly broader, generally subquadrate shield, short and stout ocular peduncles, broad right chela, and more sparsely setose ambulatory dactyls. In small specimens (shield lengths less than 4.0 mm), the ocular peduncles tend to be longer in relation to the length of the shield, as shield width increases with animal size in this species. Similarly, in small specimens the armature of the dorsal surfaces of the chelae consist of small spines and spinulose tubercles; but, with increasing animal size, these spines become blunted, and in large specimens (shield lengths in excess of 12 mm) are reduced to low, often flattened tubercles.

The chelae of *D. rubricatus* are characteristically quite broad, with the maximum breadth of the right exceeding the length of the dorsomesial margin of the palm by at least 1.50 times. However, in the largest specimen examined, a male (16.6 mm) from East of Taiaroa Heads, the right cheliped was extremely elongate, nearly as long as the entire body of the crab. Both the chela and carpus were unusually lengthened and proportionately narrower, the chela appearing almost triangular in dorsal view. The tip of the chela overreached the tips of the dactyls of the ambulatory legs by more than half the length of the fixed finger, and the maximum breadth of the palm was only 1.25 times the length of the dorsomesial margin. A second male specimen (14.9 mm) from off Napier showed a similar, although not as pronounced, lengthening and narrowing of the right cheliped; whereas a large female (16.4 mm, NZOI Stn D 121) did not exhibit this phenomenon. Thus it would appear that in very large males of *D. rubricatus* sexually dimorphic development of the right cheliped occurs.

SCHEMBRI and MCLAY (1983) give the bathymetric range for *D. rubricatus* between 20 and more than 350 m, but report it most commonly found between 40 and 220 m. Of the specimens we examined, the shallowest collection depth was 37 m, the deepest, apart from the unusual and doubtful depth 1951-2134 m (NZOI Stn E 759) from between 529 and 459 m, with the majority of specimens collected at depths between 180 and 300 m.

Diacanthurus spinulimanus (Miers, 1876) new combination

Figs 1 b-e, 2e, 7a-i

Eupagurus spinulimanus Miers, 1876a: 222; 1876b: 63, pl. 1, fig. 6. — FILHOL, 1885a: 25. — ALCOCK, 1905: 176 (list).

Eupagurus Edwardsii Filhol, 1883: 66; not *Eupagurus edwardsii* (Dana, 1852).

Eupagurus Edwardsi - FILHOL, 1885a: 25; 1885b: 412, pl. 52, fig. 6; not *Eupagurus edwardsii* (Dana, 1852).

Eupagurus edwardsi - G.M. THOMSON, 1899: 182, pl. 20, figs 6-7. — CHILTON, 1906: 266; not *Eupagurus edwardsii* (Dana, 1852).

Eupagurus intermedius Lenz, 1901: 446, pl. 32, figs 8-10. — E.F. THOMPSON, 1930: 271.

Eupagurus norae Chilton, 1911: 299. — BORRADAILE, 1916: 95.

Eupagurus chiltoni E.F. Thompson, 1930: 271.

Pagurus spinulimanus - GORDAN, 1956: 335 (lit). — PROBERT *et al.*, 1979: 381 (list). — HYDEN & FOREST, 1980: 473, fig. 3b. — RAINER, 1981: 37 (list).

'*Pagurus*' *spinulimanus* - SCHEMBRI, 1982b: 868. — SCHEMBRI & MCLAY, 1983: 34, figs 20, 25.

TYPE. — **New Zealand.** Holotype ♂ (12.7 mm; abdomen missing) (NHM 1876.4).

ADDITIONAL MATERIAL EXAMINED. — **New Zealand.** No specific locality: 1790-1795, H. FILHOL id.: 1 ♂, 1 ♀ (5.1, 5.8 mm) (MNHN). — Cook Strait, H. FILHOL id.: 1 ♀ (7.2 mm) (MNHN). — VUZ Stn GUJ 166, 1 ♀ (7.1 mm) (NMNZ). — VUZ Stn H, 1 ♀ (6.3 mm) (NMNZ). — Great Omaha Bay: 26-30 m, 17.07.1995-15.12.1995, coll. R. TAYLOR: 2 ♂, 3 ♀ (2.2-9.1 mm) (PMcL). — Colville Channel: Marine Prawn Survey Stn 90, 48 m, 14.11.1962: 1 ♂, 2 ♀ (3.4-5.7 mm) (NZOI). — Paria Rock, Hawke Bay: 12 m, 29.7.1991, coll. C. DUFFY: 4 ♂, 4 ♀ (2 ov.) (7.1-14.9 mm) (PMcL). — Off Cuvier I.: Marine Fisheries Dept., 46-51 m, 11.01.1964: 1 ov. ♀ (10.7 mm) (NZOI).

NZOI: Stn B 225, 46°50'S, 168°18'E, 31 m, 21.01.1960: 1 ♂, 1 ♀ (12.4, 13.2 mm) (NZOI). — Stn B 263, 46°55'S, 168°24'E, 53 m, 27.05.1960: 1 ♀ (10.0 mm) (NZOI). — Stn B 605, 46°23'S, 167°22'E, 73 m, 17.10.1962: 1 ♀ (3.4 mm) (NZOI). — Stn B 619, 44°42'S, 167°33.2'E, 95 m, 19.10.1962: 1 ♀ (6.5 mm) (NZOI). — Stn C 814, 37°40'S, 178°56'E, 194 m, 25.02.1962: 1 ♂ (5.4 mm) (NZOI). — Stn C 844, 41°38'S, 175°11'E, 88 m, 01.03.1962: 1 ♂, 2 ♀ (1 ov. ♀) (4.2-11.5 mm) (NZOI). — Stn C 957, 43°09'S, 175°15'E, 123 m, 07.03.1963: 1 ♂ (6.0 mm) (NZOI). — Stn E 139, 44°00'S, 176°00'E, 95 m, 16.10.1964: 1 ♀ (4.1 mm) (NZOI).

M.V. *Alert*: stn BS 173, 40°52.2'S, 114°57.2'E, 59 m, 10.08.1951: 1 ♀ (juvenile) (2.1 mm) (NMNZ). — Stn BS 186, 45°00'S, 167°20'E, 37 m, 23.03.1949: 1 ♀ (8.9 mm) (NMNZ). — Stn BS 198, 45°40'S, 167°51'E, 36 m, 13.01.1957: 1 ♂ (3.2) (NMNZ).

R.V. *Tangaroa*: stn BS 732, 37°46.5'S, 176°38.5'E, 39 m, 21.01.1979: 1 ?♂ (juvenile) (2.4 mm) (NMNZ).

DIAGNOSIS. — Shield (Fig. 2e) longer than broad. Rostrum obsolete or broadly rounded, produced nearly to level of lateral projections. Ocular peduncles 0.80 to nearly as long as shield; corneae slightly dilated, ratio of peduncular length to corneal diameter usually greater than 4:1; ocular acicles very broad basally, terminally subtriangular to ovate, with strong marginal or submarginal spine. Antennular peduncles reaching to distal margins of corneas or overreaching corneas by up to 0.5 length of ultimate segment. Antennal peduncles not reaching beyond basal margins of corneas; antennal acicles reaching nearly to distal margin of fifth peduncular segment, mesial margin with dense row of long setae.

Chelipeds with distal segments covered with dense short setae (Fig. 7b); spines and tubercles usually smaller, but more acute in smaller specimens. Dactyl of right cheliped (Fig. 7a) with dorsolateral row of spines and median row of large tubercles. Palm with maximum breadth only slightly greater than length of dorsomesial margin; strong spines on dorsomesial and dorsolateral margins at least partially obscured by dense long setae; dorsal surface with 1 or 2 longitudinal rows of widely-spaced tall, usually blunt spines, sometimes forming irregular inverted "V" medially, usually 1 or 2 more irregular rows of spines or tubercles laterally and mesially and scattered somewhat smaller spines or tubercles on palm and fixed finger; tip of fixed finger usually heavily calcified, frequently flattened. Carpus with row of strong slender spines on dorsomesial margin; dorsal surface with scattered smaller acute spines, often at least partially concealed by dense setae and longitudinal row of spines laterad of midline; ventrodiscal margin often with irregular row of small spines. Merus (Fig. 7c) with row of acute spines distally on ventrolateral margin and transverse rows of spines extending onto ventral surface proximally; ventromesial margin also with row of acute spines.

Left cheliped (Fig. 7d) with palm somewhat dorsoventrally flattened, propodal-carpal articulation twisted clockwise nearly 45°; dorsal surface of chela with mat of short dense setae. Dorsal surface of dactyl with row of spinulose tubercles or blunt spines in midline, dorsomesial margin unarmed but with dense tufts of long setae. Dorsal surface of palm with low rounded median ridge armed with row of spinulose tubercles or blunt spines nearly obscured by dense setae; slightly elevated dorsolateral margin with row of strong spines, decreasing in size on fixed finger. Carpus with dorsomesial and dorsolateral row of spines and few additional spines distally on dorsal surface, all at least partially obscured by dense setae.

Ambulatory legs (Figs 7e-h) with dactyls moderately stout, 1.35-1.75 times longer than propodi, dorsal and ventral margins and mesial faces dorsally and ventrally all with longitudinal rows of corneous spinules and stiff bristles or setae. Carpi of second pereopods each with row of spines on dorsal surface; carpi of third usually with only dorsodistal spine, occasionally also small spinule in proximal half usually obscured by tuft of setae. Sternite of third pereopods with small semicircular anterior lobe.

Male pleopods with endopods vestigial or absent. Telson (Fig. 7i) with posterior lobes laterally convex, mesially concave and drawn out into strong acute termination; 1 strong spine basally on either side of usually deep median cleft, and occasionally 1 or 2 additional spinules on inner margin.

COLOR. — Ocular peduncles white with medial light orange band; antennules light orange; antennae reddish brown with white bars; chelipeds and ambulatory legs orange-brown ground color and darker brown areas and distinctive purple and dark red patches on regions of articulation of carpi and meri (SCHEMBRI & MCLAY, 1983).

HABITAT. — Occupies variety of gastropod shells and may carry the anemone *Calliactis conchicola* on the shell; on muddy sand substrates.

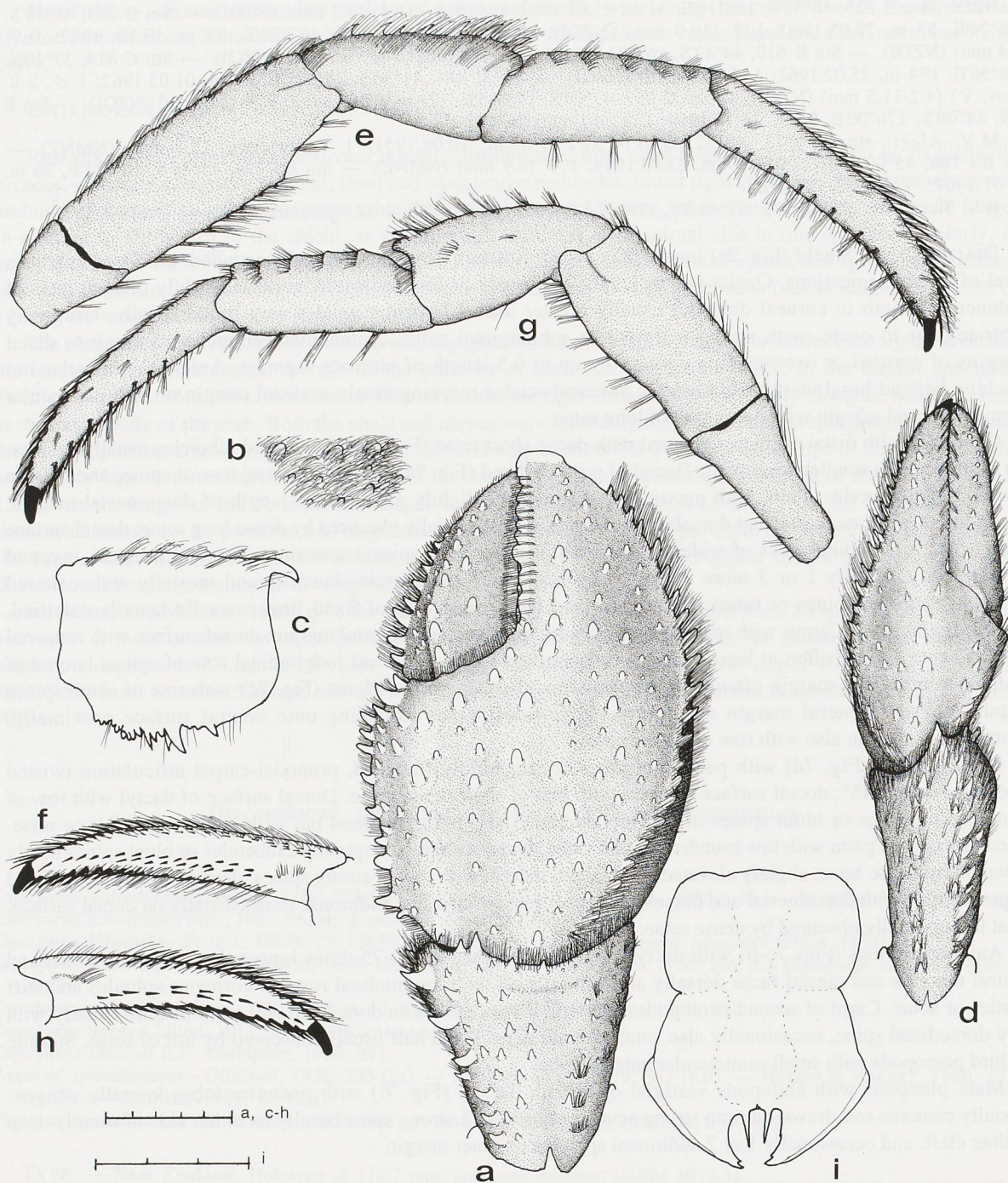


FIG. 7. — *Diacanthurus spinulimanus* (Miers, 1876), a-i, ♀ (12.0 mm) from Paria Rock, Hawks Bay, New Zealand: a, chela and carpus of right cheliped (surface setal mat not shown); b, area of dorsal surface of palm of right chela showing setal mat; c, merus of right cheliped (lateral view); d, chela and carpus of left cheliped (surface setal mat not shown); e, right second pereopod (lateral view); f, dactyl of right second pereopod (mesial view); g, left third pereopod (lateral view); h, dactyl of left third pereopod (mesial view); i, telson.

Scales equal 3.0 mm (i) and 5.0 mm (a, c-h).

DISTRIBUTION. — New Zealand and Chatham Islands; 12-194 m.

REMARKS. — The questionably juvenile male specimen (2.4 mm) has much longer and more acute spines of the dorsal surface of the palm of the left cheliped than any other specimens examined within the size range of 2.1 to 2.6 mm, but in all other respects agrees with small specimens of *D. spinulimanus*.

Diacanthurus spinulimanus is immediately distinguished from all other species of the genus by the much longer and more slender ocular peduncles, and only slightly dilated corneas (peduncular length to corneal diameter equal to or greater than 4:1). As previously indicated, *D. spinulimanus* appears most closely allied to *D. richeri* sp. nov. The irregular rows of large, widely-spaced tubercles on the dorsal surface of the palm of the right chela of *D. spinulimanus* immediately distinguishes this species from *D. richeri*.

DISCUSSION

The species of *Diacanthurus* present an extremely similar morphological module, despite their broad latitudinal range (Japan to southern Western Australia and southern New Zealand). Not only the unique structure of the telson, which immediately sets the species now assigned to *Diacanthurus* apart from other species of *Pagurus*, but several additional characters, taken in concert, demonstrate this homogeneity and provide the rationale for establishing a separate genus. These characters include the very clearly two-segmented ocular peduncles, the distinctive ocular acicles, the shape of the left chela and its propodal-carpal articulation, the strong molar-like dentition of the cutting edges of the dactyl and fixed finger of the right chela, the covering of the dorsal surfaces of the chelae with mats of fine setae, and the masking of the male gonopores by prominent tufts of long setae.

Although POWAR (1969) reported a three-segmented peduncle for *Diogenes miles* Fabricius, 1787 and several other decapod taxa, we accept the views of JACKSON (1913) and MAKAROV (1938, 1962) that a two-segmented ocular peduncle is characteristic of pagurids, as it is typical for decapods in general (cf. BALSS, 1940). However, the basal segment is usually small and there is relatively little flexibility between the two segments. In *Diacanthurus* the basal segment is enlarged; the extensive articulating membrane between the two segments permits considerable intersegmental flexibility. The ocular acicles are exceptionally prominent, broad, flattened, terminally straight, blunt or subacute, and with one or two very large marginal or submarginal spines.

The conformation of the left chela, although not unique, is unusual and seen consistently only in one other pagurid genus, i.e., *Australeremus* McLaughlin, 1981. The proximal portion of the dorsolateral margin of the palm is often considerably expanded, always strongly armed, and generally elevated above the dorsolateral surface, whereas this margin on the fixed finger, while still armed, is depressed well below the dorsolateral surface. The propodal-carpal articulation is rotated clockwise 15-60° from the horizontal plane, giving the palm an oblique flexion. SCHEMBRI (1982a) suggested that the expanded lateral margin in *D. rubricatus* was an adaptation for digging, while the more concave ventral surface provided an efficient scoop for collecting sediment.

Similarly, the strong molar-like armature of the cutting edges of the dactyl and fixed finger of the right chela is not unique to *Diacanthurus* (e.g., see MCLAUGHLIN, 1974), but the relative uniformity of development among its members suggests similarities in feeding behavior. SCHEMBRI (1982a) suggested that this dentition in *D. rubricatus* was an adaptation for cracking molluscan shells. SCHEMBRI (1982b) described feeding in *D. rubricatus* and *D. spinulimanus* as practically identical.

Tufts of setae in close proximity to male gonopores are not uncommon among pagurids; however, in certain genera the presence of a distinctive tuft masking the gonopore is considered a diagnostic character, i.e. a prominent tuft masks the right gonopore in *Pagurixus* Melin, 1939 or left gonopore in *Paguridium* Forest, 1961. In *Diacanthurus* such tufts of stiff setae mask both gonopores.

The fossil record of pagurids is poor and specimens usually consist only of chelae or remnants of them (e.g., VAN STRAELEN, 1925; RATHBUN, 1926, 1935), some of which can only questionably be assigned to the Section Paguridea (sensu FOREST, 1987). GLAESSNER (1969) reported the first records for the Section in general, as Late Jurassic, and the Paguridae, in particular, as the Late Cretaceous; FÖRSTER (1985) placed pagurids first in the Early Liassic. However, these early records are derived from chelae attributed to genera such as *Goniochirus*

Étallon, 1861, *Orhomalus* Étallon, 1861 and *Paleopagurus* Van Straelen, 1925, whose assignment to the Paguridea is uncertain, at best. As previously indicated, "*Pagurus*" *clifdenensis* is from the Altonian stage, Early Miocene, and only one of two fossil hermit crabs reported from New Zealand: FELDMAN and KEYES (1992) mentioned *Pagurus* sp. (without description) from the southern portion of North Island, from the Late Miocene to the Early Pleistocene.

"*Pagurus*" *clifdenensis*' position within the Paguridae is without question; it is preserved occupying the shell of *Struthiolaria subspinosa* Marwick. That it is correctly assignable to *Diacanthurus* is based on the structure, armature, and apparent indications of setation of both chelipeds. HYDEN and FOREST (1980) compared the fossil with *D. spinulimanus*; however, an even greater similarity is seen between *D. clifdenensis* and *D. ephyma* sp. nov. In both species the dorsal surface of the palm of the right chela is covered, but not densely, with small spines or tubercles, the margins each carry a row of spines, those of the dorsolateral margin smaller on the palm, but increasing in size on the fixed finger; the dorsal surfaces of the dactyls each have several longitudinal rows of small spines or tubercles and a marginal row of spines. Like all other species of *Diacanthurus*, the cutting edge of the dactyl and fixed finger each is provided with a row of strong molar-like teeth. The armature of the palms of the left chelas of the fossil and *D. ephyma* also are very similar. The illustrations of the in situ carpi of the right and left chelipeds of *D. clifdenensis* (HYDEN & FOREST, 1980: text-fig. 2), while distinct from, are comparable with those of *D. ephyma*, in having a marginal row of spines on the right accompanied by an irregular adjacent row; the left carpi of both species have two rows of strong dorsal spines, with a prominent dorsodistal spine.

There appears to be an evolutionary trend in the shape and armature of the chelipeds in species of *Diacanthurus* in the following in sequence, fossil included: *D. richeri*, *D. ophthalmicus*, *D. clifdenensis*, *D. spinulimanus*, *D. ephyma*, *D. rubricatus*. Beginning with *D. richeri* where the right palm is almost symmetrical, without any expansion of the dorsomesial margin and weak armature, a pattern of enlargement of the dorsal surface, expansion of the dorsomesial margin, and increasing strength of armature can be followed through *D. ophthalmicus*, *D. clifdenensis* and *D. spinulimanus* to *D. ephyma* and *D. rubricatus*. A similar, but not as distinctive progression can be seen in expansion and armature of the dorsolateral margin of the left palm, and among Recent species in the amount of rotation in the propodal-carpal articulation. In *D. richeri* there is little, if any, marginal expansion; the armature is weak; and the rotation slight. *Diacanthurus ophthalmicus*, *D. clifdenensis*, *D. spinulimanus*, and *D. ephyma*, all exhibit slightly greater expansions of the dorsolateral margin, and increases both in the strength of the marginal spines, and in the Recent species, the degree of propodal-carpal rotation. Expansion and rotation reach the maximum in *D. rubricatus*, although the marginal spines tend to become more blunted with increasing animal size.

ACKNOWLEDGEMENTS

We very much appreciate the willingness of Paul CLARK, The Natural History Museum, and Elizabeth LANG, Musée zoologique, Université Louis Pasteur, Strasbourg to loan their type specimens. We are indebted to Alain CROSNIER and Bertrand RICHER DE FORGES, ORSTOM; Elliot DAWSON, formerly with the New Zealand Oceanographic Institute; Diana JONES, Western Australian Museum; Tomoyuki KOMAI, Natural History Museum & Institute, Chiba; and Richard WEBBER and John YALDWYN, Museum of New Zealand Te Papa Tongarewa, for making materials from their collections available for study. Gifts of specimens by Clinton DUFFY, New Zealand Department of Conservation; Michio IMAFUKU, Kyoto University; and Richard TAYLOR, University of Auckland to P. McLAUGHLIN are also gratefully appreciated. We also wish to acknowledge, with thanks, the contributions made by Michèle DE SAINT LAURENT, who, during a preliminary study of the New Zealand material with the second author, recognized the generic distinction of *D. spinulimanus* and *D. rubricatus*, and who, at the time, identified many of the specimens used in this study. This is a scientific contribution from Shannon Point Marine Center, Western Washington University and Muséum national d'Histoire naturelle, Paris.

REFERENCES

- ALCOCK, A., 1905. — Catalogue of the Indian Decapod Crustacea in the collections of the Indian Museum. Part II. Anomura. fasc. I, Pagurides. i-xi + 1-197, pls 1-16. Indian Museum, Calcutta.
- BABA, K., 1986. — In: Baba, K., K-I. Hayashi and M. Toriyama. Decapod crustaceans from continental shelf and slope around Japan. Japan Fisheries Resource Conservation. 1-336, 17 figs, 176 pls. Tosho Printing Co. Ltd., Tokyo.
- BALSS, H., 1940. — Decapoda (Zehnfüsser) Erforschungsgeschichte. In: Bronns Klassen und Ordnungen des Tierreichs, 5(1): Crustacea, Book 7, part 1: 1-160, figs 1-205. Leipzig, Akademische Verlagsgesellschaft M.B.H. Hamburg Museum.
- BORRADAILE, L.A., 1916. — Crustacea. Part I. Decapoda. In: British Antarctic ("Terra Nova") Expedition, 1910. *Natural History report. Zoology*, 3 (2): 75-110, figs 1-16.
- BRANDT, J.F., 1851. — Krebse. In: A. Th. V. Middendorff, Reise in den Äussersten Norden und Osten Sibiriens während der Jahre 1843 und 1844. 2 (1) (Zoologie): 77-148, pls 5, 6.
- CHILTON, C., 1906. — Report of some Crustacea dredged off the coast of Auckland. *Transactions of the New Zealand Institute*, 38: 265-268.
- CHILTON, C., 1911. — Crustacea. In: Scientific results of the New Zealand government trawling expedition, 1907. *Records of the Canterbury Museum*, 1: 285-312, fig. 1, pl. 58.
- DANA, J.D., 1852. — Crustacea. In: United States Exploring Expedition during the Years 1838, 1839, 1840, 1841, 1842. Under the command of Charles Wilkes, U.S.N. 13 (1): vii + 685 pp. Philadelphia, C. Sherman. Reprinted 1972 Lochem, Netherlands, Antiquariaat Junk.
- ÉTALLON, A., 1861. — Notes sur les crustacés jurassiques du Bassin du Jura. *Mémoires de la Société d'Agriculture Sciences et Lettres de la Haute Saône*, 9: 129-171, pl. 2, figs 7-9.
- FABRICIUS, J. C., 1775. — Systema Entomologiae, sistens insectorum classes, ordines, genera, species, adiectis synonymis, locis, descriptionibus, observationibus: i-xxxii + 1-832. Flensburgi et Lipsiae Officina Libraria Kortii.
- FABRICIUS, J.C., 1787. — Mantissa insectorum sistens eorum species nuper detectas adiectis characteribus genericis, differentiis specificis, emendationibus, observationibus. 1: xx + 348 pp. Hafniae.
- FELDMAN, R.M. & KEYES, I.W., 1992. — Systematic and stratigraphic review with catalogue and locality index of the Mesozoic and Cenozoic decapod Crustacea of New Zealand. *New Zealand Geological Survey Record* (45): 1-73, fig. 1.
- FILHOL, H., 1883. — Note sur quelques espèces nouvelles d'*Eupagurus* recueillies en Nouvelle-Zélande. *Bulletin de la Société Philomatique de Paris*, (7) 8 (2): 66-68.
- FILHOL, H., 1885a. — Considérations relatives à la faune des Crustacés de la Nouvelle-Zélande. *Bibliothèque de l'École des Hautes Études, Section des Sciences naturelles*, 30 (2): 3-60.
- FILHOL, H., 1885b. — Recueil de Mémoires, Rapports et Documents relatifs à l'Observation du Passage de Vénus sur le Soleil du 9 Décembre 1874. Mission de l'île Campbell. *Zoologie*, 3 (2) 1: 349-510, pls 38-55. Institut de France, Académie des Sciences.
- FOREST, J., 1961. — Pagurides de l'Afrique occidentale. Scientific Results of the Danish Expedition to the coasts of tropical West Africa 1945-1946. *Atlantide Report*, (6): 203-250, figs 1-19.
- FOREST, J., 1987. — Les Pylochelidae ou "Pagures symétriques" (Crustacea Coenobitoidea). In: Résultats des campagnes MUSORSTOM, volume 3. *Mémoires du Muséum national d'Histoire naturelle, Série A Zoologie*, 137: 1-254, figs 1-81. pls 1-9.
- FÖRSTER, R., 1985. — Evolutionary trends and ecology of Mesozoic decapod crustaceans. *Transactions of the Royal Society of Edinburgh*, 76: 299-304, figs 1-5.
- GLAESSNER, M.F., 1969. — Decapoda. In: R.C. MOORE (ed.), Treatise on Invertebrate Paleontology. Part R Arthropoda. 2: R400-R651, figs 217-397. The Geological Society of America & University of Kansas.
- GORDAN, J., 1956. — A bibliography of pagurid crabs, exclusive of Alcock, 1905. *Bulletin of the American Museum of Natural History*, 108: 253-352.

- HAND, C., 1975. — Behaviour of some New Zealand sea anemones and their molluscan and crustacean hosts. *New Zealand Journal of Marine and Freshwater Research*, **9** (4): 509-527.
- HENDERSON, J.R., 1888. — Report on the Anomura collected by H.M.S. "Challenger" during the years 1873-76. Scientific Results of the Exploratory Voyage of HMS *Challenger*, (Zoology) **27**: i-xi + 1-221, pls 1-21.
- HYDEN, F.M. & FOREST, J., 1980. — An in situ hermit crab from the early Miocene of southern New Zealand. *Palaeontology*, **23** (2): 471-474, figs 1-3.
- JACKSON, H.G., 1913. — *Eupagurus*. Liverpool Marine Biology Committee, *Memoirs* **21**: i-viii + 1-79, text figs 1-2, pls 1-6.
- LENZ, H., 1901. — Ergebnisse einer Reise nach dem Pacific (Schauinsland 1896-1897). Crustaceen. *Zoologische Jahrbücher. Abtheilung für Systematik, Geographie und Biologie der Thiere*, **14** (5): 429-482, pl. 32.
- MAKAROV, V.V., 1938. — Rakoobraznye Anomura. [Crustacés Décapodes Anomures]. In: A.A. SHTAKEL'BERG (ed.), Fauna SSSR, (n. ser.) (16) **10** (3): i-x + 1-324, text-figs 1-113, pls 1-5. Moscow and Leningrad: Akademii Nauk SSSR.
- MAKAROV, V.V., 1962. — Fauna of U.S.S.R. Crustacea, Anomura, 10(3): 1-278, figs 1-113, pls 1-5. Jerusalem: Israel Program for Scientific Translation. Published for the National Science Foundation and Smithsonian Institution, Washington, D.C. (English translation).
- McLAUGHLIN, P.A., 1974. — The hermit crabs (Crustacea Decapoda, Paguridea) of northwestern North America. *Zoologische Verhandelingen*, (130): 1-396, figs 1-101, pl. 1.
- McLAUGHLIN, P.A., 1981. — Revision of *Pylopagurus* and *Tomopagurus* (Crustacea: Decapoda: Paguridae), with the descriptions of new genera and species: Part I. Ten new genera of the Paguridae and a redescription of *Tomopagurus* A. Milne Edwards and Bouvier. *Bulletin of Marine Science*, **31** (1): 1-30, figs 1-8.
- McLAUGHLIN, P.A., 1997. — Crustacea Decapoda: Hermit crabs of the family Paguridae from the KARUBAR cruise in Indonesia. In: A. CROSNIER & P. BOUCHET (eds), Résultats des Campagnes MUSORSTOM, volume 16. *Mémoires du Muséum national d'Histoire naturelle*, **172**: 433-572, figs 1-40.
- MELIN, G., 1939. — Paguriden und Galatheiden von Prof. Dr. Sixten Bocks Expedition nach den Bonin-Inseln 1914. *Kungliga Svenska Vetenskapsakademiens Handlingar*, (3) **18** (2): 1-119, figs 1-71.
- MIERS, E.J., 1876a. — Descriptions of some new species of Crustacea, chiefly from New Zealand. *Annals and Magazine of Natural History*, (4) **17**: 218-229.
- MIERS, E.J., 1876b. — Catalogue of the stalk- and sessile-eyed Crustacea of New Zealand. i-xii, 136 pp., 3 pls. Colonial Museum and Geological Survey Department, London.
- MIYAKE, S., 1975. — Anomura. In: Freshwater and marine animals: 187-342, pls 110-119. Gakushu-kenkyusha, Tokyo. (in Japanese).
- MIYAKE, S., 1978. — The crustacean Anomura of Sagami Bay: 1-200 (English), 1-161 (Japanese), figs 1-72, pls 1-4. Hoikusha Publishing Co, Tokyo.
- MIYAKE, S., 1982. — Japanese crustacean decapods and stomatopods in color. Vol. 1. Macrura, Anomura and Stomatopoda: 1-261, pls 1-56. Hoikusha Publishing Co., Tokyo (in Japanese).
- ORTMANN, A., 1892. — Die Decapoden-Krebse des Strassburger Museum, mit besonderer Berücksichtigung der von Herrn Dr. Döderlein bei Japan und bei den Liu-Kiu-Inseln gesammelten und zur Zeit im Strassburger Museum aufbewahrten Formen. IV. Die Abtheilungen Galatheidea und Paguridea. *Zoologischen Jahrbüchern. Abtheilung für Systematik, Geographie und Biologie der Thiere*, **6**: 241-326, pls 11, 12.
- POWAR, C.B., 1969. — Musculature of the eyestalk in Crustacea. *Acta Zoologica*, **50**: 127-141, figs 1-11.
- PROBERT, P.K., BATHAM, E.J. & WILSON, J.B., 1979. — Epibenthic macrofauna off southeastern New Zealand and mid-shelf bryozoan dominance. *New Zealand Journal of Marine & Freshwater Research*, **13** (3): 379-392, figs 1-4.
- RAINER, S.F., 1981. — Soft-bottom benthic communities in Otago Harbour and Blueskin Bay, New Zealand. *New Zealand Oceanographic Institute Memoir*, (80): 1-38, figs 1-7.
- RATHBUN, M.J., 1926. — The fossil stalk-eyed Crustacea of the Pacific slope of North America. *Bulletin of the United States National Museum*, **138**: i-viii + 1-155, figs 1-6, pls 1-39.
- RATHBUN, M.J., 1935. — Fossil Crustacea of the Atlantic and Gulf coastal plain. *Special Paper of the Geological Society of America*, (2): i-vii + 1-160, figs 1, 2, pls 1-26.

- RICHER DE FORGES, B., 1990. — Les campagnes d'exploration de la faune bathyale dans la zone économique de la Nouvelle-Calédonie. In: A. CROSNIER (ed.), Résultats des Campagnes MUSORSTOM, volume 6. *Mémoires du Muséum national d'Histoire naturelle*, (A) **145**: 9-54, figs 1-12.
- RICHER DE FORGES, B., 1993. — Les campagnes d'exploration de la faune bathyale faites depuis mai 1989 dans la zone économique de la Nouvelle-Calédonie. Listes des stations. In: A. CROSNIER (ed.), Résultats des Campagnes MUSORSTOM, volume 10. *Mémoires du Muséum national d'Histoire naturelle*, **156**: 27-32.
- RICHER DE FORGES, B. & CHEVILLON, C., 1996. — Les campagnes d'échantillonnage du benthos bathyal en Nouvelle-Calédonie, en 1993 et 1994 (BATHUS 1 à 4, SMIB 8 et HALIPRO 1). In: A. CROSNIER (ed.), Résultats des Campagnes MUSORSTOM, volume 15. *Mémoires du Muséum national d'Histoire naturelle*, **168**: 33-53, figs 1-5.
- SCHEMBRI, P.J., 1982a. — Functional morphology of the mouthparts and associated structures of *Pagurus rubricatus* (Crustacea: Decapoda: Anomura) with special reference to feeding and grooming. *Zoomorphology*, **101**: 17-38, figs 1-12.
- SCHEMBRI, P.J., 1982b. — Feeding behaviour of fifteen species of hermit crabs (Crustacea: Decapoda: Anomura) from the Otago region, southeastern New Zealand. *Journal of Natural History*, **16**: 859-878, figs 1-9.
- SCHEMBRI, P.J., 1988. — Bathymetric distribution of hermit crabs (Crustacea: Decapoda: Anomura) from the Otago region, southeastern New Zealand. *Journal of the Royal Society of New Zealand*, **18** (1): 91-102, figs 1-3.
- SCHEMBRI, P.J. & MCLAY, C.L., 1983. — An annotated key to the hermit crabs (Crustacea: Decapoda: Anomura) of the Otago region (southeastern New Zealand). *New Zealand Journal of Marine and Freshwater Research*, **17**: 27-35, figs 1-26.
- SCHUCHERT, P., 1996. — Athecate hydroids and their medusae (Cnidaria: Hydrozoa). *New Zealand Oceanographic Institute Memoir*, (106): 1-159, figs 1-85.
- TERAO, A., 1913. — A catalogue of hermit-crabs found in Japan (Paguridea excluding Lithodidae), with descriptions of four new species. *Annotationes Zoologicae Japonenses*, **8**(2): 355-391, figs 1-4.
- THOMPSON, E.F., 1930. — Contributions for a revision of the New Zealand Crustacea of the family Paguridae. *Records of the Canterbury Museum*, **3** (4): 263-273.
- THOMSON, G.M., 1899. — A revision of the Crustacea Anomura of New Zealand. *Transactions and Proceedings of the New Zealand Institute*, **31**: 167-197.
- VAN STRAELEN, V., 1925. — Contribution à l'étude des crustacés décapodes de la période jurassique. *Mémoires de l'Académie Royale, Bruxelles*, **2**: 1-462, pls 1-10.
- YOKOYA, Y., 1933. — On the distribution of decapod Crustacea inhabiting the continental shelf around Japan, chiefly based upon the materials collected by S.S. "Soyo Maru" during the years 1923-1930. *Journal of the College of Agriculture, Imperial University, Tokyo*, **12** (1): 1-236, figs 1-71.