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A Revision of the Two Southern Temperate Shore Crabs *Leptograpsus variegatus* (Fabricius) and *Plagusia chabrus* (Linnaeus) (Crustacea, Decapoda, Grapsidae)

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Abstract

Morphological variation between and, where possible within, local populations of *L. variegatus* and *P. chabrus* is analysed. The two species vary widely with age and sex in features such as carapace shape, relative proportions of limbs and in meristic features. It is concluded that both are widespread forms, none of the local populations deserving separate taxonomic status. *L. variegatus* occurs from western Australia through New Zealand to Chile. *P. chabrus* occurs from South Africa through Australia and New Zealand to Chile. The distinctions between *P. chabrus* and the very similar *P. dentipes* are examined. The latter is considered a distinct species throughout the subtropical Pacific from Japan and eastern Australia to Easter Island.

Introduction

Grapsid crabs are among the most conspicuous of intertidal animals in temperate latitudes. It is a characteristic of the history of the taxonomy of these, and other, animals that around the middle of the nineteenth century, as expeditions brought their collections back from distant shores, a very large number of species were described as new without adequate comparison with already described forms. The same animal from different areas came to be known under different names. Later, many of these were amalgamated and the number of recognised species thereby reduced. Sometimes this move was made without study of an adequately large sample of specimens.

The two species dealt with in this report have each been considered, in recent years, to be widespread throughout much of the southern temperate region from South Africa to Chile. This study examines the justification for such a view. The two species are highly characteristic of rocky intertidal shores in southern temperate latitudes (Griffin, 1971).

Material has been obtained from throughout most of the geographic range of each. Terminology follows that used by Rathbun (1918). The abbreviations c.l. and c.w. refer to carapace length and width respectively. The synonymies for each species give the original and major literature references only. Localities from which the material used in the present study came are listed and previous geographic records are also given. A brief description of each species follows and the morphological variation is then examined.

Sources of Material

The following is a list of the Museums from which material used in this study was obtained. The abbreviations given are those used in the text.

Australian Museum, Sydney	AM
National (Dominion) Museum, Wellington	DM
Smithsonian Institution, Washington	USNM
South African Museum, Cape Town	SAM
Tasmanian Museum, Hobart	TM
Western Australian Museum, Perth	WAM

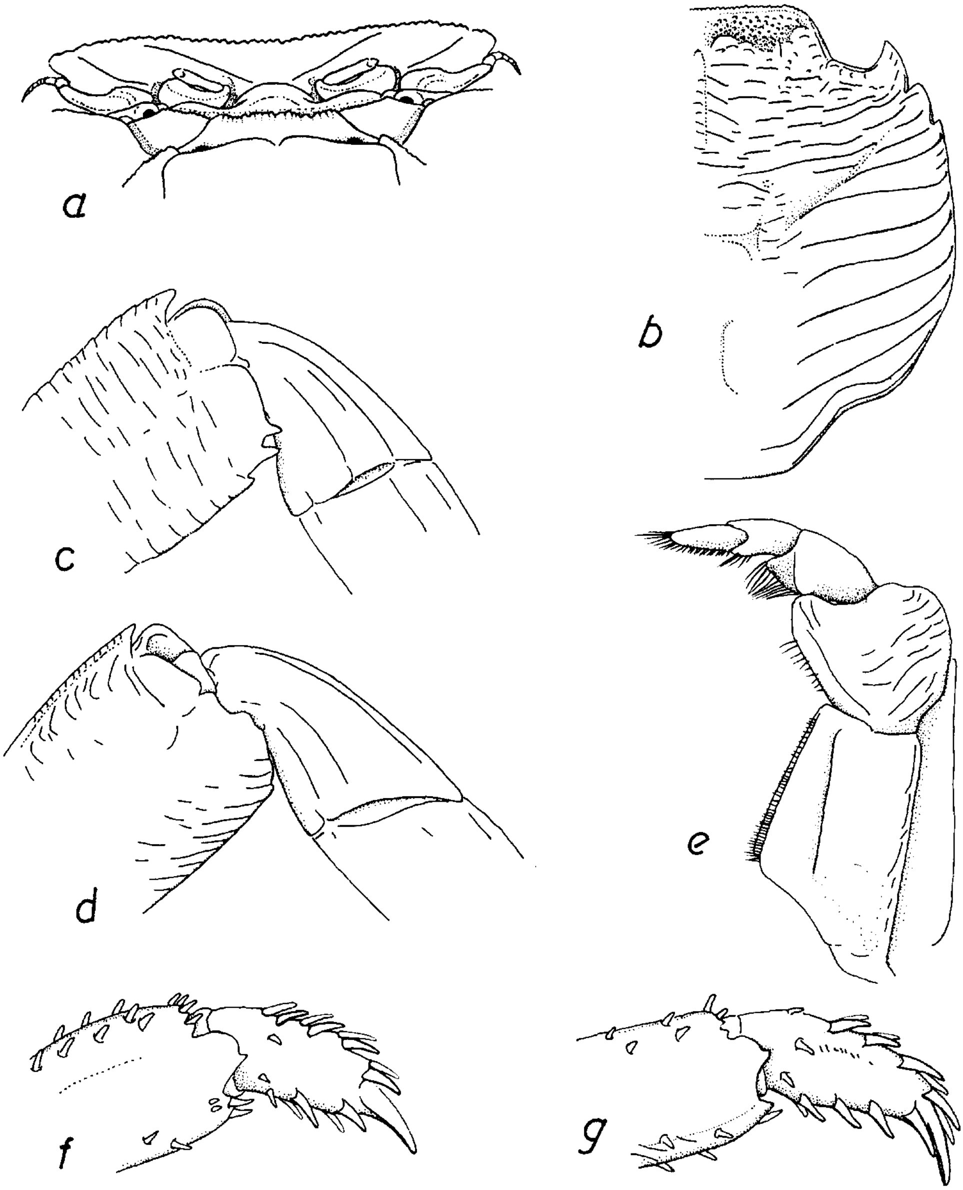

FIG. 1.—*Leptograpsus variegatus.* Male, c.l. 53 mm (WAM 240.62), Dorre I., Shark B., W.A.: a, front of carapace, ventral aspect; b, right half of carapace, dorsal aspect; c, right front ambulatory leg, merus and carpus, posterior aspect; d, right fourth ambulatory leg, merus and carpus, posterior aspect; e, left third maxilliped, outer aspect; f, right first ambulatory leg, propodus and dactyl, posterior aspect; g, right fourth ambulatory leg, propodus and dactyl, posterior aspect.

SYSTEMATICS

Leptograpsus variegatus (Fabricius) (Figs 1–6)
Cancer variegatus Fabricius, 1793, p. 450.
Grapsus variegatus Latreille, 1803, p. 71.
Grapsus personatus Lamarck, 1818, p. 249.

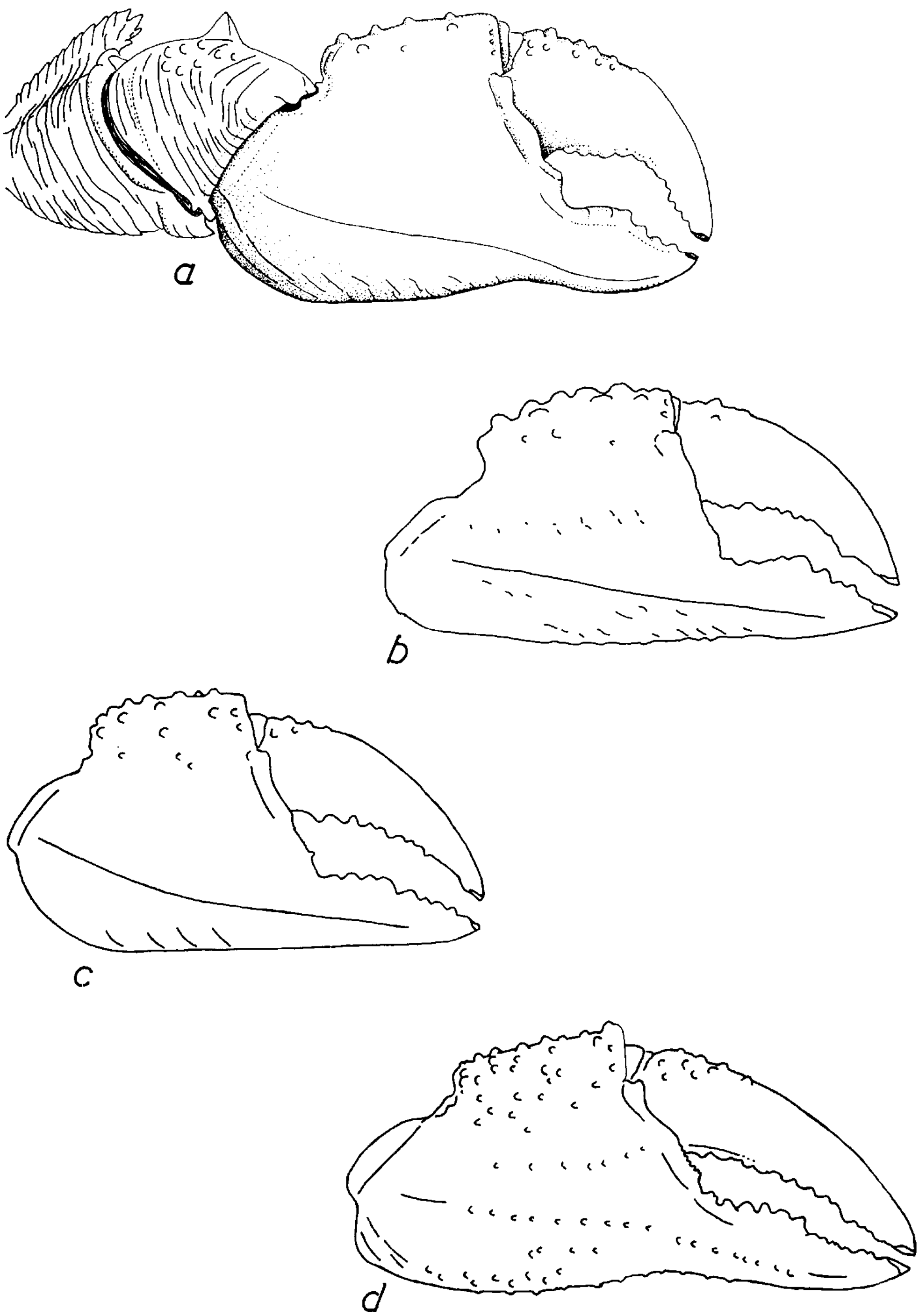

FIG. 2.—*Leptograpsus variegatus*. Right chelipeds: a, male, c.l. 53 mm (WAM 240.62), Dorre I., Shark B., W.A.; b–d, chela only; b, female, c.l. 35.7 mm (AM P.12455), Eddystone Pt., Tas.; c, male, c.l. 46.7 mm (WAM 236.62), Abrolhos Is., W.A.; d, male, c.l. 67.3 mm (WAM 239.62), Abrolhos Is.

Grapsus strigilatus White, 1842, p. 78.
Grapsus planifrons Dana, 1852, p. 249.
Leptograpsus variegatus.—H. Milne Edwards 1853, p. 172. Rathbun, 1918, p. 234, pl. 56.—Hale, 1927a, p. 180, fig. 181.—Garth, 1957, p. 94.—McNeill, 1962, p. 38, fig.—Bennett, 1964, p. 80.—Dell, 1965, p. 51; 1968, p. 26.—Morton and Miller, 1968, p. 89, pl. 22–5.—Griffin, 1969, p. 324; 1972, p. 85.—Healy and Yaldwyn, 1970, p. 98.—Griffin and Yaldwyn, 1971, p. 58.
Leptograpsus Ansoni H. Milne Edwards, 1853, p. 172.
Leptograpsus Gayi H. Milne Edwards, 1853, p. 172.
Leptograpsus Verreauxi H. Milne Edwards, 1853, p. 172.
Sesarma pentagona Hutton, 1875, p. 41.
Leptograpsus planifrons.—Cano, 1889, pp. 92, 99, 238.

TYPES AND TYPE LOCALITIES

Cancer variegatus Fabricius—"In Americae Meridionalis Insulis"; type not extant; see Rathbun, 1918.
Grapsus personatus Lamarck—"New Holland"; types not extant; pers. comm. D. Guinot, 11 April 1972.
Grapsus strigilatus White—New Zealand; British Museum (Natural History), London; R. W. Ingle, pers. comm., 10 April 1972.
Grapsus planifrons Dana—Chile; Smithsonian Institution, Washington.
Leptograpsus Ansoni H. Milne Edwards—Juan Fernandez; three syntypes, Muséum Nationale d'Histoire Naturelle, Paris; D. Guinot, pers. comm.
Leptograpsus Gayi H. Milne Edwards—Chile; type material not extant; D. Guinot, pers. comm.
Leptograpsus verreauxi H. Milne Edwards—Australia; two syntypes, Muséum Nationale d'Histoire Naturelle, Paris; D. Guinot, pers. comm.
Sesarma pentagona Hutton—New Zealand; Location of types unknown.

MATERIAL EXAMINED: A total of 127 specimens (65 ♂♂, 62 ♀♀, c.l. 9.3–67.3 mm).

Localities: Australia: Western Australia: Doore I. and Berniet I., Shark B.; North I., W. Wallabi I. and Southern Group, Abrolhos Islands; Pt. Gregory Reef, N. of Geraldton; Rat I.; Lancelin I.: Garden I.; Clifton St. Beach; Bunbury; 1 mile E. of Frenchman B., near Albany; N.E. Mondrain I. and N. Wilson I., Recherche Archipelago. Bass Strait: Citadel I., Glennie Group; Currie Harb., King Island; Deal I. Tasmania: Swan I. Eddystone Pt.; Binalong B.; Bicheno; Sleepy B.; Coles B.; C. Forestier; Maria I.; Fossil I., Pirates B.; Remarkable Cave. New South Wales: Shellharbour; Trial B.; Shark I.; Pt. Hacking; Long Reef, Collaroy; Coogee; Fairy Bower, Manly; 2 miles S. of entrance of Tuggerah Lakes; Pt. Stephens; Flat Rock, N. of entrance to Richmond R. Queensland: Noosa Hd; Pt. Cartwright.

New Zealand: Waihau B. nr. C. Runaway; Otatau I., Auckland.

Pacific Ocean: Middleton Reef, Tasman Sea.

South America: Talcahuano, Chile.

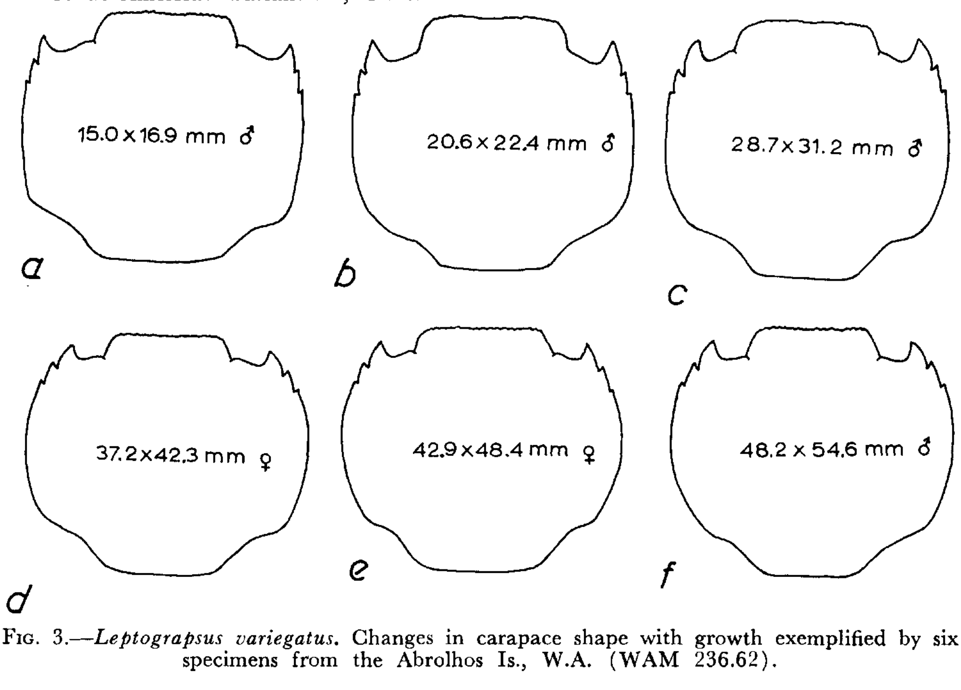

FIG. 3.—*Leptograpsus variegatus*. Changes in carapace shape with growth exemplified by six specimens from the Abrolhos Is., W.A. (WAM 236.62).

Localities Previously Reported

Australia: Fourteen localities from Shark B. (Western Australia) in the north-west, through South Australia and Bass Strait, to Rockhampton (Queensland) in the north-east (Balss, 1935).

New Zealand: Fifteen localities from C. Maria van Dieman in the north to Dunedin in the south (Chilton and Bennett, 1929; Bennett, 1964); Cape Maria van Diemen to Kaikoura, Hokianga to Westport (Dell, 1968).

Pacific Ocean: Middleton Reef, Tasman S. (McNeill, 1937); Norfolk I. (Grant and McCulloch, 1907); Sunday I., Kermadecs (Chilton, 1911); Easter I. (Rathbun, 1918; Porter, 1937).

South America: Twenty-seven localities from Paita, Peru, in the north to Valparaiso, Chile, in the south, Juan Fernandez I. (Garth, 1957).

DESCRIPTION

Carapace. Slightly broader than long, strongly depressed; lateral margins strongly and uniformly convex, two teeth behind external orbital angle, first tooth the larger, distance between teeth slightly less than length of exorbital tooth along its outer border. Regions of dorsal surface moderately well defined, especially posteriorly mid-dorsally, cervical and branchiocardiac grooves evident. Branchial regions with seven to nine prominent, equidistant, weakly curved, obliquely transverse ridges tending posteriorly towards midline, sixth and eighth ridge sometimes interrupted or short; intermediate ridges sometimes present between sixth and seventh and eighth major ridges, arising at or not far from lateral edge. Hepatic regions with four or five short unequal ridges parallel to those of branchial regions.

Post-frontal lobes strong, lateral two (above inner border of orbits) narrower and further advanced than medial two (epigastrics). Frontal and protogastric regions covered by tubercles which are prominent except close to frontal border, those on post-frontal lobes larger and broader; a few short transverse ridges posteriorly. Mesogastric regions with a few weak transverse ridges anteriorly, smooth posteriorly. Other mid-dorsal regions smooth.

Front broad, projecting almost horizontally, edged by numerous small tubercles.

Orbits with posterior edge inwardly notched, sloping posterolaterally towards stout, sharp exorbital tooth which is not as far advanced as front.

Antennular fossae small, transversely oval. Basal antennal article small, broadly triangular, set obliquely, antennae small. Suborbital tooth immediately outside basal antennal article, narrow, acute and ventrally keeled. Suborbital border with several small spinules. Ventral edge of exorbital tooth with a few small spines at base.

Anterior border of mouthfield prominently concave, minutely tuberculate. Palate with three longitudinal ridges.

Epistome moderately broad. A tuberculate lateral ridge extending obliquely forwards from anterior border of mouthfield to opening of "green gland".

Pterygostomian regions smooth. Subhepatic regions with interrupted transverse ridges.

Thoracic sternum smooth or very weakly punctate weakly, hirsute anteriorly.

Third maxillipeds.—Mostly smooth. Merus with a few interrupted oblique to transverse ridges and a sharp, low ridge close to medial edge, lateral edge straight or very weakly and irregularly curved, anterolateral angle obtusely rounded.

Chelipeds.—Massive in adult male.

Ischium with inner border distally with a few blunt tubercles.

Merus subtrigonal, ventromedial edge a strong, flattened crest, dorsally crossed by strong, transverse, interrupted ridges extending on to crest to give its edge a strongly tuberculate appearance, crest distally expanded and terminating in about four very strong blunt spines or tubercles; ventrolateral edge also strongly tuberculate; ventral surface smooth and concave.

Carpus with weak, short, transverse ridges on dorsal surface and some blunt tubercles towards medial edge; dorsomedial edge bearing midway along a short, broad, blunt spine; dorsolateral edge weakly tuberculate.

Chela extremely stout; palm compressed, as high as long, dorsal surface with numerous strong tubercles which extend part way down outer surface; ventral edge with slightly smaller tubercles or interrupted transverse ridges especially dense around base of fixed finger; outer surface otherwise with a line of tubercles or a single uninterrupted ridge extending obliquely from middle of outer surface proximally to tip of fixed finger. Fingers stout and very strongly toothed on inner edges, especially at base of dactyl; widely gaping proximally in adults, fixed finger with inner edge more or less strongly angled midway along, basal portion sometimes weakly toothed or smooth in adults. Dactyl almost twice as long as palm, strongly curved, inner edge concave, dorsal surface tuberculate proximally.

Ambulatory legs.—Long and strongly compressed, third leg the longest (slightly more than 1½ times carapace length), second leg only slightly shorter.

Coxa of second and third legs with an erect, flattened, distally acute lobe.

Merus in all legs with posterior surfaces bearing interrupted transverse ridges which extend around ventral edge and over crested dorsal edge giving the latter a tuberculate appearance and on to dorsal part of anterior surface; ridges weakly developed in last leg; dorsal crest terminating in a small, sharp spine; distal edge of all except last leg with three or four blunt spines posteroventrally, last leg sometimes weakly tuberculate, or, more often, smooth posteroventrally.

Carpi with a single dorsal ridge terminating in a broad sharp spine; another ridge, with a line of short hairs just below it, on posterior surface.

Propodi of almost uniform width throughout their length, distal edge with a few short, slender spines posteroventrally; dorsal and ventral surfaces with short, spine-like hairs; a row of short simple hairs posterodorsally on first to third legs, posteroventrally on last leg and sometimes sparse or even absent.

Dactyls terminating in a sharp spine and armed on both dorsal and ventral edges with a double row of long, stout, spine-like hairs.

Male abdomen.—Elongate triangular, of seven distinct segments, widest at middle of laterally convex third segment, edges of following segments weakly sinuous, fifth and sixth segments laterally convex, seventh segment laterally weakly concave and distally rounded; sixth and seventh segments of equal length, 1.3 times length of fifth segment. Surfaces generally smooth.

Male first pleopod.—Stout, narrowing slightly distally, densely setose distally, setae especially dense on abdominal portion of tip, in a slightly sparser clump around edge of flap at end of short lateral groove, also extending part way down lateral surface.

Colour.—Variable. Red and yellow mixed, or dotted with violet red, or sometimes whitish. Bluish grey, everywhere transversely lineated and blotched with black; feet often reddish (Rathbun, partly after Stimpson). Ranging from dark grey to various shades of red and yellow; claws blue or purple (Tweedie, 1942).

REMARKS. The following characters were studied in detail in this species:

1. Carapace: total length and width, frontal and interorbital width and antero-lateral length (i.e., distance along lateral margin from the tip of the exorbital spine to the widest part of the carapace); number of tubercles along the frontal border between the lateral grooves on the ventral surface running up from close to the basal antennal article, the number of tubercles on the anterior border of the mouthfield and on the suborbital border; and the number of major branchial ridges behind the second anterolateral tooth.

2. Chelipeds: length and height of the chela and length of the dactyl; number of spines or tubercles on the ventromedial edge and distal crest of the merus, number of tubercles on the dorsal and dorsolateral surfaces of the palm and number of teeth on the proximal half of the inner edge of the fixed finger.

3. Ambulatory legs: length and greatest width of the ambulatory meri of all legs; number of spines on the posterior ventrodistal border of all meri.

The results show no differences between the samples in any of these characters significant enough to warrant specific or subspecific separation. This is especially true for dimensions of the carapace where analysis of first order relationships (carapace width/carapace length, etc.) give almost identical values for each of the samples. Changes in some of these dimensions do occur with growth. Thus, while the ratio carapace width/length remains fairly constant (1.08–1.18), there are very slight changes in other ratios, interorbital width and frontal width decreasing in relation to carapace width and the length of the anterolateral margin increasing. Fig. 3 shows these changes in the shape of the carapace. In juveniles (a) the carapace is almost straight-sided and the front is relatively narrow in relation to the interorbital width but wide in relation to total width. In large adults (e, f) the sides of the carapace are strongly convex and the front is wide in relation to total width. Throughout growth there appears to be little difference between the frontal width and the anterolateral margin length. In Fig. 4A the growth of three dimensions of the carapace are shown in relation to carapace length.

In the case of the ambulatory meri, the relative dimensions of which show only slight changes with increased size of the body, there are slight differences between the samples in the ratio length/width. However, these differences between the sample values are not statistically significant below the 0.05 probability level (see Table 1).

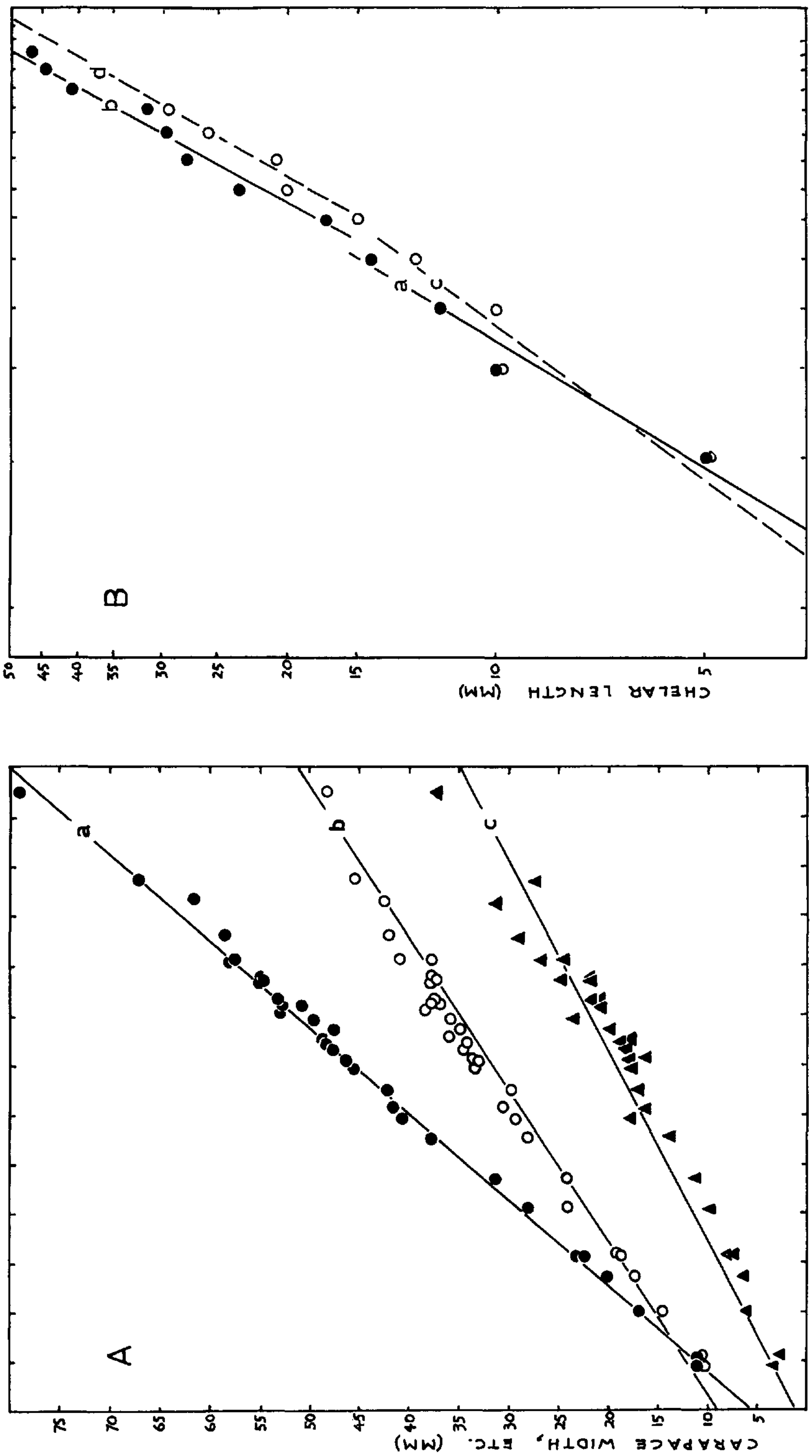

FIG. 4.—*Leptograpsus variegatus*. A, relative growth of three dimensions of the carapace: a, carapace width; b, interorbital width; c, antero-lateral margin length. Regression lines calculated from data for all material examined grouped into 5 mm classes; data shown are from 32 specimens from N.W. Australia (Abrolhos Is. and Shark B.). B, relative growth of the chelae in males (closed circles) and females (open circles) plotted logarithmically. Regressions calculated as in A: a and c, c.l. up to 27 mm, b and d, 28 mm or more.

TABLE 1.—Geographical variation in the ratio length/width of the ambulatory meri of *L. variegatus*. The upper row of each set gives the mean (together with its standard error) and the lower, the range.

Merus number	Locality (number of specimens)				
	N.W.A.[1] (33)	S.W.A.[2] (23)	E.A.[3] (29)	N.Z.[4] (9)	Chile (2)
1	1.95 (0.018)	2.01 (0.026)	2.12 (0.018)	2.07 (0.030)	1.95–
	1.7–2.2	1.7–2.1	1.9–2.3	1.9–2.2	1.9–2.0
2	1.92 (0.020)	2.00 (0.028)	2.08 (0.044)	2.06 (0.032)	2.0 –
	1.7–2.2	1.7–2.3	1.9–2.3	1.9–2.2	2.0
3	1.90 (0.020)	1.91 (0.021)	2.02 (0.017)	2.03 (0.036)	1.9 –
	1.7–2.2	1.7–2.2	1.8–2.2	1.9–2.2	1.9
4	1.77 (0.019)	1.79 (0.020)	1.90 (0.016)	1.86 (0.041)	1.80 –
	1.5–2.0	1.6–2.0	1.7–2.1	1.6–2.0	1.7–1.9

[1] Shark B. and Abrolhos Is; [2] remainder of Western Australia; [3] Queensland, New South Wales and Tasmania; [4] New Zealand.

The dimensions of the chela, which are subject to secondary sexual dimorphism, show the features of relative growth found in most brachyurans. From Fig. 2, which shows the chelae of four specimens including an adult female (b) and a juvenile male (c), it is apparent that there is little difference in the relative dimensions either between the sexes or with increasing size. There is rather wide variation in the form of the lower edge (usually smoothly curved proximally but sometimes sharply angled, and concave to straight at the junction of the fixed finger) and in the shape of the dactyl (usually strongly curved in adults but sometimes almost straight); Fig. 2a shows a rather typical specimen and 2d, an unusual one. In Fig. 4B, growth of the chela in males and females is shown in relation to carapace length. The chela in males increases at a low rate of allometry throughout, *a* (in equation $y = bx^a$) being 1.18 in juveniles and 1.25 in adults (over 27 mm carapace length); in females growth is isometric in juvenile females ($a = 0.99$) and allometric in adult females ($a = 1.27$). There do not appear to be any significant interpopulation differences in these features.

The following numerical (meristic) characters exhibit relative constancy with growth and little geographical variation: number of major branchial ridges (8 or 9), number of spines on the distal posteroventral edge of the ambulatory meri (merus 1: 2–5; merus 2: 2–4; merus 3: 1–4; merus 4: 0–1) and the number of spines on the distal medial crest of the merus of the cheliped (4–6, seldom 3, 7 or 8).

However, the number of tubercles on the frontal border, on the anterior border of the mouthfield and on the suborbital border show wider variation within populations and very slight interpopulation differences (Table 2). The trends in these characters are much the same as those shown by the ambulatory meri and the differences between the sample values are not significantly different below the 0.05 probability level. The number of tubercles on the ventromedial edge of the merus of the cheliped shows similarly wide variation.

TABLE 2.—Geographical variation in meristic characters in *L. variegatus*. Arrangement of data as in Table 1.

Character	Locality (number of specimens)				
	N.W.A. (33)	S.W.A. (23)	E.A. (29)	N.Z. (8)	Chile (2)
Number of frontal	28.7 (0.78)	29.0 (0.71)	23.7 (0.59)	24.5 (1.04)	23 (–)
tubercles	22–38	21–35	19–28	20–31	22–24
Number of tubercles on anterior border of mouth-	14.4 (0.43)	12.4 (0.51)	11.4 (0.39)	12.7 (0.70)	15 (–)
field	11–22	7–16	6–16	9–16	14–15
Number of spines on suborbital	15.4 (0.42)	13.9 (0.70)	13.6 (0.37)	12.7 (0.99)	14 (–)
border	12–20	7–18	9–18	10–17	14

Lastly, the number of tubercles on the dorsal surface of the palm of the cheliped and the number of teeth on the proximal part of the inner edge of the fixed finger of the chela show small changes with growth, the former increasing (from 3–10, in individuals of carapace width less than 20 mm, to around 20 in individuals of more than 50 mm carapace length) and the latter decreasing (generally 3 teeth but individuals of carapace length around 40 mm or above sometimes lack teeth and therefore have this proximal portion smooth).

Thus, the concept of *L. variegatus* comprising widespread populations forming a single conspecific unit is strongly supported by the present study. As Rathbun (1918, p. 235) states, this is a "variable species. Individuals differ in width of carapace and legs, in the curvature of the side margins and the size of their teeth, in the prominence of the frontal lobules and of the posterior cardiac region, and of the sculptural lines." They differ widely in colour also.

Of the many synonyms, two, Lamarck's *Grapsus personatus* and White's *G. strigilatus,* were included in the synonymy of *L. variegatus* by Milne Edwards in 1853. The last author's *L. verreauxi, L. ansoni* and *L. gayi* were separated from *L. variegatus* on the basis of absolute size, colour, shape and relative width of the carapace, prominence of the tubercles of the carapace and of the anterolateral teeth, relative size and tuberculation of the chelae and prominence of the striations of the ambulatory meri. Every one of these characters varies with age, sex or locality. De Man (1890) attempted to justify separation of *L. ansoni, L. gayi* and *L. variegatus* on the basis of some of the characters used by Milne Edwards and apparent differences in the relative width of the ambulatory meri. The last character is here shown to be very variable and not significantly different in any of the various populations. De Man agreed with Milne Edwards that *Grapsus planifrons* Dana and *L. gayi* may be synonymous.

Bennett (1964, p. 80) recently included, without comment, *Sesarma pentagona* Hutton in the synonymy of *L. variegatus*. According to Hutton's original description (repeated by Miers, 1876, p. 44), *S. pentagona* was based on a small specimen ("0.67 inches long"), carapace 1.27 times as broad as long, subquadrate and smooth. It agrees with *L. variegatus* in the almost vertically deflexed front with four raised "projections", obliquely striated branchial regions, anterolateral margin with two "teeth", pterygostomian regions (area on each side of mouthfield) with moniliform transverse striae, trigonal, striated merus of the cheliped ("arms"), very broad and compressed ambulatory meri ("third joint of legs") and distal segments of the ambulatories ("outer joints and claws") tomentose. There are no important differences from small specimens of *L. variegatus* and the subquadrate shape of the carapace is characteristic of the latter. It seems quite probable, therefore, that Hutton's species is to be included in *L. variegatus*.

Amongst the synonyms of this species listed by Kingsley was the name, *Grapsus marginatus,* attributed by Kingsley to Latreille (1803). Dr L. B. Holthuis (personal communication) has kindly informed me that this name was not used by Latreille nor can he find any use of it by an author prior to Kingsley. It is therefore apparent that the name is a *nomen nudum* since no description was given of it. I can find no record of the name being used by more recent authors. As a *nomen nudum* the name has no nomenclatorial standing. The following names listed by Kingsley (1880) under *L. variegatus* are also not to be included in the synonymy of this species:

Grapsus pictus Quoy and Gaimard, 1824, p. 523, pl. LXXVI, fig. 2 (type locality: "Isle Guam") (= *Grapsus rudis* H. Milne Edwards, 1853 = *Grapsus tenuicrustatus* Herbst, 1783—see Banerjee, 1960; not *Grapsus pictus* Latreille, 1803 = *Grapsus grapsus* (Linnaeus, 1758)—see Rathbun, 1918).

Leptograpsus Bertheloti H. Milne Edwards, 1853, p. 172 (type locality: "Iles Canaries") (? = *Pachygrapsus marmoratus* (Fabricius, 1787)—see Rathbun, 1918).

The illustrations of *L. variegatus* given here are designed to parallel those given for species of *Grapsus* by Banerjee (1960).

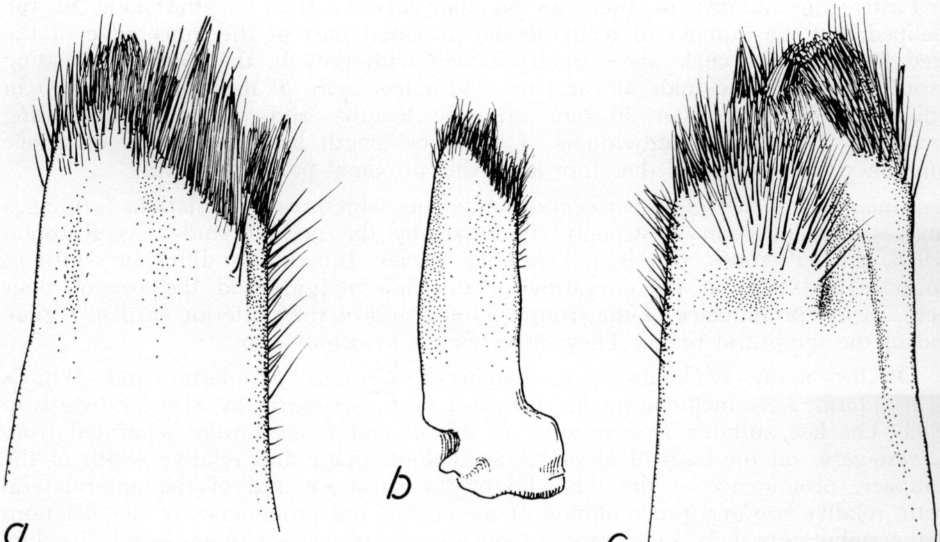

FIG. 5.—Male left first pleopod of *Leptograpsus variegatus* (Fabricius), c.l. 53 mm (WAM 240.62), Dorre I., Shark B., W.A.

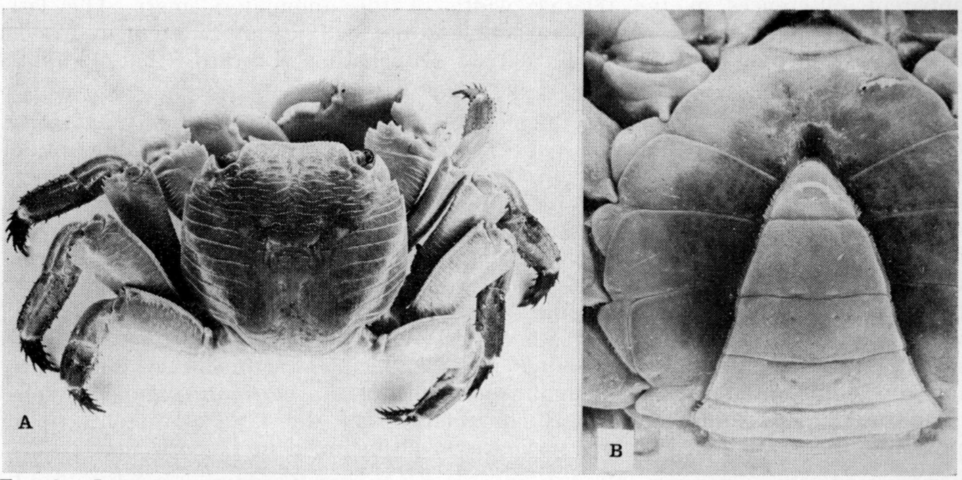

FIG. 6.—*Leptograpsus variegatus,* male, c.l. 53 mm, Dorre I., Shark Bay, Western Australia (WAM 24062). A, whole animal, dorsal view. B, abdomen.

DISTRIBUTION

Southern warm temperate Indian and Pacific Oceans from Western Australia to western South America. The records of this species from Shanghai (Heller, 1862) and Pernambuco, Brazil (Kingsley, 1880) were refuted by Balss (1935, p. 142) but are repeated by Garth (1957). As Dr L. B. Holthuis (personal communication, Jan. 1966) says, Dr Wilson, who donated the material from Pernambuco on which Kingsley's record was based, was a rich citizen of Philadelphia who often bought natural history objects and presented these to the Philadelphia Academy of Sciences. It is therefore possible that mislabelled specimens were obtained by him. Since the species has not been recorded from Brazil since 1880, Kingsley's record is best regarded as highly dubious at least.

In the tropical Pacific, western Indian and Atlantic Oceans species of the genus *Grapsus* Lamarck occupy a habitat similar to that occupied by *L. variegatus* in southern temperate latitudes.

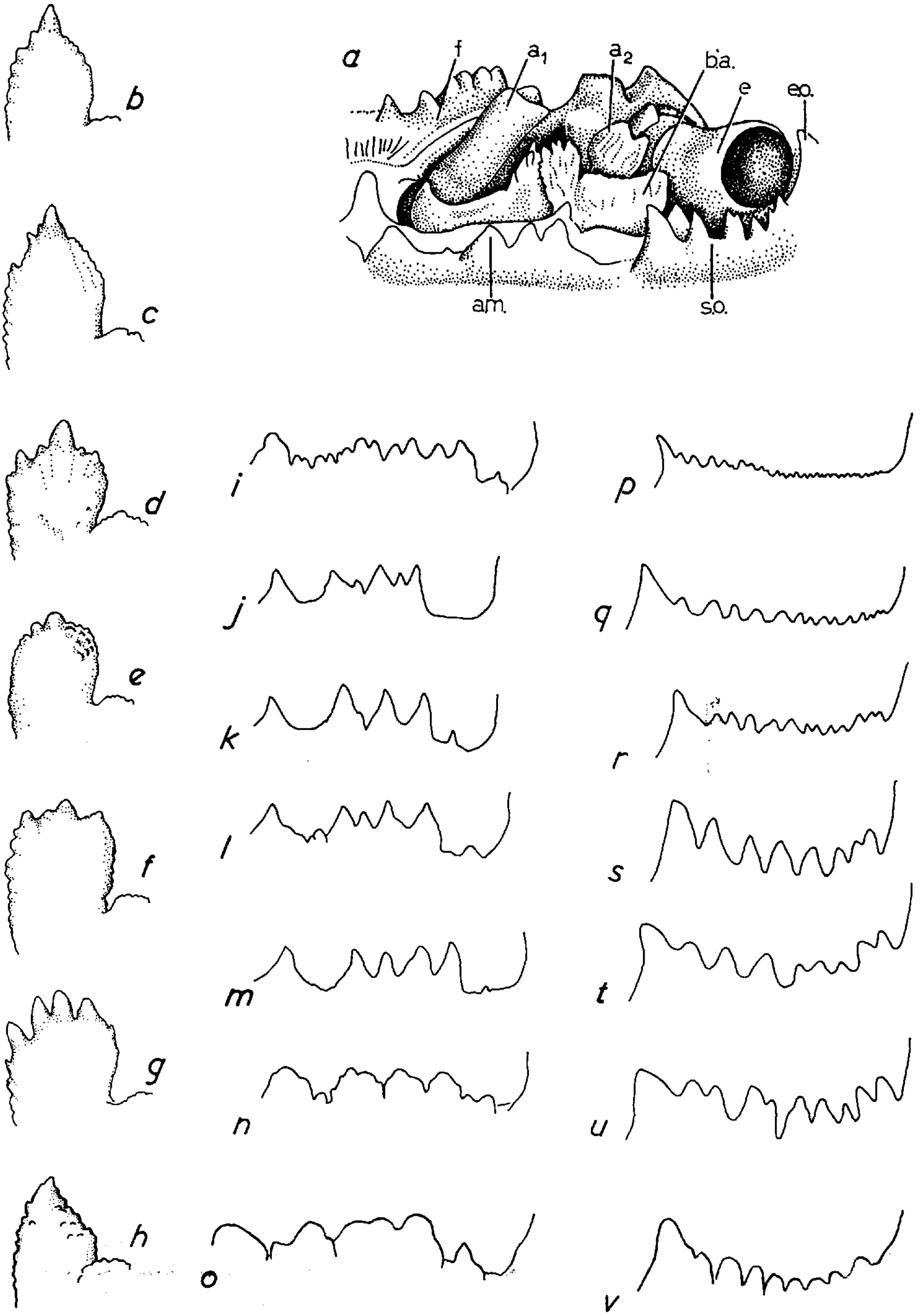

FIG. 7.—Morphological variation in some features of *Plagusia* species: a, *P. chabrus*, male, carapace length 62.8 mm (DM Cr. 1223), Castlepoint, New Zealand: front of carapace and orbit (left hand side), ventral aspect, abbreviations: a_1, antennule; a_2, antenna; a.m., anterior border of mouthfield; b.a., basal antennal article; e, eye; e.o., external orbital spine; f, front; s.o., suborbital border. b–g *P. chabrus*, variation in ornamentation of inner lobe of left basal antennal article: b, male, c.l. 37.9 mm (SAM), South Africa; c, male, c.l. 38.9 mm (DM Cr. 1003), Goat Is., New Zealand; d, male, c.l. 44.0 mm (WAM 219.62), 1 m E. of Frenchman B., Western Australia; e, female, c.l. 44.9 mm (WAM 221.62), Radar Reef,

Rottnest I., Western Australia; f, male, c.l. 56.4 mm (WAM 9013), Garden I., Western Australia; g, male, c.l. 62.8 mm (DM Cr. 1223), Castlepoint, New Zealand. h, *P. dentipes* de Haan, male, c.l. 45.2 mm (USNM 33234), Easter I., inner lobe of left basal antennal article. i–n, *P. chabrus,* anterior border of mouthfield; i, female, c.l. 14.5 mm (WAM 212.62), Busselton, Western Australia; j, female, c.l. 17.2 mm (DM Cr. 1080), Goat I. New Zealand. k, female, c.l. 19.4 mm (DM M. 1186), Lottin Pt., New Zealand; l, male, c.l. 36.2 mm, Tasmania; m, male, c.l. 38.9 mm (DM Cr. 1080), Goat I., New Zealand; n, male, c.l. 56.4 mm (WAM 9013), Garden I., o, *P. dentipes,* male, c.l. 45.2 mm (USNM 33234), Easter I., anterior border of mouthfield. p–u, *P. chabrus,* suborbital border (L.H.S.); p, female, c.l. 9.6 mm (WAM 229.62), Chatham I., Western Australia; q, female, c.l. 14.5 mm (WAM 212.62), Busselton, Western Australia; r, male, c.l. 20.2 mm (WAM 219.62), 1 m. E. of Frenchman B., Western Australia; s, female, c.l. 44.9 mm (WAM 221.62), Radar Reef, Rottnest I., Western Australia; t, male, c.l. 56.4 mm (WAM 9013), Garden I., Western Australia; u, female, c.l. 58.0 mm (WAM 9013), Garden I., Western Australia. v, *P. dentipes,* male, c.l. 45.2 mm (USNM 33234), Easter I., suborbital border.

Plagusia chabrus (Linnaeus), (Figs 7–13, 14A, 15A)

Cancer chabrus Linnaeus, 1758, p. 628; 1764, p. 438.
Grapsus (*Plagusia*) *capensis* De Haan, 1835, p. 58.
Plagusia tomentosa H. Milne Edwards, 1837, p. 92.
Plagusia spinosa Macleay, 1838, p. 66.
Plagusia chabrus.—White, 1846, p. 497.—Rathbun, 1918, p. 336, pl. 104.—Hale, 1927a, p. 185, fig. 186.—Barnard, 1950, p. 136, fig. 26a–f.—Capart, 1951, pp. 194–96, fig. 28.—Garth, 1957, p. 102.—Bennett, 1964, p. 85.—Dell, 1968, p. 26.—Griffin, 1968, p. 212, pl. 1; 1969, p. 334; 1972, p. 86.—Healy and Yaldwyn, 1970, p. 98, fig. 52.
Plagusia gaimardii H. Milne Edwards, 1853, p. 178.
Plagusia capensis.—Stebbing, 1905, p. 47.—Balss, 1935, p. 143.—McNeill, 1962, p. 38, fig.; Morton and Miller, 1968, p. 89, pl. 23–2.
Plagusia capense (sic).—Dell, 1965, p. 57.

TYPES AND TYPE LOCALITIES

The type material of *Cancer chabrus* Linnaeus and *Plagusia capensis* De Haan have already been dealt with (Griffin, 1968). The lectotype of *Plagusia capensis* was selected as the **neotype of** *Cancer chabrus.* The type material is in the Rijksmuseum van Natuurlijke Historie, Leiden. Details for other types are as follows:

Plagusia tomentosa H. Milne Edwards—5 syntypes, Cape of Good Hope and Chile; Muséum National d'Histoire Naturelle, Paris; D. Guinot, pers. comm., 11 April 1972.

Plagusia gaimardii H. Milne Edwards—Tongatabou; one syntype, Muséum National d'Histoire Naturelle, Paris; D. Guinot, pers. comm.

Plagusia spinosa Macleay—South Africa; location of type unknown.

MATERIAL EXAMINED. A total of 81 specimens (41 ♂♂, 39 ♀♀, c.l. 8.2–71.2 mm).

Localities. Australia: Western Australia: Lancelin I.; reef flat at Yanchep; West End Reef and Radar Reef, Rottnest I.; Fremantle; Garden I.; Clifton St. Beach, Bunbury; Busselton; Chatham I., near Nornalup; Albany; 1 m. E. of Frenchman B., Albany; Cheyne Beach; Hopetoun; Esperance. South Australia: "South Australia". Victoria: Pt. Phillip. Bass Strait: Currie Harb., King I. Tasmania: "Tasmania"; off Stanley; Eddystone Pt.; Grant Pt.; Bicheno; Sleepy B.; C. Forestier; Maria I.; Fossil I., Pirates B.; Tasman I.; Adventure B., Bruny I. New South Wales: Shellharbour; S.W. Rocks, Trial Harb.; Hungry Pt., Port Hacking; Port Jackson; Coogee; Long Reef, Collaroy; Bondi Beach; Fort Denison; Fairy Bower, Manly.

New Zealand: Goat I. Beach, Leigh; Otatau I., Auckland; Lottin Pt., C. Runaway; Castlepoint.

South America: Juan Fernandez I.

South Africa: "South Africa".

Localities Previously Reported: Australia: Rottnest I.; Casuarina Point; Fremantle; Bunbury (Balss, 1935). North Beach, south western Australia (Montgomery, 1931). Kangaroo I. (Hale, 1927b). "Bass Strait" (Fulton and Grant, 1906; Rathbun, 1923). "Tasmania" (Haswell, 1882; Tweedie, 1942). Near Georgetown (Miers, 1878). Pt. Puer and Port Arthur (Guider, 1956). "New South Wales" (Haswell, 1882). Illawarra, New South Wales (Dana, 1852). Port Jackson (Whitelegge, 1889).

New Zealand: Eighteen localities from Doubtless B. in the north to Otago in the south (Chilton and Bennett, 1929; Bennett, 1964); "rare in the south, common in the north" (Bennett, 1964); Parengarenga Harbour to Lyttelton Harbour, Manukau Harbour to Nelson (Dell, 1968).

Pacific Ocean: Lord Howe I. and Norfolk I. (Chilton, 1911). Sunday I., Kermadecs (Chilton, 1911). Tonga (H. Milne Edwards, 1853).

South America: Five localities from Bay of Taltal in the north to Los Vilos, Chile, in the south; Juan Fernandez I. (Garth, 1957).

South Africa: Numerous localities from Pt. Nolloth on the west coast to Pt. Stephens, Natal, on the east coast (Barnard, 1950).

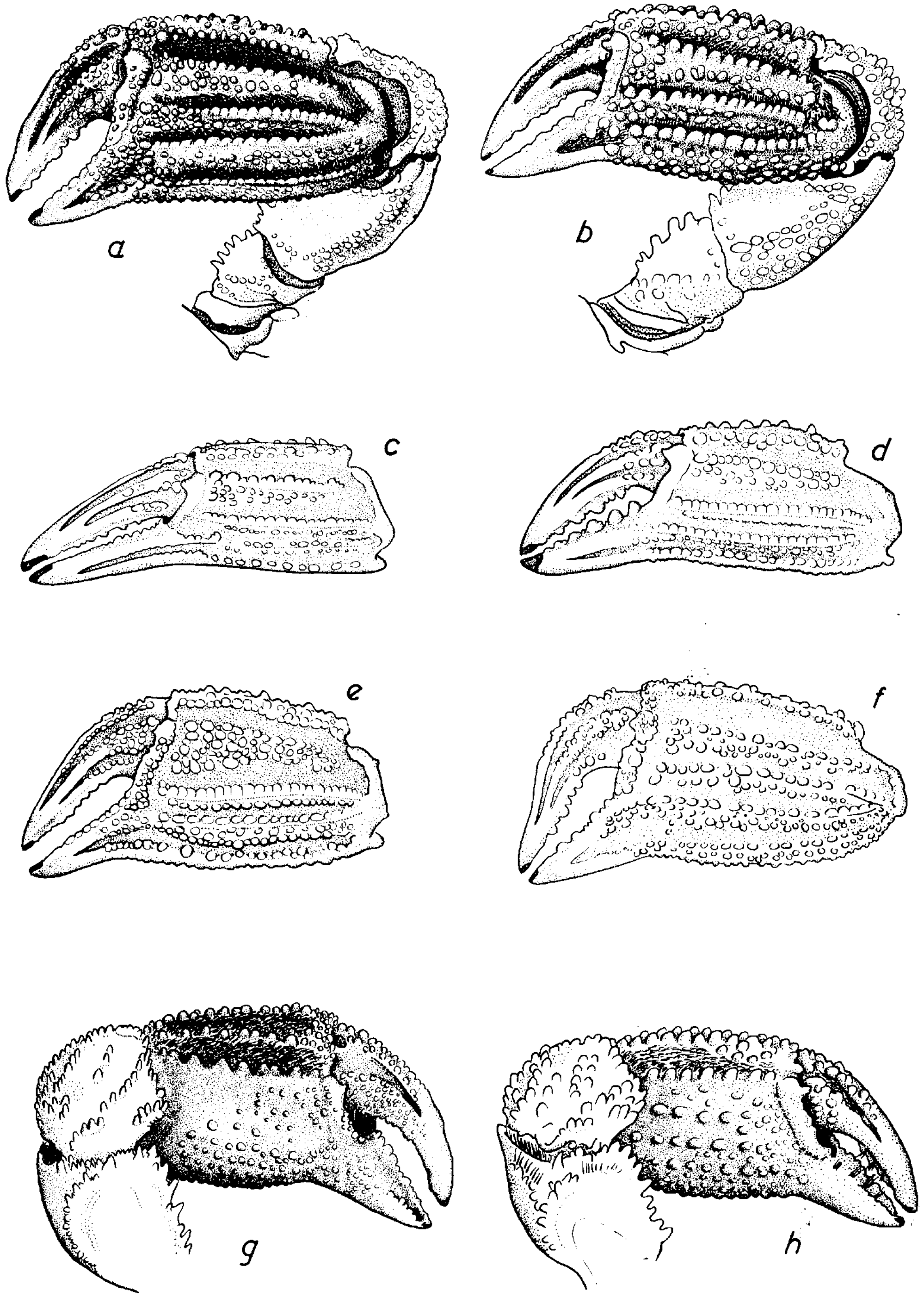

FIG. 8.—Chelipeds of *Plagusia chabrus* de Haan (a, c–g) and *P. dentipes* de Haan (b, h). a, b, whole chelipeds in outer aspect and g, h, inner aspect; a, g, male, c.l. 62.8 mm (DM Cr. 1223), Castlepoint, New Zealand; b, h, male, c.l. 45.2 mm (USNM 33234), Easter I. c–f, left chela outer aspect; c, female, 67.0 mm (TM) Tasmania; d, male, c.l. 31.0 mm (DM M1186), Lottin Pt.; e, male, c.l. 56.4 mm (WAM 9013), Garden I., W.A.; f, male, c.l. 65.4 mm (AM P.9453), Fort Denison, N.S.W.

DESCRIPTION

Carapace.—As wide as long, greatest width about half carapace length from front, lateral margins convex, bearing anterolaterally three equidistant, strong, forwardly directed, sharp, subtriangular spines, the last at widest part of carapace. Surface mostly smooth, covered nearly everywhere by a mat of short curled hairs. A shallow, semicircular groove centrally. Three short, oblique, weakly tuberculate ridges on branchial regions posterolaterally close to edge; a naked, blunt tubercle just behind, and slightly medial to, each orbit; a pair of sharp spines situated transversely immediately behind front.

Front weakly concave and deflexed, bearing 10–14 broad, spines or blunt tubercles around edge. A shallow medial groove extending posteriorly from weak central notch on edge of front to opposite posterior border of orbit.

Orbits deep, U- or V-shaped, margins smooth, weakly notched medially, inwardly bearing a strong, blunt spine anteriorly, outer margin formed by a broad, strong, weakly curved spine. Suborbital border a ridge of 6–15 flattened spines variously grouped into lobes.

Antennular fossae deeply incised into front, narrow, U-shaped, bound laterally by a vertically bilobate ridge. Antennules folding longitudinally and almost vertically.

Basal antennal article L-shaped, consisting of a slender vertical lobe medially, and broad, short, horizontal portion laterally, the former terminating in about three spinules or tubercles, medial edge minutely spinulous. Antennae short.

Anterior border of mouthfield with a narrow incision medially and bearing on each side a single submedial spine and, separated from this by a broad U-shaped hiatus, three broad flattened lobes variously incised into smaller lobes or spines.

Third maxillipeds.—Merus subquadrate, lateral edge bearing midway along a lobe with several low tubercles in a transverse row, surface medially raised proximally and very weakly tuberculate, at least more distally.

Chelipeds.—Moderately long and enlarged in the adult male, ischium, merus and carpus subtrigonal, chela strongly compressed.

Ischium with two ventral ridges each of 4–7 blunt spines.

Merus with two strongly spinous or tuberculate ridges, spines of ventromedial and dorsal ridges long, those of ventrolateral ridge short.

Carpus with blunt spines in six rows dorsally and laterally, spines in mid-dorsal row sharper, medial 3 rows short, others extending full length of carpus, lateral 2 rows proximally convergent.

Chela in adult male massive, deep, enlarged towards distal part of palm. Palm with 3 lobate ridges extending longitudinally along outer surface, each ridge divided longitudinally into two parts, a narrow dorsal row of close-set, large, rounded tubercles and a broad ventral part comprising smaller scattered tubercles. Ventral surface with a single ridge, outwardly distinctly lobate, inwardly comprising small scattered tubercles. Dorsal surface bearing three single rows of laterally compressed tubercles those towards inner surface spinous. All ridges separated by broad areas covered by a dense mat of curled hairs. Inner surface with scattered tubercles, in rows which are sometimes ill-defined, more dense ventrally and in a group distally toward dorsal surface, otherwise smooth. Fingers short, widely gaping throughout their length, inner edges bearing a few large blunt teeth, fixed finger inwardly excavated and spooned distally. Dactyl with a single lobate ridge on outer surface and a mid-dorsal and mid-ventral ridge leaving a single medial smooth area on inner surface; all ridges bearing numerous large tubercles proximally, tubercles decreasing in number and size distally; distal half of dactyl smooth. Fixed finger weakly bent from palm, with a mid-ventral ridge only and smooth distally.

Chela in juvenile and adult female small, palm tapering slightly distally, fingers as long as palm, inner edges adjacent throughout their length.

Ambulatory legs.—Long, third the longest (about twice length of carapace), second slightly shorter, strongly compressed, bases and ischia subcylindrical, meri subtrigonal, long hairs in a dense fringe on posterior surfaces arising from ventral ridge on meri, from both dorsal and ventral ridges of carpi and propodi and from dorsal ridge of dactyli.

Coxae with an erect, truncate or spinate flattened lobe arising posteriorly.

Meri rather deep, dorsal edge convex, bearing numerous short, compressed, distally curved, sharp spines, the most distal the largest; surface covered by a dense mat of curled hairs in three narrow rows on anterior surface and in three very broad rows on posterior surface separated by two narrow longitudinal ridges, the more dorsal finely serrate along its upper edge, the more ventral one smooth. A narrow mid-ventral area of hairs bounded by two ridges extending whole length of meri.

Carpi and propodi with fine narrow elevated smooth ridges, one dorsal, two ventral, one on anterior surface and one on posterior surface; a dense mat of curled hairs between ridges.

Dactyls ventrally bearing two rows of stout, spine-like hairs.

Sternum.—In male covered by short curled hairs, surface close to edge of each sternite usually naked and smooth; tuberculate lobules sometimes projecting in from edge.

Male abdomen.—Of seven segments, all wider than long, first two segments very short, narrowing distally; widest at base of third segment; following segments tapering, laterally very weakly concave, sixth segment weakly convex laterally, seventh segment subtriangular, proximal width slightly exceeding length, edge laterally weakly concave, tip rounded. Surface covered by a fine mat of hairs leaving naked only a broad transverse line across each segment not far from base and another close to distal edge, the two joined by a central longitudinal naked ridge, a naked area also around lateral edge; central ridge

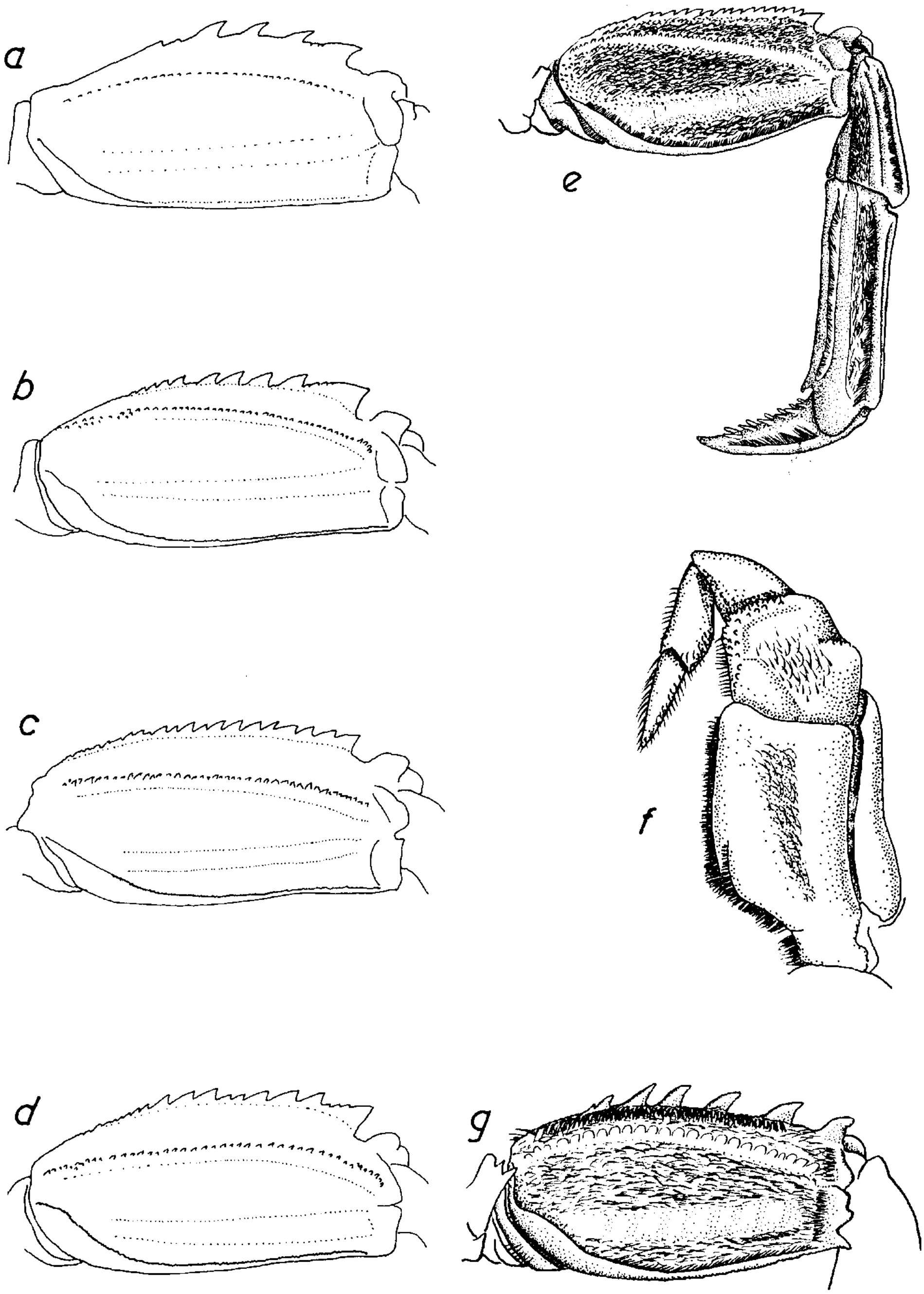

FIG. 9.—Right third ambulatory leg, posterior aspect, of *Plagusia chabrus* (a–e) and of *P. dentipes* (g) and left third maxilliped, outer aspect (f), of *P. chabrus;* c, e and f, male, c.l. 62.8 mm (DM Cr. 1223), Castlepoint, N.Z.; g, male, c.l. 45.2 mm (USNM 33234), Easter I., a–d, merus only; a, male, c.l. 18.1 mm (SAM), South Africa; b, male, c.l. 56.4 mm (WAM 9013), Garden I., W.A.; d, male, c.l. 71.2 mm (TM), Tasmania.

of sixth segment extending from base of segment to transverse ridge, in seventh segment only central longitudinal ridge and marginal ridges present.

Male first pleopod.—Stout, trigonal, medially strongly concave, distally slightly expanded, tip truncate; groove on sternal surface close to medial edge terminating in a large sternal flap. Tip bearing short, stout hairs completely encircling short, broad, concave, horny apical process, surface of pleopod elsewhere naked.

Colour.—Carapace, chelipeds and ambulatory legs various shades of red, naked ridges on dorsal surfaces darker, hairs yellowish. Undersides pale or creamy.

REMARKS

In assessing the variation within and between populations of *P. chabrus* particular attention was paid to the following characters:

1. Carapace: total length, width at the third, second and first lateral spines, interorbital width and frontal width; number of tubercles on the front, on the anterior border of the mouthfield and suborbital border and number of spinules or tubercles around the tip of the inner lobe of the basal antennal article; degree of tuberculation of the carapace behind the orbits and close to the posterolateral edge and of the sternum and abdomen of the male.

2. Chelipeds: length and height of the chela; arrangement of tubercles on carpus and chela.

3. Ambulatory legs: length of the merus of the third leg; number of spines on the dorsal edge of the third merus.

Analysis of the samples shows no differences between samples which would warrant specific or even subspecific separation of the widespread populations. A large number of characters show significant changes with growth.

In the growth of the carapace there is a very slight relative increase in the width of the carapace from the front to the widest part of the carapace at the third lateral spine. This is reflected in a gradual decrease in the ratios frontal width/carapace width, interorbital width/carapace width, etc., most marked in those for the anterior dimensions (see Fig. 11). The regressions for the carapace width/carapace length calculated from the data from all specimens grouped into 5 mm classes, give the following values of a and b (in equation $y = a + b^x$): width of carapace at third spine, $a = 0.63$, $b = 1.06$; width of carapace at second spine, $a = 0.59$, $b = 0.97$; width of carapace at first spine, $a = 2.99$, $b = 0.79$; interorbital width, $a = 4.46$, $b = 0.54$; frontal width, $a = 1.25$, $b = 0.20$.

Relative growth of the chela proceeds in the usual brachyuran fashion with a very marked difference in the relative size and relative height of the chela between juveniles and females on the one hand and adult males on the other (Fig. 8c–f). The dactyl in adult males is typically weakly curved; Fig. 8f shows an unusual but not unique specimen with the dactyl very strongly hooked and curved proximally.

Of the wide variation in meristic characters, nearly all are correlated with growth. They are of two kinds: those in which the rate of change in juveniles is markedly greater than in adults (e.g., number of tubercles or spines around the frontal margin, number of tubercles along the suborbital border—Fig. 12) and those in which the number appears to be constant from juveniles to adults (number of tubercles on the anterior border of the mouthfield, number of spinules or tubercles on the tip of the inner lobe of the basal antennal article, number of spines on dorsal border of the ambulatory meri).

The changes in the number of tubercles on the suborbital border and number of spines on the dorsal edge of the ambulatory meri are the most marked. In the former (Fig. 7p–u; 11) there is a decrease which is very rapid in juveniles (b, in equation $y = a + bx$, being -1.55), very small specimens (Fig. 7p) possessing a very large number of spinules (20–30) which are particularly minute laterally. In adults (c.l. 27 mm) the decrease is still significant ($b = -0.073$) but the rate much less, the border comprising 8–12 more or less broad lobes.

There is a constant rate of increase (b = 0.18) in *P. chabrus* in the number of spines on the dorsal edge of the third ambulatory merus with growth (Fig. 9a–d; 13), small specimens having a few large spines whilst in adults there are a very large number of small spines.

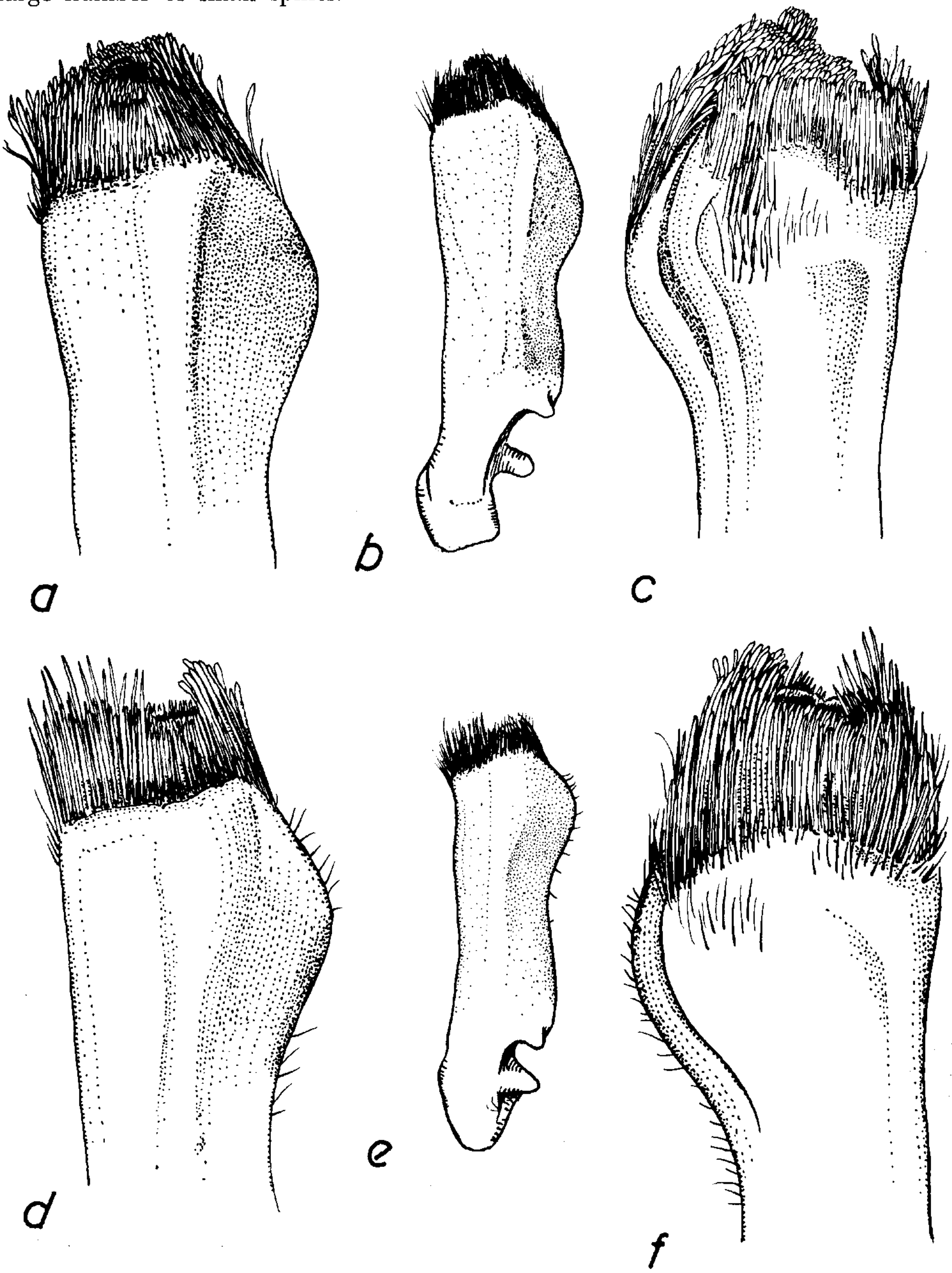

FIG. 10.—Male right front pleopod of *Plagusia* species; a–c, *P. chabrus*. Male, c.l. 62.8 mm (DM Cr. 1223), Castlepoint, N.Z.; d–f, *P. dentipes* de Haan. Male, c.l. 32.2 mm (USNM 45534), Misaki, Japan. Tip in abdominal aspect to the left and in sternal aspect to the right, whole pleopod in abdominal aspect in the centre.

There is a sharp increase in juveniles in the number of spines on the front. In very small specimens there are less than 10 spines around the front. In adults,

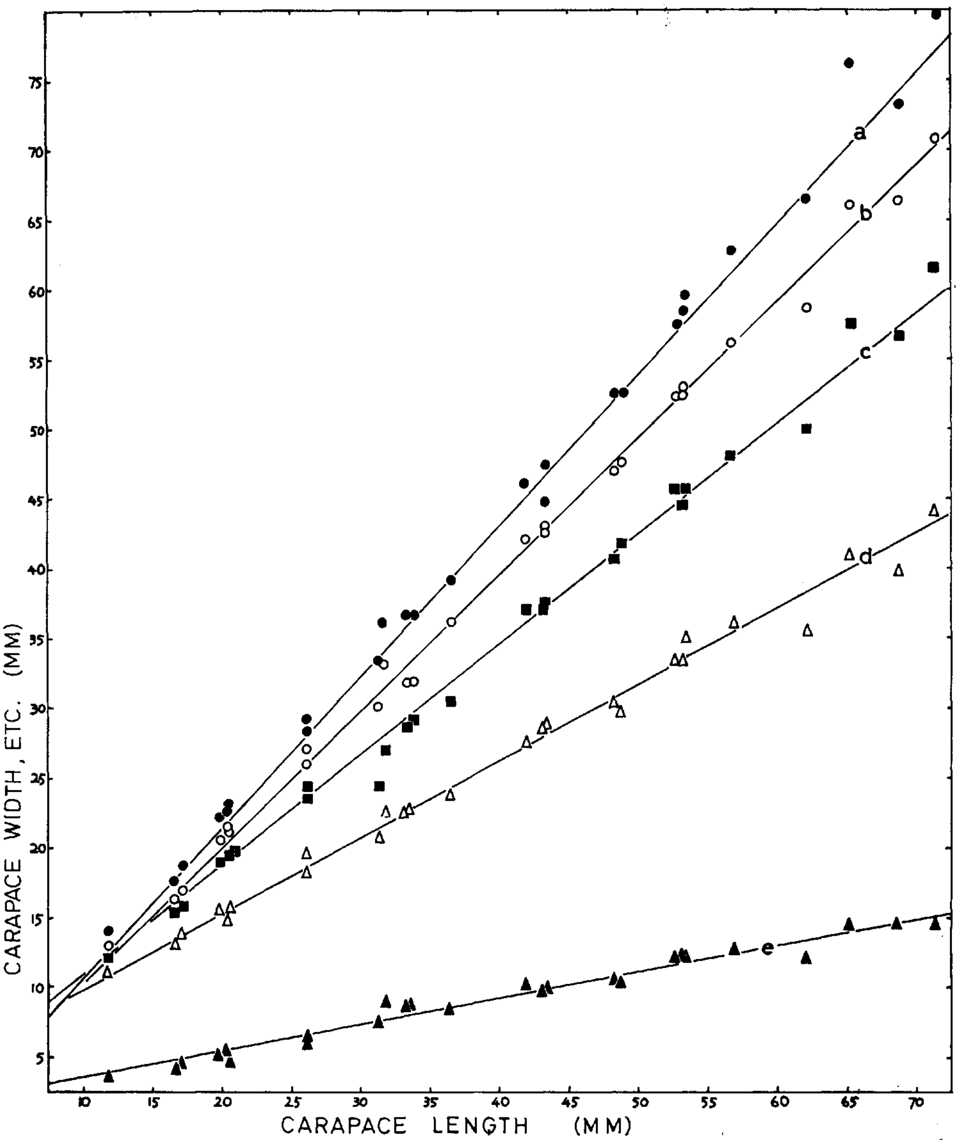

FIG. 11.—Relative growth of five dimensions of the carapace in *Plagusia chabrus;* a, carapace width at third anterolateral spine; b, carapace width at second spine; c, carapace width at first spine; d, interorbital width; e, frontal width. Regression lines calculated from data for all specimens examined grouped into 5 classes; data shown is from 26 specimens from eastern Australia.

in which there is no significant change with growth, the average number is 13.27 ($\pm$ 1.848 in 52 specimens).

In the spinulation of the apex of the inner lobe of the basal antennal article (Fig. 7b–g), there is with increasing size a significant, though small, increase in the number of spinules or lobes—from 1–3 in juveniles to 4–6 in some large adults ($b = 0.040$).

There is no significant increase in the number of tubercles in the anterior border of the mouthfield (Fig. 7i–n), the basic arrangement, of one lobe medially on each side of the midline separated from three lateral lobes, being the same throughout growth, although the tips of the lobes in some small specimens (Fig. 7i) are in turn divided into a number of smaller lobes. In this character there is very wide variation.

Other variable characters include the form of the erect lobe on the coxae of the ambulatory legs (sometimes distally divided into two to four small spines anu sometimes concave or truncate); the number of distal spines on the dorsomedial surface of the carpus of the cheliped (usually two or three in adults but sometimes none in juveniles) and the degree of separation of the most ventral of the ridges on the outer surface of the palm from the mid-ventral ridge, the two ridges tending to be incompletely separated close to the origin of the fixed finger in adults.

The arrangement of tubercles on the dorsal surface of the carpus of the chelipeds is fairly constant. In all, there are five longitudinal rows, the outer two convergent proximally and comprising a larger number of tubercles.

In all the characters so far mentioned there appear to be only very small interpopulation differences.

Lastly, the presence of a strong tubercle behind each orbit, the degree of tuberculation of the three ridges on the posterolateral part of the dorsal surface

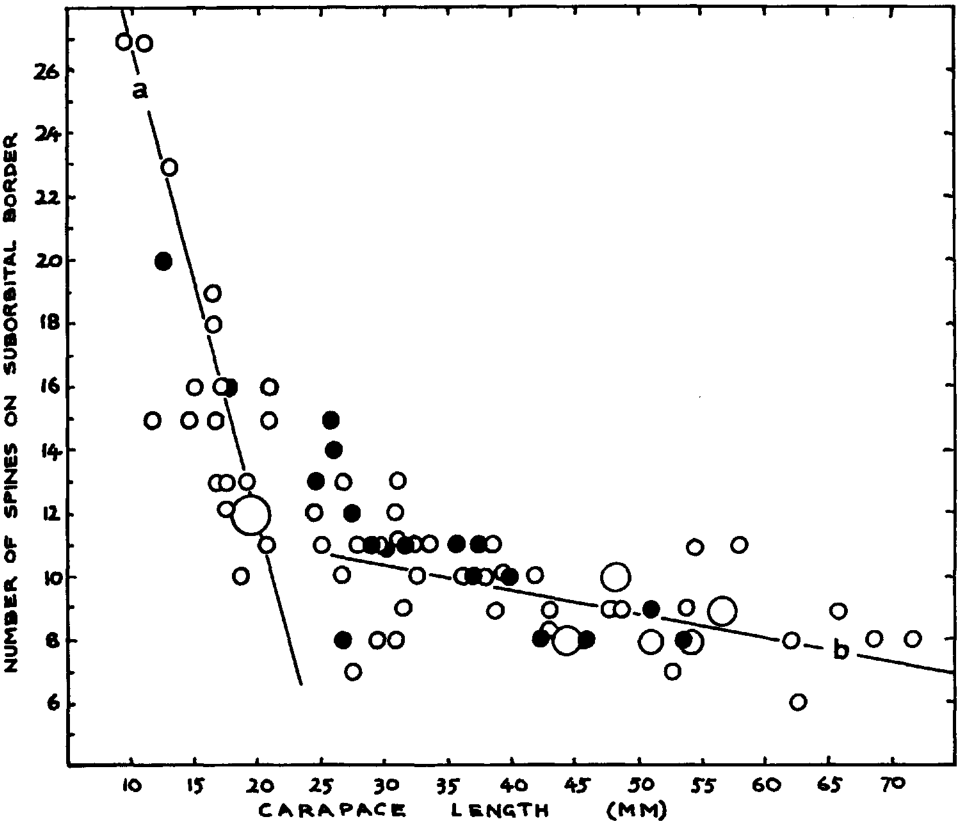

FIG. 12.—Variation with growth in the number of suborbital spines in *Plagusia chabrus* (open circles) and *P. dentipes* (closed circles). Regression lines calculated from all data for *P. chabrus* only, grouped into 5 mm size classes (a, refers to specimens with carapace length less than 22 mm; b, carapace length more than 25 mm). Size of circles proportional to number of specimens (from 1–4).

well developed and sometimes tuberculate and the naked areas on the sternum

of the carapace and the extent and degree of tuberculation of the naked areas on the male sternum are subject to considerable change with age. In all cases there is an increase in the prominence of tubercles. In small specimens the small area behind each orbit is naked or weakly hirsute, the posterolateral ridges are faint and the naked areas of the sternum are smooth. In large adults there is a strong, sometimes spinous, tubercle behind each orbit, the posterolateral ridges are are moderately extensive and sometimes tuberculate (Figs 14A, 15A). Miers (1886, p. 273—footnote) stated that the posterolateral areas of the carapace were smooth, or almost so, in two South African specimens but bearing well-developed ridges in some New Zealand specimens. Barnard (1950, p. 136) stated that South African specimens examined by him, except in the case of a large specimen, lacked a prominent tubercle behind the orbit. Specimens examined during the present study hardly support taxonomic separation of South African populations on the basis of these characters; the absence of tubercles or ridges in South African specimens is understandable since in Australian and New Zealand material such a tuberculate appearance is only found in rather large specimens (carapace length greater than 55 mm). Miers and Barnard both apparently had access only to specimens smaller than this. However, these characters do appear to vary clinally, being weakly expressed in South African specimens and strongly in Australian and New Zealand ones but this is certainly masked by variations due to age.

Milne Edwards's two species, *P. tomentosa* from the Cape of Good Hope and *P. gaimardii* from Tongatabou were only briefly diagnosed originally. It appears that their description as distinct species from *P. chabrus* was based mainly on the appearance and number of the spines or tubercles on the frontal border. As has been pointed out already above, there is wide variation in this character; South African specimens are well within the range of the material from other areas. Stebbing (1905, p. 48) quoted Krauss as considering *Plagusia tomentosa* to be "extraordinarily near to *P. dentipes*". This is not supported by the present study. Mme Daniele Guinot (Paris) has kindly sent me photographs of one of the syntypes of *P. tomentosa,* a male measuring 50 × 45 mm, in the Museum's collections. This specimen possesses all the characteristics of *P. chabrus* as set out above. In particular, there are no strong tubercles on the dorsal surface of the carapace, the front possesses a large number of tubercles and the dorsal borders of the ambulatory meri possess numerous small spines. Photographs of the single syntype of *P. gaimardii,* a male 58 × 53.5 mm, were sent to me by Mme Guinot. This specimen agrees with *P. chabrus* in the same features.

DISTRIBUTION

A partly circumpolar southern hemisphere cool temperate species confined to the Indo-Pacific from South Africa to Chile. The records of this species from Lord Howe I., Norfolk I. and the Kermadecs are almost certainly *P. dentipes.* Material of *P. dentipes* from these localities was examined in this study and is reported on below. The locality of Tonga given by Milne Edwards for *P. gaimardii* does not conform with the known distribution of *P. chabrus.*

Amongst the several other species of the genus *Plagusia, P. chabrus* is undoubtedly most closely related to the subtropical Indo-West Pacific species, *P. dentipes* De Haan (type locality: Japan). Among the features in which the two species both differ from other species of the genus are the presence of several spines on the dorsal border of the ambulatory meri in addition to a terminal spine and the almost smooth, rather than strongly tuberculate, carapace (Tesch, 1918, p. 128; Rathbun, 1918, p. 332). There are also other differences in the shape of the male abdomen and first pleopod.

Grant and McCulloch (1907, p. 153) enumerated five differences separating *P. chabrus* and *P. dentipes;* these concerned: 1, the presence of a spine on the lower distal border of the ambulatory meri; 2, the size of spines on the dorsal border of the ambulatory meri; 3, the number of spines on the front; 4, the presence of tubercles on the hepatic (anterolateral) and branchial (posterolateral) regions of the carapace; and 5, the presence of hairs around these latter prominences. Chilton (1911, p. 558) considered only the first and fourth of Grant and

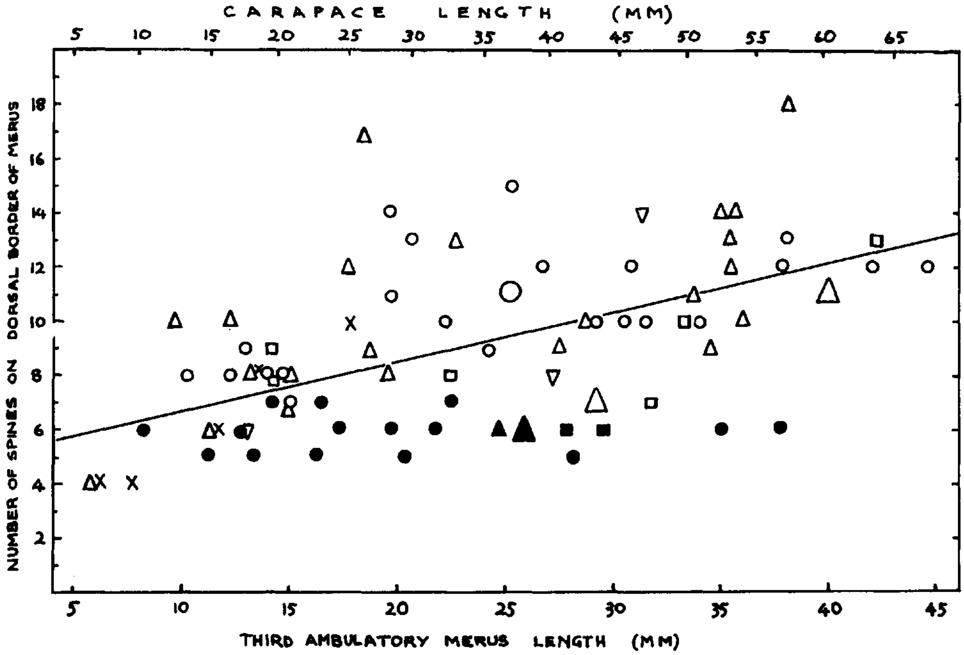

FIG. 13.—Geographical and age variation in spination of third ambulatory merus of *Plagusia chabrus* (open circles, etc.) and *P. dentipes* (filled circles, etc.). Regression line calculated for data from all specimens of *P. capensis* grouped into 5 mm size classes. ○ eastern Australia, △ Western Australia, ▽ South Africa, □ New Zealand, × Chile, ● Queensland and Lord Howe I., ▲ Japan, ■ Easter I. Size of circles, squares, etc., proportional to number of specimens (from 1–3).

McCulloch's differences to be valid. Tesch (1918, p. 129—in key) mentioned one additional difference, the tuberculation of the grooves between the main ridges of large tubercles on the outer surface of the chela in the male.

Considering the doubts expressed already of the validity of some characters in separating the two species and the possibility that there might be a gradation of characters between the two which would warrant subgeneric unification, a moderately large series of specimens of *P. dentipes* was examined. The specimens (15 males, 16 females, c.l. 5.7–53.5 mm: Australia: C. Moreton (Berman Shoals), Pt Cartwright, Caloundra and Coolangatta (Queensland); Pacific Ocean: Norfolk I., Lord Howe I., Easter I.; Japan: Misaki (Sagami B.), Enoshima) were obtained from the collections of the Australian Museum, the Smithsonian Institution and Western Australian Museum (see Figs 7h, o, v; 8b, h; 9g; 10d–f; 12; 13; 14B; 15B).

Study of these specimens shows the two species to be easily separable on the basis of seven characters (see Table 4).

The two species can be less easily separated on the basis of the better defined, longitudinal arrangement of the tubercles on the inner surface of the palm and the slightly greater tuberculation of the grooves between the principal ridges on the outer surface of the male chela in *P. dentipes*. The most ventral of the outer ridges and the mid-ventral ridge are not separated at the origin of the fixed finger (Fig. 8b, h) and the dorsal tubercles of the carpus of the cheliped are in groups rather than rows (Fig. 8h). The male first pleopod in *P. dentipes* bears longer hairs distally (Fig. 10d–f).