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**A revision of the genus *Pachygrapsus* Randall, 1840  
(Crustacea: Decapoda: Brachyura, Grapsidae),  
with special reference to the Southwest Pacific species**

JOSEPH POUPIN, PETER J. F. DAVIE & JEAN-CHRISTOPHE CEXUS



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## A revision of the genus *Pachygrapsus* Randall, 1840 (Crustacea: Decapoda: Brachyura, Grapsidae), with special reference to the Southwest Pacific species

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### Table of contents

Abstract .....	4
Résumé .....	4
Introduction .....	4
Methods .....	5
Systematic account .....	6
Grapsidae MacLeay, 1838 .....	6
Grapsinae MacLeay, 1838 .....	6
<i>Pachygrapsus</i> Randall, 1840 .....	6
<i>Pachygrapsus corrugatus</i> (von Martens, 1872) .....	8
<i>Pachygrapsus crassipes</i> Randall, 1840 .....	9
<i>Pachygrapsus fakaravensis</i> Rathbun, 1907 .....	12
<i>Pachygrapsus gracilis</i> (de Saussure, 1858) .....	15
<i>Pachygrapsus laevimanus</i> Stimpson, 1858 .....	18
<i>Pachygrapsus loveridgei</i> Chace, 1966 .....	23
<i>Pachygrapsus marmoratus</i> (Fabricius, 1787) .....	25
<i>Pachygrapsus maurus</i> (Lucas, 1846) .....	28
<i>Pachygrapsus minutus</i> A. Milne-Edwards, 1873 .....	31
<i>Pachygrapsus planifrons</i> De Man, 1888 .....	34
<i>Pachygrapsus plicatus</i> (H. Milne Edwards, 1837) .....	37
<i>Pachygrapsus propinquus</i> De Man, 1908 .....	42
<i>Pachygrapsus transversus</i> (Gibbes, 1850) .....	44
Discussion .....	50
Remarks on <i>Pachygrapsus polyodous</i> Stebbing, 1921 .....	50
Biogeography .....	52
Morphology .....	52
Morphological Relationships .....	54
Key to species of <i>Pachygrapsus</i> .....	54
Acknowledgements .....	56
Literature cited .....	56
Appendix .....	64

## Abstract

The genus *Pachygrapsus* Randall, 1840 is revised with particular attention to the five Southwest Pacific species: *P. fakaravensis* Rathbun, 1907, *P. laevimanus* Stimpson, 1858, *P. minutus* A. Milne-Edwards, 1873, *P. planifrons* De Man, 1888, and *P. plicatus* (H. Milne Edwards, 1837). *Pachygrapsus laevimanus* Stimpson, 1858 is redescribed and a neotype is designated because of confusion of this species with *P. transversus* (Gibbes, 1850). Seven other species were examined: *P. corrugatus* (von Martens, 1872), *P. crassipes* Randall, 1840, *P. gracilis* (de Saussure, 1858), *P. loveridgei* Chace, 1966, *P. marmoratus* (Fabricius, 1787), *P. maurus* (Lucas, 1846), and *P. transversus* (Gibbes, 1850). The type specimens of *P. striatus* A. Milne-Edwards, 1873, and *P. laevis* Borradaile, 1900, were re-examined and found to be junior synonyms of *P. plicatus* (H. Milne Edwards, 1837), and *P. planifrons* De Man, 1888, respectively. *Pachygrapsus kraussii* (Dana, 1852) is considered a junior synonym of *P. plicatus* H. Milne Edwards, 1837. *Pachygrapsus polyodous* Stebbing, 1921, is excluded from *Pachygrapsus* and provisionally placed in *Euchirograpsus* H. Milne Edwards, 1853. *Pachygrapsus propinquus* De Man, 1908, is probably a junior synonym of *P. minutus* A. Milne-Edwards, 1873, but its status needs to be confirmed with the collection of new material from the type locality. *Pachygrapsus* now includes twelve species, thirteen if *P. propinquus* De Man, 1908, proves to be a separate species. A key to all thirteen species is given.

**Key words:** Crustacea, Decapoda, Brachyura, Grapsidae, *Pachygrapsus*, Systematics

## Résumé

Une révision du genre *Pachygrapsus* Randall, 1840 est proposée, avec une attention particulière pour les cinq espèces du Sud Ouest Pacifique: *P. fakaravensis* Rathbun, 1907, *P. laevimanus* Stimpson, 1858, *P. minutus* A. Milne-Edwards, 1873, *P. planifrons* De Man, 1888, et *P. plicatus* (H. Milne Edwards, 1837). *Pachygrapsus laevimanus* Stimpson, 1858, parfois confondu avec *P. transversus* (Gibbes, 1850), est re-décrit, avec désignation d'un néotype. Sept autres espèces du genre ont été examinées: *P. corrugatus* (von Martens, 1872), *P. crassipes* Randall, 1840, *P. gracilis* (de Saussure, 1858), *P. loveridgei* Chace, 1966, *P. marmoratus* (Fabricius, 1787), *P. maurus* (Lucas, 1846), et *P. transversus* (Gibbes, 1850). Les spécimens types de *P. striatus* A. Milne-Edwards, 1873, et de *P. laevis* Borradaile, 1900, ont été revus et ces deux espèces sont proposées comme synonymes de *P. plicatus* (H. Milne Edwards, 1837), et *P. planifrons* De Man, 1888, respectivement. *Pachygrapsus kraussii* (Dana, 1852) est considéré comme un synonyme de *P. plicatus* H. Milne Edwards, 1837. *Pachygrapsus polyodous* Stebbing, 1921, est exclu du genre et placé provisoirement dans le genre *Euchirograpsus* H. Milne Edwards, 1853. *Pachygrapsus propinquus* De Man, 1908, est considéré comme une espèce valide bien qu'il s'agisse d'un synonyme potentiel de *P. minutus* A. Milne-Edwards, 1873. Après cette révision *Pachygrapsus* compte douze espèces, treize si *P. propinquus* De Man, 1908, s'avère être une espèce distincte. Une clé pour les treize espèces est donnée.

## Introduction

This study has its origins in the large collections of crustaceans made by the first author in French Polynesia. Among the intertidal crabs were a number of grapsids belonging to the

genus *Pachygrapsus* Randall, 1840. All *Pachygrapsus* species are intertidal, and collected among rubble, algae, and rocks. Most species, such as *P. minutus* A. Milne-Edwards, 1873, *P. planifrons* De Man, 1888, and *P. plicatus* (H. Milne Edwards, 1837), are widespread through the Indo-West Pacific region, but two, *P. fakaravensis* Rathbun, 1907, and *P. laevimanus* Stimpson, 1858, are less common, and in need of taxonomic revision. *Pachygrapsus fakaravensis* was described from Fakarava Atoll in the Tuamotu Archipelago during the 1899–1900 Expedition of the Albatross. It is apparently a rare species despite being widely distributed. The G1 of this species, an important character for species differentiation among most brachyuran crabs, had never been described. *Pachygrapsus laevimanus* was briefly described from Sydney, Australia. This species was long confused with *P. transversus* (Gibbes, 1850). So obscure was its identity that it was completely overlooked in Serène's (1968) checklist of Indo-West Pacific crabs. A redescription of this species was thus necessary.

To clarify taxonomic issues with the French Polynesian collections it became necessary to examine specimens of a number of other species in the genus: *P. corrugatus* (von Martens, 1872), *P. crassipes* Randall, 1840, *P. gracilis* (de Saussure, 1858), *P. laevis* Borradaile, 1900, *P. loveridgei* Chace, 1966, *P. marmoratus* (Fabricius, 1787), *P. maurus* (Lucas, 1846), *P. striatus* A. Milne-Edwards, 1873, *P. transversus* (Gibbes, 1850). The current status of three additional species, *P. kraussii* (Dana, 1852), *P. polydous* Stebbing, 1921, and *P. propinquus* De Man, 1908, was also in need of revision. Keys to the species of *Pachygrapsus* were given by Kingsley (1880: 198), Tesch (1918: 75), Edmondson (1959: 168), Crosnier (1965: 26), Sakai (1976: 635), and Dai & Yang (1991: 510). These, however, are now outdated or have been restricted to species of particular regions.

## Methods

Collections of *Pachygrapsus* were made at a variety of locations in French Polynesia between 1986 and 1991 during cruises of RV *Marara*. The objective of these cruises was the sampling of the deepwater crustacean fauna by mean of traps (see Poupin, 1996), but intertidal and shallow-water collections were also made. Additional collections were made in 2002 during the BENTHAUS Expedition to the Austral Is. (mostly Rapa, the southernmost of the islands) organised by the Institut de Recherche pour le Développement (IRD) and the Muséum national d'Histoire naturelle, Paris (MNHN). Other collections from the Tuamotu Archipelago (Rangiroa Atoll) were also made available by G. Paulay, University of Florida. Additional specimens were collected at Clipperton Atoll, in January–February 2005, during the Jean-Louis Etienne Expedition, or examined by the first author at MNHN during several short stays in 2003 and 2004, and at the Smithsonian Institution, Washington D.C. (USNM), during a one-month stay in 2004. Specimens in the Queensland Museum (QM) were examined by the second author. Species are listed alphabetically even though emphasis has been placed on the Southwest Pacific species.

Measurements are of carapace length (cl) taken from the front to posterior margin; maximum carapace width (cw) usually taken behind the exorbital angle. Frontal breadth is expressed as a proportion of the width between the exorbital angles. Terminology used for male gonopods follows Garth (1958: 13). The concave surface that lies against the sternum is referred to as the sternal surface; that lying against the abdomen, the abdominal surface. Full synonymies are not necessarily given but key references containing more exhaustive literature references and distributions are always listed. Morphological characters were coded via the DELTA Editor (Dallwitz, 1980; Dallwitz *et al.*, 1999, 2000). The data matrix was used to compute a key to the species and has been processed with MATLAB® software to perform a Principal Component Analysis (PCA).

Museums abbreviations were used as follows: Australian Museum, Sydney (AM), Academy of Natural Sciences Philadelphia (ANSP), The Natural History Museum, London (BMNH), California Academy of Science, San Francisco (CAS), Natural History Museum of Los Angeles County, California (LCMN), Muséum d'Histoire naturelle, Genève, Switzerland (MHNG), Muséum national d'Histoire naturelle, Paris (MNHN), Museo Nacional de Historia Natural, Santiago, Chile (MNHNS), Musée Zoologique, Strasbourg, France (MZS), Naturhistorisches Museum, Vienna (NHMW), National Science Museum, Tokyo (NSMT), Queensland Museum, Brisbane (QM), Rijksmuseum van Natuurlijke Historie, Leiden, The Netherlands (RMNH), Scripps Institution of Oceanography, San Diego, California (SIO), Senckenberg Museum und Forschungsinstitut, Frankfurt (SMF), Florida Museum of Natural History, University of Florida, Gainesville (UF), University Museum of Zoology, Cambridge, U.K. (UMZC), National Museum of Natural History, Smithsonian Institution, Washington (USNM), Museum für Naturkunde (Zoologisches Museum), Humboldt-Universität, Berlin (ZMB), and Zoological Museum, Göttingen, Germany (ZMG).

Other abbreviations used are: F, female; G1, male first gonopod; juv., juvenile; M, male; METEI, Medical Expedition to Easter I.; ov., ovigerous; P2, P5, second pereopod, fifth pereopod.

### **Systematic account**

#### **Grapsidae MacLeay, 1838**

#### **Grapsinae MacLeay, 1838**

#### ***Pachygrapsus* Randall, 1840**

*Pachygrapsus* Randall, 1840 (type species *Pachygrapsus crassipes* Randall, 1840, subsequent designation by Kingsley, 1880; gender masculine; type locality was originally indicated as Hawaiian Is. but this is probably an error as it has not been subsequently reported from this locality; the Pacific coast of the United States is more likely).

*Goniograpsus* Dana, 1851 (type species *Goniograpsus innotatus* Dana, 1851, a subjective junior synonym of *Pachygrapsus transversus* (Gibbes, 1850), subsequent designation by Manning & Holthuis, 1981; gender masculine).

#### Diagnosis

Carapace subquadrate or with lateral margins convergent backwards; dorsal surface slightly convex, feebly or strongly striated. Anterolateral margins entire or with one or two teeth behind exorbital angles. Length of front more than half carapace width. Third maxilliped widely gaping; merus as broad as or broader than long with no oblique setal crest. Inner sub-orbital lobes small, allowing antennae to enter orbits.

#### Remarks

*Pachygrapsus* Randall is morphologically close to *Planes* Bowdich, 1825, and *Metopograpsus* H. Milne Edwards, 1853. The latter two genera include species that have been sometimes placed in *Pachygrapsus*. *Planes* differs from *Pachygrapsus* by having a more convex carapace that is subcircular, smooth or only feebly striated; a natatory fringe of setae on the propodi of the ambulatory legs; and an open-water habitat (among pelagic seaweeds or crawling on floating objects). It includes three species: *P. major* (MacLeay, 1838), *P. minutus* (Linnaeus, 1758), and *P. marinus* Ratbhun, 1914. *Planes marinus* Ratbhun, 1914 is somewhat intermediate in morphology between *Planes* and *Pachygrapsus*. Its carapace is more subquadrate and striated, the chelae resembling those of *Pachygrapsus*, and the natatory fringe of setae on the ambulatory legs can be reduced. This led Chace (1951: 72) to transfer the species to *Pachygrapsus*, mentioning that, except for its much smaller size, it is very similar to *Pachygrapsus crassipes* Randall, 1840. Chace (1966: 647) after observing the well-developed natatory fringes on specimens of *Pachygrapsus marinus* from St. Helena I., decided that the similarities in shape of the carapace and chelae were probably not very important, and that the presence of natatory fringes and the shape of the G1 were the most important characters for defining *Planes*. He thus reinstated *Planes marinus*, and this generic placement is now widely accepted (see Prado & Melo, 2002). These generic changes, however, serve to highlight the close morphological relationship between *Planes* and *Pachygrapsus* species.

*Pachygrapsus* is also morphologically close to *Metopograpsus* H. Milne Edwards, 1853, the two being separated only on the basis of whether the antennae are able to enter the orbital hiatus (*Pachygrapsus*) or are excluded (*Metopograpsus*). This character is nevertheless not always reliable. We agree with Tesch (1918: 78), Tweedie (1949: 466, footnote), and Crosnier (1965: 25) that *M. thukuhar* (Owen, 1839) may have a distinct gap between the inner sub-orbital lobes and the outer angles of the front, and that it is thus possible for the antenna to enter the orbit. This has also been reported for *M. quadridentatus* Stimpson, 1858 (Tesch, 1918; Tweedie, 1949). This minor difference between the genera led to confusion in the past. Tweedie (1936) described *P. quadratus* from specimens collected from Singapore, but later realised (Tweedie, 1949) that he had confused it with *M.*

*quadridentatus* Stimpson, 1858. Further work is needed to decide if such a variable orbital character is enough to separate *Pachygrapsus* Randall and *Metopograpsus* H. Milne Edwards.

***Pachygrapsus corrugatus* (von Martens, 1872) (Figures 1a–d, 14f, 15f)**

*Grapsus* (*Leptograpsus*) *corrugatus* von Martens, 1872: 107, pl. 4, fig. 8, 8b [type locality: Cuba].  
*Pachygrapsus corrugatus* —Kingsley, 1880: 200 (key). —Rathbun, 1918: 252, pl. 160, fig. 4 (Cuba); 1933: 89 (Puerto Rico). —Chace & Hobbs, 1969: 167 (Virgin Is.). —Manning, 1963: 159–160 (Bahamas). —Holthuis *et al.*, 1980: 46 (St Paul's Rocks). —Manning & Chace, 1990: 66, fig. 43 (Ascension I.). —Melo, 1996: 452, fig. 1 (Brazil); 1998: 499 (Brazil).

*Type material*

Three females and one male in alcohol with the label “*Leptograpsus corrugatus*, collector Gundlach, Cuba” (ZMB 3702). These are not indicated as types but many types in this collection are not marked as such (C. O. Coleman, pers. comm.). The smallest specimen (ZMB 3702) is a male approximately 12 x 14 mm, probably the specimen that is described in von Martens (1872: 107). It is herein designated as lectotype and the remaining three females are the paralectotypes.

*Material Examined*

**West Atlantic. Virgin Is.:** St. Croix, on coastal rocks Judith Fancy Bay, coll. H. A. Beatty, 1935–1936, 1 ov. F. 13.6 x 15.2 mm (USNM 72340). **Bahamas,** Treasure I., Salt Cay, Chaplin-Bahama collection, stn 247, south shore of western tip, coll. J. C. Briggs *et al.*, 14 August 1955, 1 M 15.4 x 17.3 mm (USNM 122786).

**South Central Atlantic. Ascension I.:** south of Collyer Point, intertidal rocky flat around blow-hole adjacent to Cable and Wireless Beach, hand and poison, coll. R. B. Manning, 25 May 1971, 1 M 8.6 x 10.2 mm (USNM 252325).

*Diagnosis*

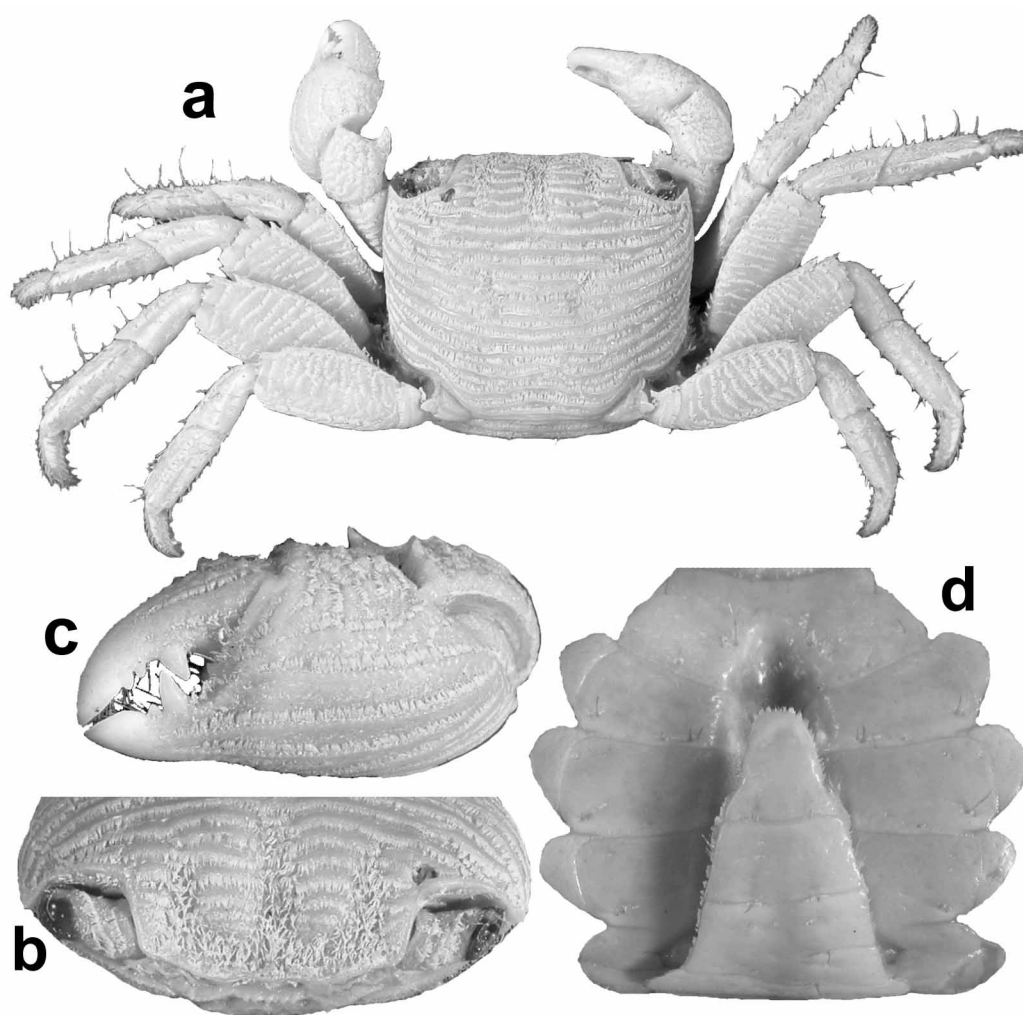
Very similar to *Pachygrapsus fakaravensis* (see diagnosis and remarks for that species). The two species differ by the striation of the abdomen, which is less pronounced in *P. corrugatus* than in *P. fakaravensis*.

Measurements: medium size; carapace of specimens examined ranging from 8.6 x 10.2 to 15.4 x 17.3 mm. For Ascension I., Manning & Chace (1990: 66) indicated a smaller cl, ranging from 3.2 to 8.5 mm.

*Distribution*

**West and south central Atlantic:** Brazil, Bahamas, Cuba, Puerto Rico, the Virgin Is., St. Paul's Rocks, Ascension I.





**FIGURE 1.** —*Pachygrapsus corrugatus* (von Martens, 1872). a) dorsal view; b) front; c) left chela, outer face; d) male abdomen. a–c, ov. female 13.6 x 15.2 mm, Virgin Is. (USNM 72340); d) male 15.4 x 17.3 mm, Bahamas (USNM 122786).

*Habitat*

Intertidal rock pools often around algae.

***Pachygrapsus crassipes* Randall, 1840 (Figures 2a–e, 14g, 15g, 16)**

*Pachygrapsus crassipes* Randall, 1840: 127 [type locality: Hawaiian Is. but according to Rathbun (1918) and Edmonson (1959) this locality must be erroneous]. —Stimpson, 1858: 48 [102] (California, Japan); 1907: 116 (Japan). —Ortmann, 1894: 708 (California; Japan). —Rathbun, 1918: 241 (California; Galápagos Is., Japan, Korea; but not Chile, see distribution). —Tesch, 1918: 76 (Key). —Garth, 1957: 103 (invalid record in Chile; see distribution). —Edmonson, 1959: 168 (California). —Sakai, 1976: 634, pl. 218, fig. 1 (Japan, Korea; references). —Dai &

Yang, 1991: 511 (China sea, Guangdong, Fujian, and Zhejiang). —Hendrickx, 1995: 140 (east Pacific from Oregon to Gulf of California and Rocas Alijos; references). —Cuesta & Schubart, 1998: 1501 (California). —Ng *et al.*, 2001: 40 (Taiwan; references).

*Grapsus eydouxi* H. Milne Edwards, 1853: 170 [136] (Chile; probably an erroneous locality, see distribution).

*Leptograpsus gonagrus* H. Milne Edwards, 1853: 173 [139] (type locality unknown).

#### *Type material*

Male preserved in alcohol (ANSP CA 901) (P. Callomon, pers. comm.).

#### *Material Examined*

**East Pacific. California:** Pacific Grove, 1 M 27.0 x 30.8 mm (MNHN B12892); coll. J. E. Benedict, June 1905, 3 M 26.5 x 29.8–37.2 x 42.9 mm, 4 ov. F 27.3 x 30.1–31.9 x 36.8 mm, 2 F 25.6 x 28.4, 34.0 x 39.6 mm, plus numerous other specimens not examined (USNM 32234). **West Pacific. Japan:** Enoshima, Sagami Bay, coll. M. Takeda, 15 August 1980, 1 M 31.9 x 36.6 mm (NSMT Cr7516). —Sotobo, Chiba Prefecture, coll. T. Habe, 25 March 1975, 2 M 16.8 x 18.9, 24.9 x 29.3 mm (NSMT Cr 6822).

#### *Diagnosis*

Carapace with dorsal surface weakly convex, striated on gastric, hepatic, branchial regions; striae without setae. Cardiac, intestinal regions smooth or only with faint striae. Lateral margins convergent posteriorly, with single tooth behind exorbital angle (Fig. 2a). Front 0.6 times exorbital width, anterior margin slightly sinuous with 2 lobules distally (Fig. 2b). Infraorbital margin weakly dentate on inner half, deeply dentate on outer half; outer notch deep (Fig. 14g).

Outer face of chelae smooth with faint longitudinal line near lower margin, becoming clearly noticeable only on outer face of fixed finger; upper margin slightly carinated; tip of fingers spoon-like, glabrous (Fig. 2c). Ambulatory legs almost totally glabrous; carpi, propodi with several short mobile spines; dactyli with longitudinal rows of long mobile spines, ending with strong, corneous claw. Lower margin of P5 merus smooth with rounded distal angle (Fig. 2d).

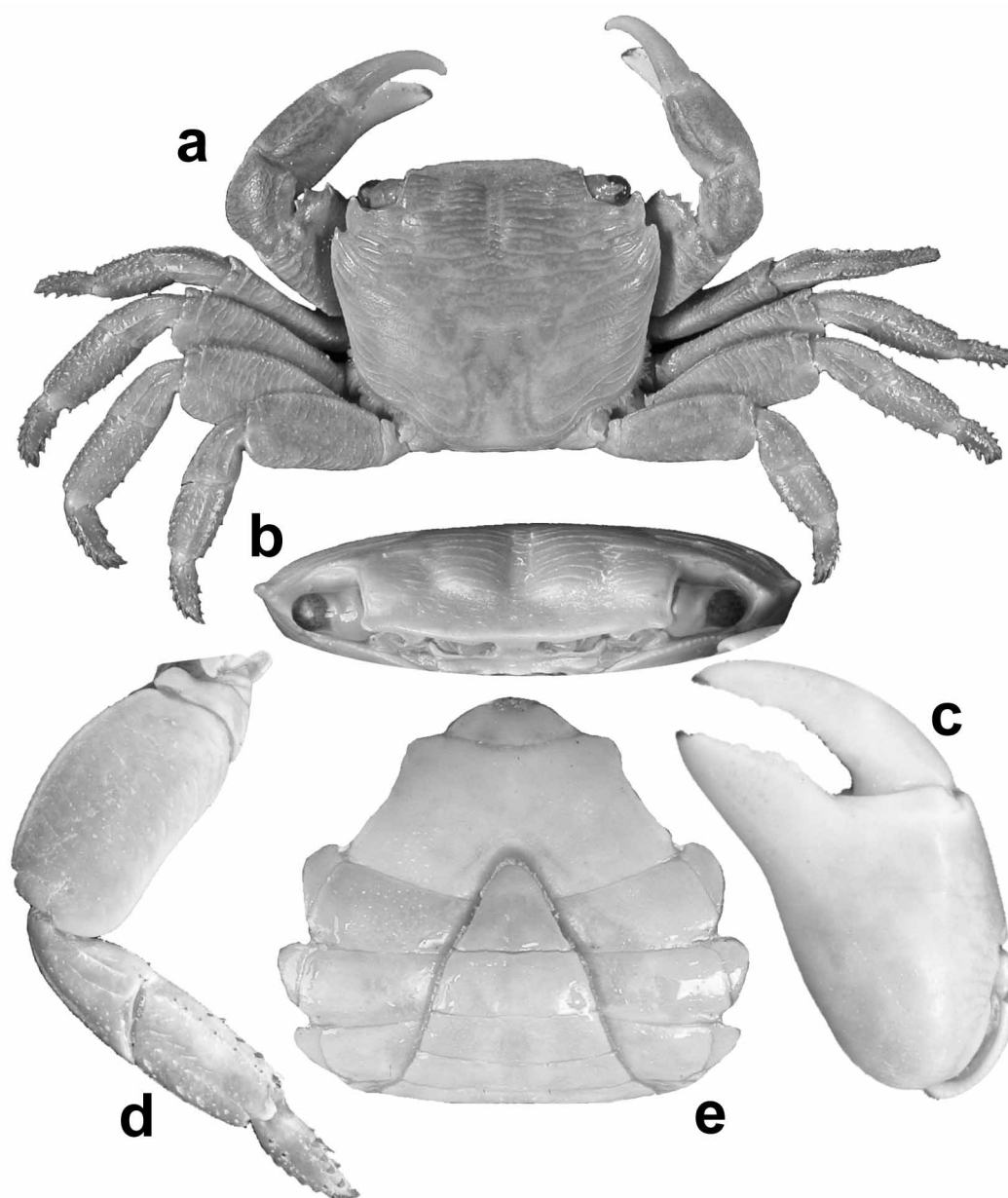
Abdominal tergites smooth; sixth somite of abdomen plus telson triangular in male (Fig. 2e). G1 bluntly truncated with small horn-like process distally (Fig. 15g).

Colour: very variable on photographs examined. Carapace green to almost totally black. Chelipeds light pink to purple or black, with a marbled pattern on the chelae. Ambulatory legs light green or purple to almost totally black.

Measurements: large size; carapace of specimens examined ranging from 26.5 x 29.8 mm to 37.2 x 42.9 mm.

#### *Distribution*

**East Pacific.** Oregon and California, Mexico, Galápagos. **West Pacific.** China, Japan, Korea, Taiwan.



**FIGURE 2.** —*Pachygrapsus crassipes* Randall, 1840. a) dorsal view; b) front; c) left chela outer face, d) left P5, e) male abdomen. a) male 26.5 x 29.8 mm, California (USNM 32234); b–e, male 27.0 x 30.8 mm, California (MNHN B12892).

The type locality given by Randall (1840), the Hawaiian Is., is certainly erroneous as this large-size and common species has never again been recorded from the islands. The type specimen was most probably collected on the California coast. *Pachygrapsus crassipes* was also listed as occurring in Chile by Rathbun (1918: 241) based on the fact that this is the type locality given for *Grapsus eydouxi* H. Milne Edwards (1853: 170). The

type of *G. eydouxi* has not been found at the MNHN. Garth (1957: 105) considered the type locality of Chile for *G. eydouxi* to be erroneous, and thus he did not include *P. crassipes* as part of the Chilean fauna.

#### *Habitat*

Intertidal on rocky shores.

#### *Remarks*

*Pachygrapsus crassipes*, together with *P. gracilis*, *P. laevimanus*, *P. loveridgei*, *P. maurus*, and *P. transversus*, belongs to the group of species with only one tooth behind the exorbital angle. It clearly differs from these species by the shape of its G1 (Fig. 15). Of this group it is morphologically close to *P. transversus*, another large-size species. The two can be separated by the presence of striae on the cardiac and intestinal regions of the carapace being marked only in *P. transversus* (Fig. 2a, 13a); the longitudinal stria on the outer face of the chela is unclear in *P. crassipes*, but deep in *P. transversus* (Fig. 2c, 13c); the ventro-distal angle of the P5 merus is rounded in *P. crassipes*, but it has spines in *P. transversus* (Fig. 2d, 13d); and the male abdomen is regularly triangular at its tip only in *P. crassipes* (Fig. 2e, 13e).

*Pachygrapsus crassipes* is common on the Pacific coasts of North and South America from Oregon to Mexico and the Galápagos Is. Stimpson (1907: 116) was the first to record it from the west Pacific, indicating that he was “unable to find a distinguishing character, however minute, between the specimens from Japan and those from California”. *Pachygrapsus crassipes* was reported several times thereafter from the west Pacific, including Korea (Rathbun, 1918), Japan (Sakai, 1976), China (Dai & Yang, 1911), and Taiwan (Ng *et al.*, 2001). This amphi-Pacific distribution is rather unusual, the fauna of the east and west Pacific normally being distinct. The G1 of Asian *P. crassipes* appears to have never been figured or compared with the American *P. crassipes*. The examination of the G1 of Japanese specimens (NSMT Cr7516, Cr 6822) shows them to be very similar to the American *P. crassipes*. Despite this, preliminary DNA analyses by C. Schubart (pers. comm.) indicate genetic differences between the Asian and American populations and, if these are confirmed by additional data (morphology, larval development, colour pattern), the two could be considered separate species.

#### ***Pachygrapsus fakaravensis* Rathbun, 1907 (Figures 3a–f; 14a; 15a)**

*Pachygrapsus fakaravensis* Rathbun, 1907: 29, pl. 5, fig. 1, pl. 9, fig. 6, 6a [type locality: Fakarava Atoll, Tuamotu Archip., French Polynesia]. —Tesch, 1918: 76 (Key). —Sakai, 1976: 636, pl. 218, fig. 3 (Japan). —Hwang & Yu, 1980: 153, pl. 11-2 (Taiwan). —Monteforte, 1984: 172, annex I, tab. a (Tuamotu Archip.). —Poupin, 1994: 62, fig. 58, pl. 7e (Tuamotu Archip.). —Davie, 1998a: 63 (Hawaiian Is.). —DeFelice *et al.*, 2001: 45 (Hawaiian Is.). —Ng *et al.*, 2001: 40, fig. 8e (Hawaiian Is., Taiwan; references).

*Type material*

Male holotype, 18.0 x 19.4 mm (USNM 32844).

*Material Examined*

**French Polynesia. Tuamotu Archip.:** Fakarava Atoll, outer reef, coll. USS *Albatross*, 12 October 1899, M holotype 18.0 x 19.5 mm (USNM 32844); Taiaro Atoll, outer reef, low tide at night, on big coral rocks, Taiaro Expedition, coll. J. Poupin, 12–20 February 1994, 1 ov. F 15.0 x 16.5 mm (MNHN B25782). —**Hawaiian I.:** Milolii, intertidal on rocks at night, coll. G. Paulay, 31 October 1997, 1 ov. F. 12.9 x 15.1 mm (UF 2255; erroneously labelled *P. plicatus*).

*Diagnosis*

Carapace subquadrate; lateral margins almost parallel with no tooth behind exorbital angle (Fig. 3a). Dorsal surface weakly convex with strong transverse striae with setae. Front 0.5 times carapace width at exorbital angles; anterior margin sinuous (Fig. 3b). Infraorbital margin dentate along entire length, separated from outer orbital tooth by deep notch (Fig. 14a).

Chelipeds equal. Merus with deep transverse striae with setae; dorsal, anterior margins with few mobile spines, inner ventrodistal lobe with 3–4 teeth. Carpus with few granules, short striae with setae; inner spine stout, blunt. Outer face of chela with several longitudinal striae formed by rounded tubercles with setae on lower half; upper half with rounded granules surrounded by setae (Fig. 3c). Tips of fingers spoon-like, glabrous.

Meri of ambulatory legs with deep transverse to oblique ridges with setae; lower margin of P5 meri without sub-median tubercle (Fig. 3d). Carpi, propodi with two longitudinal striae with setae. Dactyli ending in strong corneous claw; dorsal, ventral margins with rows of strong, moveable spines.

Male with numerous short setiferous striae on abdominal tergites, thoracic sternites; sixth somite of abdomen plus telson triangular (Fig. 3e). Female with several short setiferous striae on abdominal tergites (Fig. 3f). G1 with long, horn-like process with minute spinule medially (Fig. 15a).

Colour: overall brown to dark brown with violet hues and paler areas on ambulatory legs.

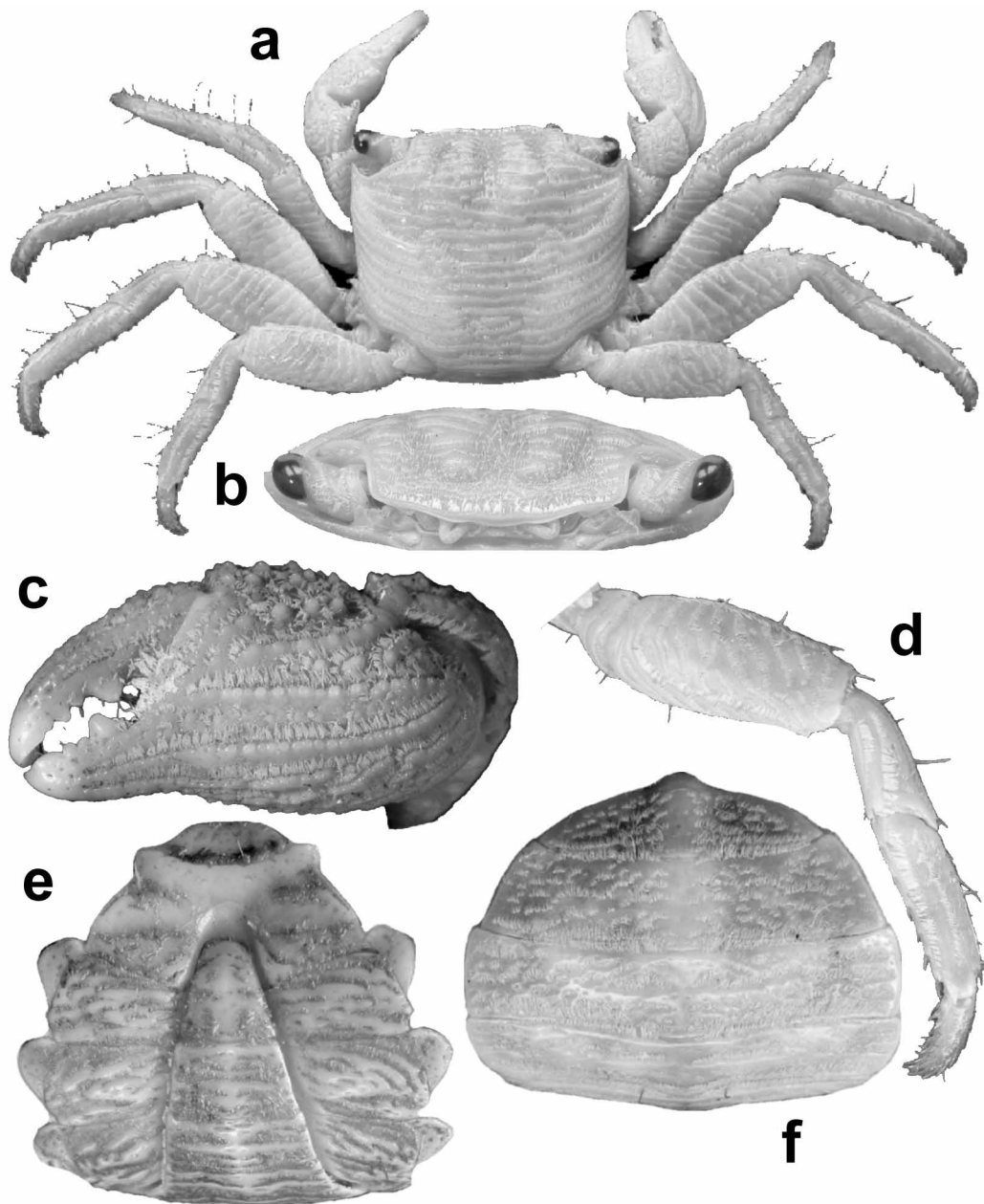
Measurements: carapace of specimens examined ranging from 12.9 x 15.1 to 15.0 x 16.5 mm.

*Distribution*

**West and Central Pacific.** Japan; Taiwan, Hawaiian Is., French Polynesia (Tuamotu Archip.: Fakarava, Makatea, Mataiva, Taiaro, Takapoto).

*Habitat*

Collected at upper level of reefs at night; uncommon.



**FIGURE 3.** —*Pachygrapsus fakaravensis* Rathbun (1907). a) dorsal view; b) front; c) left chela, outer face; d) right P5; e) male abdomen; f) female abdomen. a, b, d, f, ov. female 15.0 x 16.5 mm (MNHN B25782); c, e, holotype male 18.0 x 19.4 mm (USNM 32844).

#### Remarks

*Pachygrapsus fakaravensis* is uncommon, rarely reported in the literature. It is morphologically close to the Indo-West Pacific *P. plicatus* (H. Milne Edwards, 1837), which has similar coarse striations on the carapace and the same longitudinal striae on the outer

face of the chelae. The two species have been collected together in French Polynesia. They can be separated by the shape of the lateral carapace margins (subparallel in *P. fakaravensis*, posteriorly convergent in *P. plicatus*), the presence of setae on the longitudinal striae of the outer face of the chelae of *P. fakaravensis*, and by the abdominal tergites having short striae in *P. fakaravensis* but being smooth in *P. plicatus*. The shape of the G1, figured here for the first time for *P. fakaravensis*, also separates the two species (Fig. 15a, e).

After examining *P. corrugatus* (von Martens, 1872) from the west and central Atlantic (USNM 72340, 122786, 252325), it is clear that *P. fakaravensis* is morphologically close to the latter and may thus be considered a sibling species. It is surprising that neither Rathbun (1907) in her description of *P. fakaravensis*, nor Manning & Chace (1990) in recording and illustrating a male of *P. corrugatus* from Ascension I., mentioned this sharp similarity. Both species share a subrectangular carapace, with almost parallel lateral margins; coarse and hairy striae on the carapace; several longitudinal striae furnished with setae on the outer face of the chelae; abdominal tergites with short transverse striae; similarly shaped infraorbital margins, with a small protrusion distally followed by a deep indentation; and similar G1 (Fig. 15a, f). The two species can, however, easily be separated using the relative striation of the abdominal tergites, which is more pronounced in *P. fakaravensis* than in *P. corrugatus*. This difference is especially obvious in males. Striae are also present on the thoracic sternites of *P. fakaravensis* but absent in *P. corrugatus* (Fig. 3e, 1d).

Davie (1998a) suggested that it was likely that *P. fakaravensis* had only recently become established or possibly introduced in the Hawaiian Is. because it was unusual that such a relatively large and distinctive intertidal crab, living in a major harbour on the island of Oahu, had not been previously noticed, especially given the large collections reported by Rathbun (1906) and the extensive collections made by Edmondson (1959).

### ***Pachygrapsus gracilis* (de Saussure, 1858) (Figures 4a–e, 14h, 15h)**

*Metopograpsus gracilis* de Saussure, 1858: 443 [27], pl. 2, fig. 15 [type locality: St. Thomas, Virgin Is.].

*Grapsus* (*Leptograpsus*) *rugulosus* von Martens, 1872: 108 (Cuba), not *Leptograpsus rugulosus* H. Milne Edwards, 1863.

*Pachygrapsus gracilis* —Verrill, 1908: 324, fig. 6a, b, pl. 12, fig. 2 (Bermuda). —Rathbun, 1918: 249, pl. 60, fig. 3, pl. 61, fig. 1 (Bahamas, Jamaica, Puerto Rico, Colombia, Brazil, Bermuda; synonymy); 1921: 445, pl. 40, fig. 1 (Congo); 1933: 89 (Puerto Rico). —Capart, 1951: 187, fig. 74, pl. 3, fig. 19 (West Africa). —Monod, 1956: 419, fig. 569 (West Africa). —Holthuis, 1959: 239, pl. 10, fig. 3 (Suriname). —Chace & Hobbs, 1969: 167, fig. 51, 52j (West Indies; references). —Rodríguez, 1980: 380, pl. 59 (Venezuela). —Manning & Holthuis, 1981: 233 (Senegal to Angola; references). —Rodrigues & Brossi-Garcia, 1989: 63, fig. 1–5 (Brazil). —Melo, 1996: 453, fig. 1 (Brazil); 1998: 499 (Brazil).

*Type material*

One dry specimen (MHNG, frame n° 190, no record number) (P. J. Schwendinger, pers. comm.).

*Material Examined*

**East Atlantic. Angola:** Lobito, intertidal in oysters, 2 M 7.8 x 10.0, 9.4 x 12.0 mm, 1 F 9.2 x 12.0 mm, 4 F ov. 6.4 x 7.9–8.5 x 11.1 mm (MNHN B12903).

**West Atlantic. Florida:** Banana river, Cap Canaveral, on rock rubble and oysters, 1.8 m, coll. R. H. Gore, 10 August 1972, 3 M 11.3 x 14.3–14.9 x 19.5 mm, 2 ov. F 7.2 x 10.0, 12.4 x 16.7 mm, 3 F 10.7 x 14.1–13.5 x 14.3 mm (USNM 170178). —**French Guiana:** coll. F. Geay 1906, 1 F 11.5 x 16.0 mm (MNHN B29570; mixed with specimens of *P. transversus* under MNHN B16013).

*Diagnosis*

Carapace markedly striated on gastric, hepatic, branchial regions; cardiac, intestinal regions smooth or only with short striae; lateral margins strongly convergent posteriorly, with tooth behind exorbital angle (Fig. 4a). Front 0.6 times exorbital width; anterior margin straight (Fig. 4b). Infraorbital margin almost smooth, at most slightly granulate; without outer notch (Fig. 14h).

Outer face of chelae smooth and regularly convex, sometimes with a faint stria near lower margin, becoming more obvious on outer face of fixed finger; dorsal margin of palm with a weak carina and several oblique striae on inner side; dorsal margin of dactyl tuberculated. Cutting edges of fingers widely gaping, with small triangular teeth; tip of fingers spoon shaped, glabrous (Fig. 4c).

Ambulatory legs with few scattered long bristles and longitudinal rows of short setae on carpi, propodi; propodi without brush of setae. P5 merus with lower margin marked by several oblique striae on outer face; with a somewhat more noticeable submedian tubercle (Fig. 4d).

Abdominal tergites smooth. Male abdomen with sixth somite broader than telson, sixth somite and telson not forming triangle. G1 bluntly rounded at tip, with short corneous process (Fig. 15h).

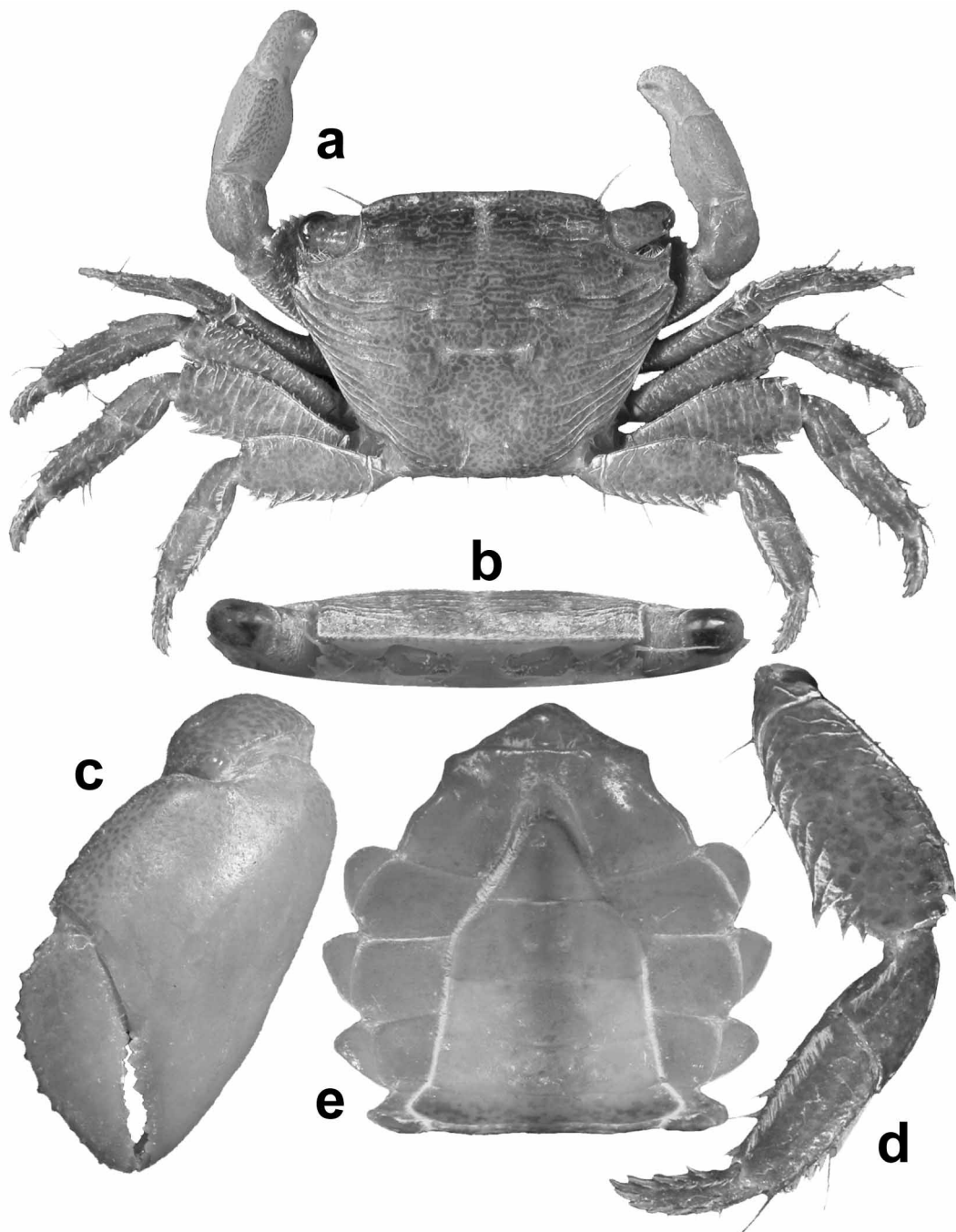
Colour (from photograph): Carapace light green to cream with transverse lines composed of small violet spots. Chelipeds and ambulatory legs pale violet with numerous darker violet spots. The spots retained on the carapace even after several years in preservative (Fig. 4a) is a useful character to recognize the species.

Measurements: medium size; carapace of specimens examined ranging from: males 7.8 x 10.0–14.9 x 19.5 mm; females 6.4 x 7.9–13.5 x 14.3 mm; smallest ovigerous female 6.4 x 7.9 mm.

*Distribution*

**West Atlantic.** Argentine, Brazil, French Guiana, Caribbean, Texas. **East Atlantic.** Senegal to Angola.





**FIGURE 4.** —*Pachygrapsus gracilis* (de Saussure, 1858). a) dorsal view; b) front; c) left chela, outer face; d) right P5; e) male abdomen. a, c–e, male 14.9 x 19.5 mm, Florida (USNM 170178); b) ov. female 8.5 x 11 mm, Angola (MNHN B12903).

*Habitat*

Intertidal. Among mangrove roots and on river banks near the sea (Chace & Hobbs, 1969).

*Remarks*

*Pachygrapsus gracilis* is morphologically close to *P. loveridgei* Chace, 1966 and *P. transversus* (Gibbes, 1850), both also Atlantic species of similar size, with only one tooth behind the exorbital angle and with the male abdomen not triangular at the tip. The three species have very distinct G1 that should not be confused (Fig. 15h, i, l). *Pachygrapsus gracilis* is also distinct by the lateral carapace margins being strongly convergent posteriorly, the straight anterior margin of the front, the infraorbital margin being almost smooth and without an outer notch, the upper margin of the dactyl of the chela being tuberculated, the absence of a brush of setae on the propodi of the ambulatory legs, and by its colour pattern, having spots that are retained on the carapace even after several years of preservation.

***Pachygrapsus laevimanus* Stimpson, 1858 (Figures 5a–f, 14b, 15b, 16)**

*Pachygrapsus laevimanus* Stimpson, 1858: 48 [102] [type locality: Port Jackson, Sydney, Australia] —Stimpson, 1907: 117 (New South Wales). —Holthuis & Gottlieb, 1958: 102 (New South Wales). —Davie, 1998b: 151, photograph (Queensland); 2002: 218 (Queensland, New South Wales, Norfolk I.). —Poore, 2004: 508, fig. 161d, h, 162b (Queensland, New South Wales, Victoria).

*Pachygrapsus transversus* —Rathbun, 1907: 29 (Easter I.); 1918: 248 (part, only specimens from Sydney and Easter I.). —Garth, 1973: 324 (Easter I.). —Báez & Ruiz, 1985: 105 (Easter I.). [Not *P. transversus* (Gibbes, 1850)]

*Type material*

Male neotype 18.0 x 21.7 mm (AM P7478), herein designated. *Pachygrapsus laevimanus* was poorly described by Stimpson (1858) from specimens collected in the vicinity of Sydney. Most of Stimpson's collections, including the types of *P. laevimanus*, were lost in the Chicago fire of 1871. As a result, this species has been ignored for many years and often confused with *P. transversus* (Gibbes, 1850), a species widely distributed in the Mediterranean, east and west Atlantic, and east Pacific. Because of this long period of confusion, and because even now there is uncertainty over the identity of specimens from Easter I. (see below), we believe that it is necessary to erect a neotype for *P. laevimanus* to ensure the future stability of this taxon.

*Material Examined*

*Neotype.* **Australia. New South Wales:** Sydney, 33°52'S, 151°15.5'E, on reef, Rose Bay, Port Jackson, coll. Mel Ward, September 1924, 1 M 18.0 x 21.7 mm (AM P7478).

*Other specimens.* **Australia. New South Wales:** Sydney, Manly, leg from AM, 3 M 6.2 x 7.9–8.3 x 10.2 mm, 1 F 6.8 x 8.4 mm (USNM 43776); Sydney, November 1926, among small stones in rock crevices, between tides marks, 1 M 10.6 x 12.6 mm, 1 ov. F 8.5 x 10.6 mm, 1 F 8.0 x 10.0 mm (MNHN B11083; leg from AM P5D07, part); Sydney, Balmoral Beach, Mosman, coll. L. B. Holthuis, 23 April 1955, 5 M 7.9 x 9.6–12.0 x 14.7 mm, 5 F

6.3 x 7.9–9.6 x 12.1 mm (RMNH 10424); Sydney, Port Jackson, bottle and glass rocks, intertidal under stone and weed, 33°50.9'S, 151°16.2'E, coll. D. J. G. Griffin, 23 October 1968, 1 M 6.7 x 8.4 mm, 1 F 7.0 x 8.7 mm, 1 juv. 3.9 x 4.9 mm, (AM P17802); Sydney, Long Bay Coast, rocky reef, between tide marks, purchase #78 S. Kellner, 3 M 6.3 x 7.4–7.5 x 9.1 mm, 1 ov. F 5.8 x 7.3 mm (USNM 98830); Sydney, 'Maulyi', AM acc. n° 25661, coll. 3 February 1889, 2 M 8.5 x 10.5, 10.5x12.5 (UNSM 17054); Twofold Bay, Murrumbulga point, 37°04.7'S, 149°53.1'E, intertidal rock platform, coll. S. Keable, 25 July 1985, 3 M 7.5 x 9.1–11.9 x 14.7 mm, 2 F 8.0 x 10.1, 9.7 x 12.1 mm (AM P36075); mouth of Clarence R., 29°26'S, 153°22'E, coll. A. A. Cameron, 1 ov. F 11.3 x 14.2 mm (QM W3306). —**Lord Howe I.:** 31°31'S, 159°04'E, Neds Beach, coll. G. Kelly, 14 September 2003, 5 M 9.6 x 11.7–12.1 x 14.4 mm, 1 ov. F 11.8 x 14.0 mm (QM W26879); 31°31'S, 159°04'E, Neds Beach, coll. G. Kelly, 30 August 2003, 1 M 14.3 x 17.4 mm (QM W26876). —**Queensland:** Caloundra, Kings Headland, 26°48'S, 153°08'E, rocky shore, under rocks, coll. J. W. Short, M. Bavins, October 1996, 3 F 8.5 x 10.4–13.8 x 16.8 mm (QM W21818); Kings Headland, 26°48'S, 153°09'E, rocky shore, under rocks, coll. J. W. Short, 27 September 1996, 1 F 8.7 x 10.5 mm (QM W21533); Kings Headland, N. end, Kings Beach, 26°48'S, 153°08'E, rocky shore, coll. M.S.A. party (Brisbane Shell Club), 13 March 1983, 1 F 7.6 x 9.3 mm (QM W10457); Kings Headland, 26°48'S, 153°08'E, rocky shore, coll. P. Davie, D. Potter, 30 July 1997, 2 M 11.6 x 14.6, 11.3 x 13.3 mm (QM W23937); Moreton Bay, 27°00'S, 153°00'E, 2 M 11.3 x 13.3, 14.7 x 17.9 mm (QM W12336). —**Tasman Sea. Middleton reef:** 29°28.5'S, 159°03.7'E, reef flat near wreck of Runic, rubble, dead coral heads, dead *Tridacna*, low tide, coll. J. K. Lowry, 4 December 1987, 9 M 3.5 x 4.6–10.3 x 12.9 mm, 7 ov. F 4.5 x 5.8–7.9 x 9.8 mm, 6 F 5.9 x 7.6–8.7 x 11.0 mm (AM P38221); 29°25'S, 159°00'E, near wreck of Runic, coll. J. W. Short, R. J. McKay, 9 May 1987, 1 M 10.6 x 13.2 mm (QM W13048), 1 M 7.1 x 9.2 mm (QM W13050). —**Elizabeth reef,** 29°55.4'S, 159°02.7'E, sand cay, north west lagoon entrance, under stone, low tide, coll. J. K. Lowry, 12 December 1987, 12 M 7.9 x 9.8–11.7 x 14.2 mm, 5 ov. F 6.5 x 8.0–8.2 x 10.2 mm, 4 F 8.3 x 9.8–10.0 x 12.7 mm (AM P38223); 29°55'S, 159°00'E, coll. J. W. Short, 6 May 1987, 1 M 12.4 x 14.9 mm (QM W13051), 4 May 1987, 4 M 4.8 x 5.9–14.3 x 17.4 mm (QM W13047).

**Norfolk I.:** Cemetery Bay, under stones on intertidal rock platform, coll. D. J. G. Griffin, 30 March 1969, 1 M 5.4 x 7.0 mm, 1 F 6.7 x 8.7 mm (AM P17329).

**Austral Is.:** Rapa I., Haurei Bay, intertidal, RV *Marara* campaign, coll. J. Poupin, 19 to 21 March 1995, 13 M 6.6 x 7.8–14.0 x 16.8 mm, 4 ov. F 8.0 x 10.0–11.1 x 13.9 mm, 4 F 8.1 x 10.3–13.9 x 17.0 mm (MNHN B29265). —**BENTHAUS Expedition:** Haurei Bay, intertidal, near wharf, among stones and rubbles, coll. J. Poupin, 2 November 2002, 14 M 4.0 x 5.0–14.8 x 17.5 mm, 7 ov. F 6.6 x 8.0–12.8 x 16.0 mm, 7 F 7.1 x 8.6–11.3 x 13.6 mm (MNHN B29266); Haurei Bay, intertidal, coll. A. Warén, 8 November 2002, 2 F 6.3 x 7.7, 6.6 x 7.9 mm (MNHN B29267); 27°37.4'S, 144°18.4'W, north of Anatakuri Bay, 2 m, in sediment under stones, coll. malacologist team, stn 38, 22 November 2002, 1 M 6.3 x 7.6

mm (MNHN B29268); Anarua Bay, 27°36.4'S, 144°22.6'W, intertidal, coll. malacologist team stn 87 (possibly 86), 25 November 2002, 1 juv. 2.6 x 3 mm (MNHN B29269).

**Easter I.:** shore, coll. RV *Albatross*, 16 December 1904, 1 F 7.6 x 9.5 mm (UNSM 33186; see remarks).

#### *Description*

Carapace 1.2–1.3 times broader than long (Fig. 5a). Dorsal surface slightly convex on anterior half, covered with strong transverse striae, smooth or with scarce setae. Median postfrontal lobes distinct, striated; mesogastric, cardiac regions with few short striae (sometimes indistinct on cardiac region); intestinal region flat, almost totally smooth. Lateral margins of carapace convex, slightly convergent posteriorly, armed with single conspicuous tooth posterior to exorbital tooth. Front 0.6 times exorbital width (Fig. 5b); anterior margin sinuous, granulate, with shallow sinuses. Orbits subrectangular in dorsal view, about one third as wide as front; infraorbital margin minutely dentate, separated by deep notch from outer orbital tooth (Fig. 14b).

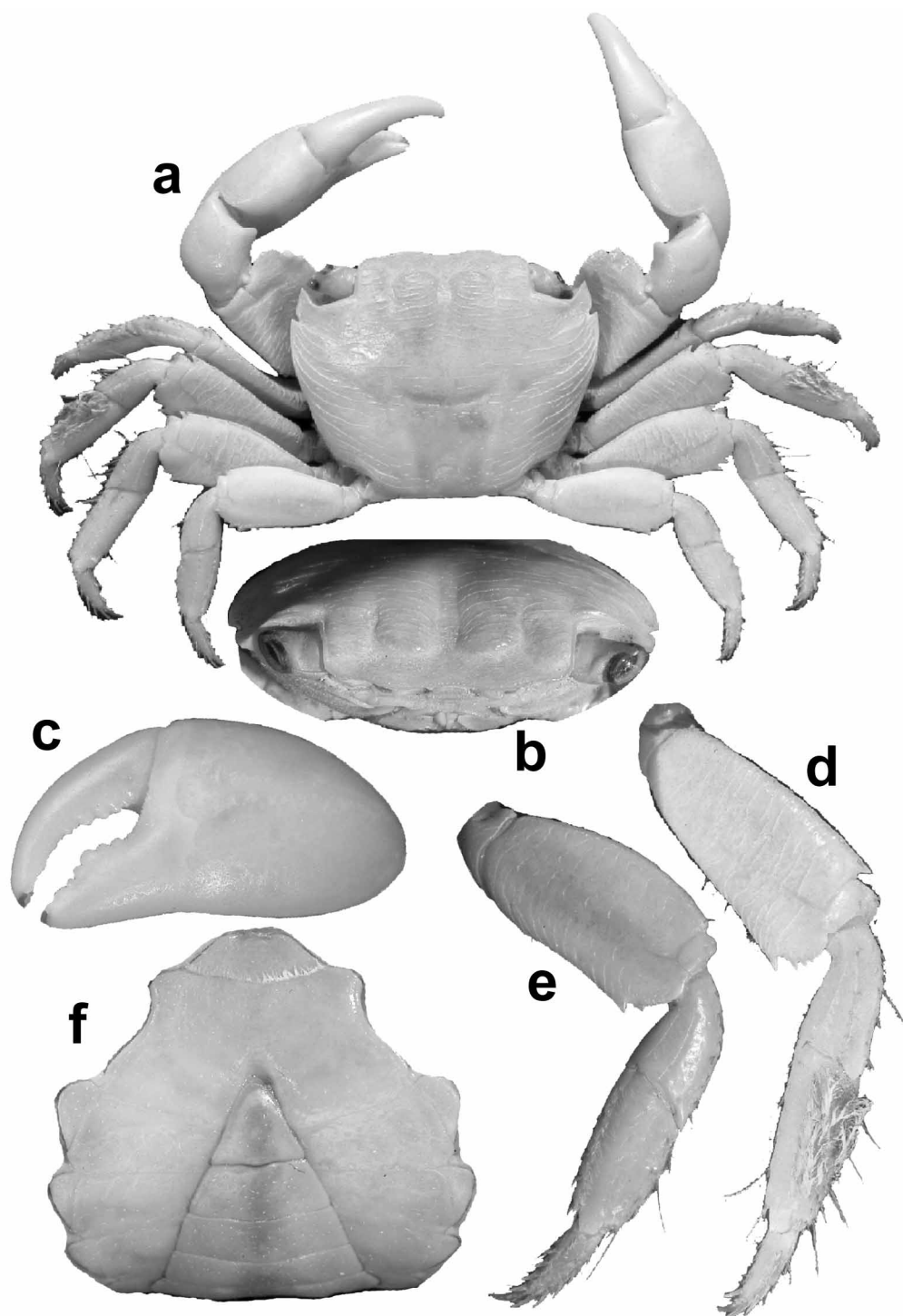
Chelipeds equal. Merus striated transversely, inner ventrodiscal lobe denticulated, with 2–6 distinct teeth. Carpus smooth on upper surface; with blunt tooth at inner distal angle. Chelae robust, height about half length (Fig. 5c). Upper margin rounded, with faint oblique striae proximally, on inner side. Outer face smooth, regularly convex; smaller specimens with weak longitudinal line on outer face of fixed finger, near lower margin. Inner surface of palm smooth. Fingers about two third as long as palm, narrowly gaping, tip corneous, spoon-like, glabrous. Cutting margin of fixed finger with 6–7 triangular teeth, larger medially; moveable finger with 3–4 triangular teeth proximally.

Ambulatory legs robust. Meri with faint transverse ridges on outer surfaces; upper margins with few moveable spines on distal half; P2–P4 with strong dorsodistal tooth, dorsodistal angle of P5 rounded or only with small tooth; lower margins unarmed except for 2–3 spines at distal angles. Dactyli slightly curved, armed with several long moveable spines, terminating in strong corneous claw. P2 propodus with row of setae on dorsal margin. P3 propodus with conspicuous brush of setae on dorsal margin (Fig. 5d); on some specimens this brush may be poorly developed or even missing. Lower margin of P5 merus slightly denticulate, usually without sub-median tubercle (Fig. 5e), except on few of smallest specimens (less than 8 x 10 mm).

Abdominal tergites and thoracic sternites smooth (Fig. 5f). Sixth somite of abdomen plus telson triangular in male. G1 (Fig. 15b) stout with distal process horn-like, strongly curved.

Colour: live colour is dark brown to black, slightly paler along transverse striations, often with paler cardiac and intestinal regions and a few small paler patches surrounding the metagastric region; chelae with inner face becoming lighter in colour ventrally and distally with tips of fingers pale.

Measurements: medium size; carapace of specimens examined ranging from: males 3.5 x 4.6–18.0 x 21.7 mm; females 4.5 x 5.8–13.9 x 17.0 mm; smallest ovigerous female was 4.5 x 5.8 mm.



**FIGURE 5.** —*Pachygrapsus laevimanus* Stimpson, 1858. Neotype male 18.0 x 21.7 mm (AM P7478): a) dorsal view; b) front; c) left chela, outer face; d) right P3; e) right P5; f) abdomen.

*Distribution*

**Eastern Australia** (New South Wales, southern Queensland, Victoria); **Tasman Sea** (Middleton and Elizabeth Reefs), Norfolk and Lord Howe islands; **French Polynesia, Austral Is.** (Rapa I.); ? **Easter I.** Between latitude 26–37°S, longitude 149°E–144°W (Fig. 16).

*Habitat*

Found in the intertidal zone among small rocks and stones, dead coral, rubble, and seaweeds.

*Remarks*

*Pachygrapsus laevimanus* is morphologically close to *P. transversus* (Gibbes, 1850) of similar size, especially in the shape of the carapace and chelae. The setation of the ambulatory legs, however, differs conspicuously between the two species. There is a brush of setae on the P2 propodus in *P. transversus* (obvious in females only), whereas it is located on P3 in *P. laevimanus*. The shape of the G1 is also very different between the two species, with the tip slender and petal-like in *P. transversus* instead of stout and horn-like in *P. laevimanus* (Fig. 15b, l).

*Pachygrapsus laevimanus* was poorly described by Stimpson (1858) from specimens collected in the vicinity of Sydney. As a result, this species was ignored for many years and often confused with *P. transversus* (Gibbes, 1850), a species with a wide distribution in the Mediterranean, east and west Atlantic, and east Pacific. Holthuis & Gottlieb (1958) were the first to point out the existence of *P. laevimanus* from specimens collected near Sydney in 1955. Davie (2002) correctly listed *P. laevimanus*, giving its distribution as New South Wales, Queensland, and Norfolk I. The specimens collected from Rapa I. greatly extend eastward the distribution of *P. laevimanus*. In French Polynesia at least, the species seems to be confined to subtropical latitudes. It is one of the commonest intertidal crabs in Haurei Bay, Rapa I. (28°S) but it has never been observed in the Austral Is., which are situated at more northern latitudes (Raevavae I., 24°S; Tubuai I., 23°S).

*Pachygrapsus laevimanus* may also be present much further east on Easter I. at the same latitude as Rapa I. Similarities between the decapods of the two islands have been shown by Poupin (2003). A *Pachygrapsus* female collected in 1904 on Easter I. (USNM 33186) and attributed to *P. transversus* by Rathbun (1907) shows that although very similar to *P. transversus* of the same size and sex from the Atlantic, it differs slightly in the setation of the ambulatory legs. Females of *P. transversus* from the Atlantic have a slight brush of setae on the P2 propodus and no setae on the P3 propodus, whereas on the Easter I. female there is no brush on P2 and a faint one on P3, a characteristic of *P. laevimanus*. Unfortunately, no male specimen of *P. transversus* was available from Easter I. to confirm this identification. Garth (1973) confirmed the presence of *P. transversus* on Easter I. but did not mention the shape of the G1 and did not compare his specimens with *P. laevi-*

*manus*. Garth's Easter I. specimens have not been located in several collections (CAS, LCMN, SIO, USNM). Other specimens from Easter I. attributed to *P. transversus* by Báez & Ruiz (1985), and deposited in the MNHNS collections, were not available for this study. While the morphology of the G1 should confirm the identification, it seems most likely that *P. laevimanus*, not *P. transversus*, is found in Easter I.

***Pachygrapsus loveridgei* Chace, 1966 (Figures 6a–e, 14i, 15i)**

*Pachygrapsus loveridgei* Chace, 1966: 640, fig. 9–10 [type locality: St. Helena I.]. —Manning & Chace, 1990: 66 (Ascension I.).

*Pachygrapsus transversus* —Miers, 1881: 432 (Ascension I.) [Not *Pachygrapsus transversus* (Gibbes, 1850)].

*Type material*

Male holotype 10.3 x 13.1 mm (USNM 112457) and 6 paratypes (USNM 112467).

*Material Examined*

**Central Atlantic. St. Helena I.:** Rupert's Bay, on buoy cable, coll. A. Loveridge, 18 March 1960, 1 M 10.3 x 13.1 mm (Holotype USNM 112457); 11 February 1963, 3 M 5.5 x 6.8–7.7 x 9.5 mm, 1 F 6.2 x 7.9 mm, 2 ov. F. 5.0 x 6.7, 7.2 x 8.6 mm (Paratype USNM 112467); 1 M 8.1 x 10.0 mm (MNHN B17836).

*Diagnosis*

Carapace dorsal surface markedly convex; with glabrous striae on protogastric, hepatic, branchial region; mesogastric, cardiac, intestinal region smooth or with only few short striae (Fig. 6a). Lateral margins convergent posteriorly, with only one tooth behind exorbital angle. Anterior margin of front sinuous, 0.5 times exorbital width (Fig. 6b). Infraorbital margin minutely denticulate, with shallow outer notch (Fig. 14i).

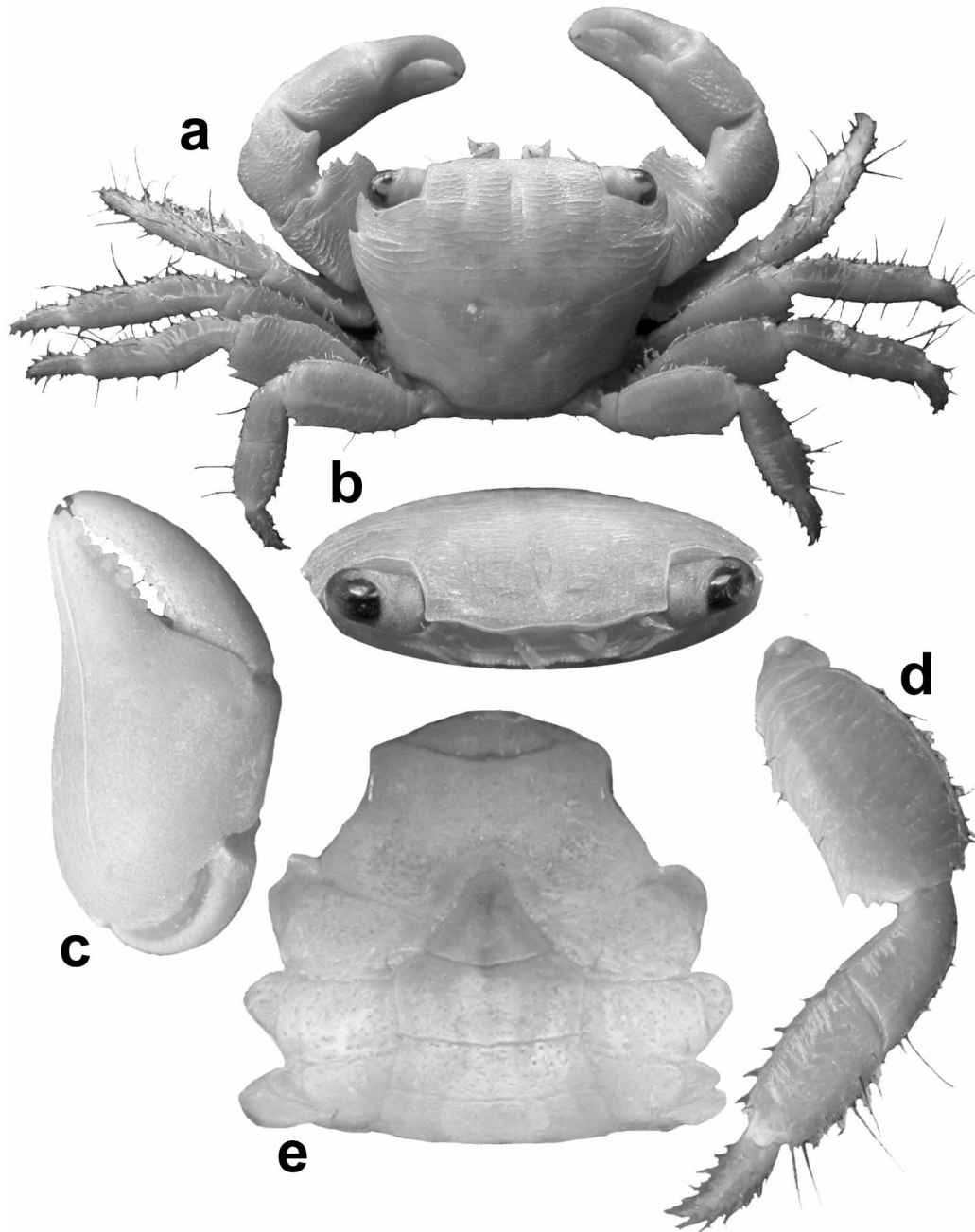
Outer face of chelae regularly convex, smooth except for conspicuous longitudinal line near lower margin, running nearly entire length of palm to tip of fixed finger (Fig. 6c). Cutting edges of fingers narrowly gaping, with several triangular teeth. Tip of fingers corneous, spoon-like, glabrous.

Ambulatory legs with several scattered long bristles. P2 propodi with plumose setae on anterodorsal surface, forming light brush of setae. Lower margin of P5 with 1–3 submedian tubercles; distoventral angle with 2–3 spines (Fig. 6d).

Abdominal tergites smooth; sixth somite of male broadly subrectangular, not triangular with telson (Fig. 6e). Distal process of G1 stout, sickle-like tip (Fig. 15i).

Colour: Live coloration unknown. Chace (1966: 643) indicated the colour of freshly preserved specimens as “the carapace is mottled grayish brown with all transverse striae dark brown; chelipeds dark reddish brown dorsally, fading to light tan on outer surface of

palm and to nearly white near tip of fingers; ambulatory legs mottled with brown, gray, and tan, proximal and distal ends of propodus and proximal end of dactyl nearly white, giving banded appearance to legs.”



**FIGURE 6.** —*Pachygrapsus loveridgei* Chace, 1966. a) dorsal view; b) front; c) left chela, outer face; d) right P5; e) male abdomen. a, d, holotype male 10.3 x 13.1 mm, St. Helena I. (USNM 112457); b, c, e, male 8.1 x 10 mm, St. Helena I. (MNHN B17836).



Measurements. Medium size; carapace of specimens examined ranging from 5.0 x 6.7–10.3 x 13.1 mm. Chace (1966) and Manning & Chace (1990) indicated that cl varies between 1.9–12.4 mm, with 3.2 mm for the smallest ovigerous females.

#### *Distribution*

**Central Atlantic:** Ascension and St. Helena islands.

#### *Habitat*

Intertidal, but also on buoys, associated with barnacles, from near the surface to 7 meters.

#### *Remarks*

*Pachygrapsus loveridgei* is morphologically close to *P. transversus* (Gibbes, 1850). Both species have only one tooth on the lateral margins of the carapace behind exorbital angle, a conspicuous line on the outer face of the chelae near the lower margin, a brush of setae on the P2 propodi, and a male abdomen that is not apically triangular. *P. loveridgei* is smaller in size, the carapace is more convex, and the chitinous terminal portion of the G1 is broadly sickle shaped, rather than obliquely T-shaped as in *P. transversus* (Fig. 15i, l).

Chace (1966: 644) indicated that 85 of the 211 specimens examined from St. Helena I. were found living near the surface on a buoy. This sporadic semi-pelagic way of life, along with its small size and markedly convex carapace, suggest affinities with species of *Planes* Bowdich, especially *Planes marinus* Rathbun, 1911, a species at one time included *Pachygrapsus* (see Chace, 1951).

#### ***Pachygrapsus marmoratus* (Fabricius, 1787) (Figures 7a–e, 14j, 15j)**

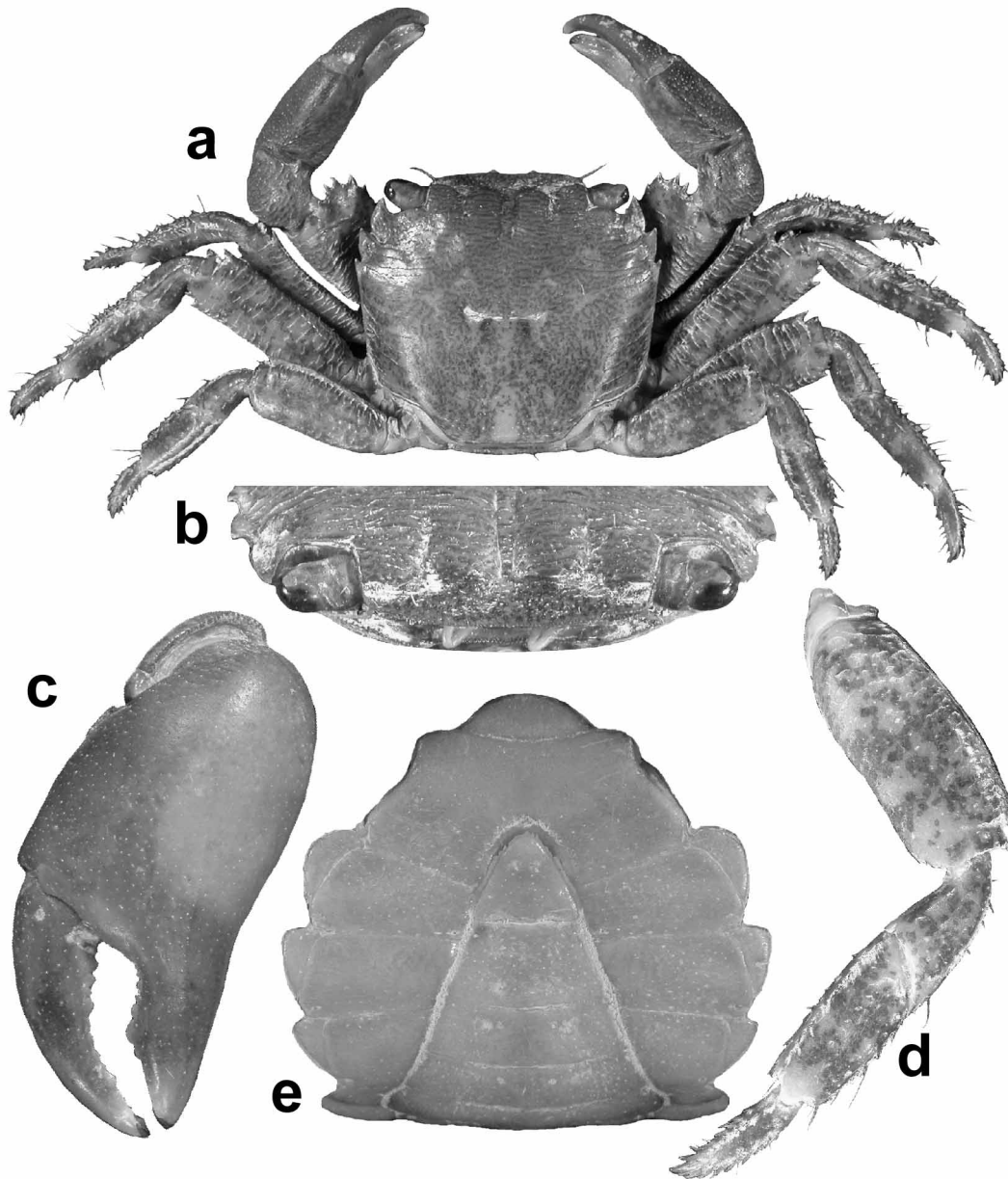
*Cancer marmoratus* Fabricius, 1787: 319 [type locality: unknown]

*Grapsus varius* Latreille, 1803: 67 (Mediterranean). —H. Milne Edwards, 1837: 88 (Brittany, Italy).

*Leptograpsus marmoratus* —H. Milne Edwards, 1853: 171 (Mediterranean)

*Pachygrapsus marmoratus* —Stimpson, 1858: 48 [102] (Madeira); 1907: 116 (Madeira). —Heller, 1863: 111, pl. 3 fig. 8-10 (Mediterranean). —Kingsley, 1880: 201 (France, Bosphorus). —Ortmann, 1894: 710 (Mediterranean). —Rathbun, 1918: 250, fig. 138, pl. 62 (Biarritz, France; Azores; synonymy). —Pesta, 1918: 451, fig. 149 (Adriatic). —Fauvel, 1929: 3 (Cotentin Peninsula). —Nobre, 1931: 103, fig. 1, 58, 59 (Portugal); 1936: 61, fig. 1 (Portugal). —Bouvier, 1940: 259, fig. 179, pl. 11, fig. 4 (warm temperate Northeast Atlantic, Mediterranean, Black sea). —Zariquiey Álvarez, 1946: 163, pl. 18, fig. e; 1968: 423, fig. 140a, 141b–e (Spain). —Holthuis & Gottlieb, 1958: 100, pl. 3, fig. 15 (Mediterranean coast of Israel; references, distribution). —Bourdon, 1965: 32 (Brittany). —Băcescu, 1967: 326, fig. 56, 138b, 139, 140a (Romania). —Ingle, 1980: 121, fig. 24, 72, 74, pl. 23b (British Channel). —González Gurriarán & Méndez, 1985: 149, fig. 56, photo 44 (Galicia). —Moyse & Smaldon, 1990: 551, fig. 10.28 (English Channel). —Falciai & Minervini, 1992: 234, pl. 16. —d'Udekem d'Acoz, 1994: 35 (Greece); 1999: 255 (references, distribution, ecology); 2005 (photographs, refer-

ences, distribution). —González Pérez, 1995: 223, photo 163 (Canary Is.). —Vincent & Le Granche, 1996: 173 (Cotentin peninsula, France). —Debelius, 1999: 103, photograph.  
 ? *Pachygrapsus pubescens* Heller, 1865: 45, pl. 4, fig. 4 [type locality, Chile; probably erroneous, see remarks]. —Kingsley, 1880: 201 (in list). —Rathbun, 1918: 252, pl. 160, fig. 1 (Chile; from Heller only). —Garth, 1957: 96 (in list). —Retamal, 1981: 35, fig. 192 (in list). —Boschi, 2000: 103 (in list). See remarks.



**FIGURE 7.** —*Pachygrapsus marmoratus* (Fabricius, 1787). Male 24.5 x 26.8 mm, Tunisia (USNM 258082): a) dorsal view; b) front; c) left chela, outer face, d) right P5, e) abdomen.

### Type material

*Cancer marmoratus* Fabricius, 1787: not located, probably not extant.

*Pachygrapsus pubescens* Heller, 1865: syntypes 1 M, 2 F (NHMW, 10263), 1 M, 1 F (NHMW, 10264). C. Schubart (pers. comm.) will designate a lectotype in a forthcoming paper.

### Material Examined

**Mediterranean Sea. Tunisia:** Gabès, port, coll. R. B. Manning *et al.*, 6 June 1973, 2 M 21.9 x 24.7, 24.5 x 26.8 mm, 1 ov. F 28.2 x 32.4 mm (USNM 258082). **Italy,** Sicily, Trapani, rocky flat south of and outside harbour, coll. R. B. Manning, 20 June 1974, 5 M 5.6 x 7.2–12.1 x 13.8 mm, 1 ov. F 16.0 x 18.1 mm, 4 F 5.9 x 6.8–6.9 x 8.8 mm (USNM 152262). **East Atlantic. France,** Prèfailles, coll. P. Chalumeau, August 1991, 1 F 12.7 x 14.3 mm (MNHN B22654).

### Diagnosis

Carapace subquadrate; lateral margins with 2 teeth behind exorbital angle. Dorsal surface flattened with transverse striae on gastric, hepatic, branchial regions; mesogastric, cardiac, intestinal regions smooth or with short striae (Fig. 7a). Anterior margin of front almost straight, 0.6 times width of exorbital length (Fig. 7b). Infraorbital margin deeply denticulated medially, outer notch deep, obliquely oriented (Fig. 14j).

Outer face of chelae regularly convex, smooth, or with an unclear longitudinal line near lower margin; upper margin of palm with few oblique lines on inner face; cutting edges of fingers broadly gaping, with triangular teeth; tip of fingers corneous, spoon-like, glabrous (Fig. 7c). P2, P3 carpi, propodi with sparse bristles but without brush of setae. P5 merus with lower margin smooth or slightly denticulated, without submedian tubercle; dis-toventral angle without spines, rounded or slightly indented (Fig. 7d).

Abdominal tergites smooth; sixth somite of abdomen plus telson triangular in male (Fig. 7e). G1 distally rounded with short corneous process (Fig. 15j).

Colour (d'Udekem d'Acoz, pers. comm.): two basic but overlapping colour patterns. Either fine purplish-black reticulations on a whitish background, or almost plain purplish black with a few small irregular white variegations.

Measurements: large size; carapace of specimens examined ranging from 5.6 x 7.2–28.2 x 32.4 mm; carapace width of 40 mm is common.

### Distribution

**West Atlantic, Mediterranean and Black seas:** Azores, Madeira, Canary Is., European coast from Bay of Biscay to Morocco, Mediterranean Sea, Sea of Marmara, Black Sea. *Pachygrapsus marmoratus* was occasionally reported from the French coast of the English Channel: Brittany (Bourdon, 1965), and twice the Cotentin peninsula (Fauvel, 1929; Vincent & Le Granche, 1996). It is possible that Fauvel's specimen was accidentally

introduced from the south by fishermen. It is not ruled out that the identification by Vincent & Le Granche (1996) results from confusion with *Hemigrapsus sanguineus* (de Haan, 1835) (P. Noël, field observation and pers. comm.). The female specimen of Vincent & Le Granche is lost. Noël found in 2004 several specimens of *H. sanguineus* at Saint-Vaast-la-Hougue, France but none of *P. marmoratus*.

#### *Habitat*

Intertidal; rocky shores and under stones on sandy mud in estuaries and lagoons. Very common in southern Europe.

#### *Remarks*

Besides *P. marmoratus* only *P. pubescens* Heller, 1865, a little-known species from Chile, has two teeth behind the exorbital angle. The syntypes of *P. pubescens* (1 male, 2 females NHMW 10263; 1 male, 1 female NHMW 10264) were not examined. C. Schubart re-examined them and in a forthcoming paper will show that *P. pubescens* is a junior synonym of *P. marmoratus* (C. Schubart, pers. comm.). P. Dworschak (pers. comm.) has suggested that the type locality could be Gibraltar rather than Chile as indicated by Heller.

Two small specimens from Juan Fernandez Is., Chile identified by M. J. Rathbun as *P. pubescens* were examined (coll. W. L. Schmitt, along boulder covered beach to left of cannery, littoral, 8 December 1926, 2 juv. 4.5 x 4.7–4.5 x 4.9 mm, USNM 70847). These juveniles are in poor condition but can be identified as *Leptograpsus variegatus* (Fabricius, 1793), a species widespread in the South Pacific, from Australia to South America, including Chile.

#### ***Pachygrapsus maurus* (Lucas, 1846) (Figures 8a–e, 14k, 15k)**

*Grapsus maurus* Lucas, 1846: 20, vol. 4, pl. 2, fig. 5 [type locality: Oran, Algeria]

*Leptograpsus maurus* —H. Milne Edwards, 1853: 173 (Algeria).

*Pachygrapsus simplex* —Stimpson, 1858: 48 [102] (Madeira); 1907: 116 (Madeira).

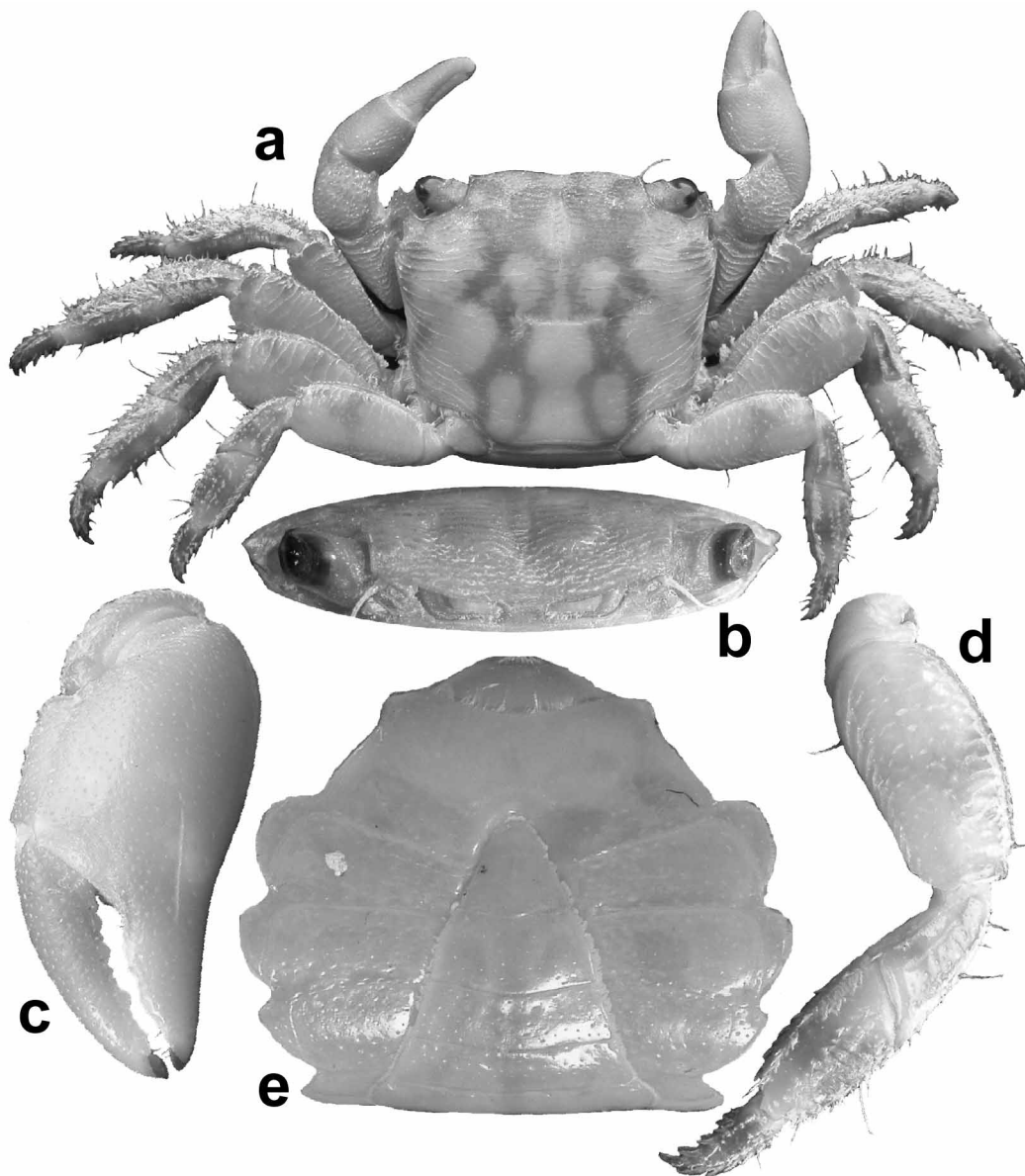
*Pachygrapsus maurus* —Heller, 1863: 112 (Algeria). —Kingsley, 1880: 199 (Key; synonymy). —Rathbun, 1918: 244 (Azores, Canary Is.; synonymy). —Bouvier, 1940: 290, fig. 180 (Algeria, Madeira, Azores). —Zariquiez Álvarez, 1948: 291, pl. 24, fig. 1-2 (Spain); 1968: 425, fig. 140b, 141a (Spain). —Falcaï & Minervini, 1992: 234. —d'Udekem d'Acoz, 1994: 36 (Greece); 1999: 255, unnumbered fig. p. 52 (references, distribution, ecology); 2005 (photographs, reference, distribution). —González Pérez, 1995: 223, photo 164 (Canary Is.).

#### *Type material*

Probably not extant. According to Rathbun (1918: 244) the type was at MNHN but the first author was unable to locate it.

*Material Examined*

**Central Atlantic. Azores:** São Miguel I., coll. Collette & R. B. Manning, 13 March 1963, 1 M 9.0 x 10.4 mm (USNM 170343). Terceira I., unknown coll., 1 F 6.5 x 7.7 mm (USNM 18627; see remarks).



**FIGURE 8.** —*Pachygrapsus maurus* (Lucas, 1846). a) dorsal view; b) front; c) left chela, outer face, d) right P5, e) male abdomen. a, c, d, female 12.7 x 14.3 mm, Banyuls-sur-Mer, France (MNHN B12933), b, e, male 8.5 x 9.9 mm, Gran Canaria I. (USNM 44529).

**East Atlantic. Madeira:** Funchal, J. Panousse, 1973, 2 M 8.7 x 10.0, 9.6 x 10.7 mm (MNHN B12931). **Canary Is.:** Gran Canaria, Guia I., coll. U.S. Fish Commission, September 1894, and unknown coll., September 1994, 3 M 6.7 x 7.9–9.2 x 10.4 mm, 1 ov. F 7.4–8.2 mm, 4 juveniles (USNM 44529). **Mediterranean Sea. France:** Banyuls, coll. and det. J. Forest, 1 F 12.7 x 14.3 mm (MNHN B12933); Spain, Cadaqués, coll. and det. J. Forest, July 1955, 4 M 6.9 x 8.4–9.4 x 10.6 mm, 1 ov. F 6.0 x 7.0 mm (MNHN B12932).

#### *Diagnosis*

Carapace with glabrous striae on gastric, hepatic, branchial regions; mesogastric, cardiac regions with shorter, fainter striae, intestinal region almost smooth; lateral margins weakly convergent posteriorly with tooth behind exorbital angle (Fig. 8a). Front 0.6 times exorbital width; anterior margin sinuous (Fig. 8b). Infraorbital margin slightly denticulated on inner half, almost smooth on outer half; outer notch deep, obliquely oriented (Fig. 14k).

Outer face of palm regularly convex with numerous small pits; distal half with faint stria above lower margin (Fig. 8c); dorsal margin of palm rounded with faint oblique lines on inner face; cutting edges of fingers with triangular teeth, tip of fingers corneous, spoon-like, glabrous (Fig. 8c). P2–P3 propodi without brush of setae, at most with a denser area of stiff setae on smallest specimens. Lower margin of P5 merus smooth; distoventral angle rounded or feebly indented (Fig. 8d).

Abdominal tergites smooth. Sixth somite of abdomen plus telson triangular in male (Fig. 8e). G1 bluntly rounded with a low corneous gutter-like process (Fig. 15k).

Colour (d'Udekem d'Acoz, pers. comm.): Large round bluish/greyish or pale yellowish spots on a black background. In some specimens the spots are confluent.

Measurements: medium size; carapace of specimens examined ranging from 6.5 x 7.7–12.7 x 14.3 mm, smallest ovigerous female 6.0 x 7.0 mm. D'Udekem d'Acoz (2005) indicates a cw of about 20 mm.

#### *Distribution*

**West Atlantic and Mediterranean.** Azores, Madeira, Canary Is. (common), Mediterranean. Patchy distribution as a result of the rarity of suitable habitats.

#### *Habitat*

Intertidal on rocks and cliffs with strong wave exposure (d'Udekem d'Acoz, 2005).

#### *Remarks*

*Pachygrapsus maurus* appears more closely related to species of *Pachygrapsus* that have no brush of setae on the P2 or P3 propodi. This brush of setae was absent on most of the specimens examined, however. It seems to be a juvenile character that disappears in adults because it was found in the three smallest specimens examined: female 6.5 x 7.7 mm, Terceira (USNM 18627), and two males 6.9 x 8.4, 7.4 x 8.4 mm, Cadaqués, Spain (MNHN B12932).

*Pachygrapsus maurus* and *P. marmoratus* occur sympatrically in the Azores, Madeira, Canary Is., and the Mediterranean. *Pachygrapsus maurus* is smaller (cw about 20 mm) than *P. marmoratus* (cw about 40 mm), and it has only one tooth behind the exorbital angle instead of two in *P. marmoratus*.

*Pachygrapsus maurus* is morphologically close to *P. transversus*, but *P. transversus* is larger than *P. maurus*. The G1 is clearly distinct, with a petal-like tip in *P. transversus* (Fig. 15l) instead of bluntly rounded with a short corneous process in *P. maurus* (Fig. 15k). Small females of these two species are more difficult to separate on a morphological basis. A small female of *P. maurus* from the Azores (USNM 18627) showed a brush of setae on the P2 propodi, and was thus very similar to females of *P. transversus* of similar size. It was identified as *P. maurus* because the distoventral angles of the P5 merus are rounded, without spines, whereas *P. transversus* has 3–4 spines.

### ***Pachygrapsus minutus* A. Milne-Edwards, 1873 (Figures 9a–d, 14c, 15c)**

*Pachygrapsus minutus* A. Milne-Edwards, 1873a: 292, pl. 14, fig. 2 [type locality: New Caledonia]. —Cano, 1889: 240 (Hawaiian Is.). —Alcock, 1900: 399 (Mergui Archipelago). —Rathbun, 1906: 840 (Hawaiian Is.); 1907: 30 (Tuamotu Archip.; Caroline Is.); 1911: 242 (Seychelles). —Tesch, 1918: 77 (Celebes; synonymy). —Balss, 1934a: 229 (Christmas I.; synonymy). —Boone, 1934: 180, pl. 91 (Samoa). —Tweedie, 1936: 46 (Christmas I.); 1950a: 94 (Malaysia). —Schmitt, 1939: 22 (Clipperton). —Holthuis, 1953: 31 (Kiribati); 1977: 158 (Red Sea). —Hertlein & Emerson, 1957: 5 (Clipperton). —Edmonson, 1959: 171 (Fiji, Samoa, Line Is., Hawaiian Is.). —Forest & Guinot, 1961: 155 (Society Is., Tuamotu Archip.). —Crosnier, 1965: 26, fig. 23, 29–30 (Madagascar). —Garth, 1965: 27, fig. 14 (Clipperton); 1992: 4 (Revillagigedo Is.). —Chace, 1966: 644, fig. 11e (Caroline Is.; synonymy). —Sakai, 1976: 635, fig. 347a–c (Japan). —Monteforte, 1984: 172, annex 1, tab. a (Society Is., Tuamotu Archip.); 1987: 9 (Society Is.). —Peyrot-Clausade, 1985: 462 (Society Is.); 1989: 113 (Tuamotu Archip.). —Dai & Yang, 1991: 510 (China sea). —Ng *et al.*, 2001: 41 (Taiwan; references). —Davie, 2002: 218 (Christmas I., Ashmore and Cartier Is., Middleton and Elizabeth reefs). —Ng & Davie, 2002: 379 (Thailand). —Paulay *et al.*, 2003: 495 (Mariana Is.). —Yeo *et al.*, 2004: 88 (Anambas Is., South China Sea).

*Sesarma murrayi* Calman, 1909: 708 (Christmas I.).

*Pachygrapsus murrayi* —Ward, 1934: 25 (Christmas I.).

#### *Type material*

Five males syntypes, 5.9 x 8.0–7.6 x 10.4 mm, poor condition (MNHN B3582). Male 7.6 x 10.4 mm is herein designated as lectotype, the remaining four specimens as paralectotypes.

#### *Material Examined*

**New Caledonia:** Types specimens, coll. M. Balansa, 5 M 5.9 x 8.0–7.6 x 10.4 mm (poor condition) (dry collection, MNHN B3582).

**Caroline Is. Palau:** landward from Ngchesau reef, supra-tidal karst, exposure on top of reef, coll. G. Paulay, 7 March 2003, 1 ov. F 7.2 x 10.3 mm (UF 3882). —**Yap:** Maap I.,

high intertidal, under rocks and plant debris, coll. G. Paulay, 1 April 2000, 1 M 3.6 x 5.1 mm (UF 8000).

**Mariana Is. Saipan:** Garapan pier, reef flat, under rocks 1 m, coll. J. Stammer, 15 November 1997, 1 M 6.6 x 9.4 mm, 4 F 5.2 x 7.4–6.1 x 8.7 mm (UF 590). —**Guam:** 13°26.74'N, 144°39.54'E, Apra Harbor on mooring buoy 16, 0–10 m, coll. G. Paulay, 23 August 2000, 1 M 6.4 x 8.7 mm (UF 3173); Tagachang reef flat, intertidal, under rocks, coll. G. Paulay, 6 July 1997, 2 M 4.4 x 6.3, 5.9 x 8.5 mm (UF 123).

**Niue:** Alofi, Utuko reef flat, exposed on reef surface, coll. B. Holthuis & G. Paulay, 13 September 1991, 1 M 3.5 x 5.4 mm (UF 2246), 1 F 4.4 x 6.6 mm (UF 2250).

**French Polynesia. Gambier Is.:** Aukena I., intertidal, RV *Marara* campaign, coll. J. Poupin, April 1995, 1 ov. F 5.7 x 8.0 mm MNHN (B29270). —**Society Is.:** Tahiti, intertidal, RV *Marara* campaign, coll. J. Poupin, November 1995, 1 M 4.2 x 5.4 mm (MNHN B29271). —**Marquesas Is.:** Nuku Hiva I., Taiohae Bay, intertidal, RV *Marara* campaign, coll. J. Poupin, 9 February 1996, 1 ov. F 3.2 x 5.0 mm (MNHN B29272). —**Tuamotu Archip.:** Moruroa Atoll, lagoon, intertidal in rubbles, RV *Marara* campaign, coll. J. Poupin, October 1995, 8 M 4.0 x 5.6–5.2 x 7.0 mm, 6 ov. F 3.3 x 4.7–5.7 x 8.0 mm, 5 F 3.3 x 4.8–4.9 x 7.0 mm (MNHN B29273).

**Clipperton Atoll.** Among rocks at low tide, Jean-Louis Etienne Expedition to Clipperton, coll. J. Poupin, February 2005, 13 M 4.0 x 5.5–7.5 x 9.0 mm, 1 ov. F 4.0 x 5.0 mm, 8 F 3.5 x 5.0–8.0 x 10.0 mm (MNHN B29860).

### *Diagnosis*

Small-size species. Carapace subtriangular, lateral margins strongly convergent posteriorly with no tooth behind external orbital angle (Fig. 9a). Dorsal surface weakly convex with faint transverse striae on protogastric, hepatic, branchial regions; striae without setae or only few; mesogastric region smooth or with few striae; cardiac, intestinal regions smooth. Front 0.5 times width at exorbital angles; anterior margin sinuous (Fig. 9b). Infraorbital margin minutely dentate over entire length, separated from exorbital tooth by very low indentation (Fig. 14c).

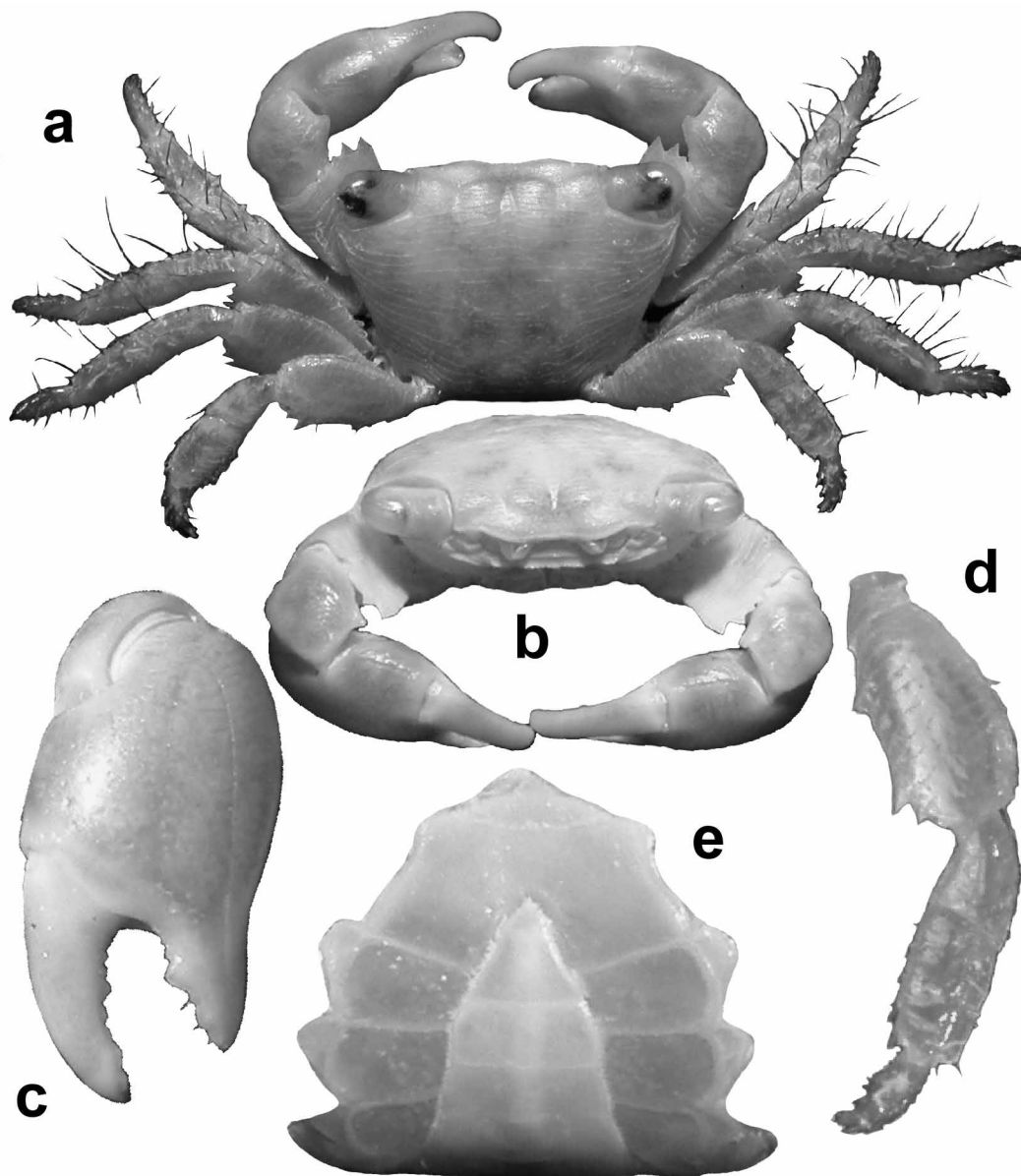
Chelipeds equal. Outer faces of chelae regularly convex, with faint longitudinal striae near lower margins, extending to fixed finger; tip of fingers spoon-like, without setae (Fig. 9c). Dorsal margins of P2–P4 carpi, propodi with scattered long setae; woolly tomentum on P2 carpi, propodi of females, juveniles. Lower margin of P5 merus with 1–2 submedian tubercles and 2 spines of unequal size at distal angle (Fig. 9d).

Abdominal tergites smooth; sixth somite of abdomen plus telson triangular in male (Fig. 9e). G1 rounded at tip with short gutter-like process at tip, vertically oriented (Fig. 15c).

Colour (from Clipperton specimens): carapace and legs with large and irregular patches of brown on a white to cream background. The brown patches form more or less transverse bands on the segments of the ambulatory legs.



Measurements: small size; carapace usually about 5 x 7 mm; carapace of specimens examined ranging from: males 3.5 x 5.4–6.6 x 9.4 mm; females 3.3 x 4.4–7.2 x 10.3 mm; smallest ovigerous female is 3.2 x 5.0 mm.



**FIGURE 9.** —*Pachygrapsus minutus* A. Milne-Edwards, 1873. Male 4.3 x 5.9 mm Moruroa, French Polynesia (MNHN B29273): a) dorsal view; b) front; c) right chela, outer face; d) right P5; e) abdomen.

*Distribution*

**Indo-West Pacific from Red Sea to Mexican oceanic islands:** Madagascar, Thailand, Indonesia, Australia, China, Japan, west and east Pacific islands (Caroline Is., Mari-

ana Is., Fiji, Niue, Kiribati, Samoa, Hawaiian Is., Line Is., French Polynesia, Clipperton, Revillagigedo Is.).

#### *Habitat*

Rocks and rubble in the intertidal zone.

#### *Remarks*

*Pachygrapsus minutus* is conspicuous by its small size. It is morphologically close to the similar-sized *P. planifrons* De Man, 1888, but the two can be easily separated. The front is straighter in *P. planifrons* (Fig. 9b, 10b) than in *P. minutus*, the tips of the cheliped fingers are furnished with setae in *P. planifrons* but are absent in *P. minutus* (Fig. 9c, 10c), the submedian tubercle on the lower margin of the P5 merus is absent in *P. planifrons* (Fig. 9d, 10d), and the G1 has a rounded tip with a short vertical gutter-like process in *P. minutus* (Fig. 15c) instead of a petal-like tip in *P. planifrons* (Fig. 15d). *Pachygrapsus minutus* is also morphologically close to *P. propinquus* De Man, 1908. The similarities between the two are discussed under *P. propinquus*.

#### ***Pachygrapsus planifrons* De Man, 1888 (Figures 10a–f, 14d, 15d)**

*Pachygrapsus planifrons* De Man, 1888: 368, pl. 16, fig. 2 [type locality: Noordwachter Island = Jaga Utara, Java Sea off Java, Indonesia, 05°12'S, 106°27'E]. —De Man, 1908: 218 (remarks on *P. longipes* status). —Tesch, 1918: 77 (Indonesia; synonymy). —Ward, 1934: 25 (Christmas I.). —Tweedie, 1936: 45 (Christmas I.); 1950b: 130 (Cocos-Keeling Is.). —Holthuis, 1953: 31 (Kiribati; Tuamotu Archip.). —Edmonson, 1959: 173, fig. 10b (Hawaiian Is.; synonymy). —Garth, 1965: 30, fig. 15–16 (Clipperton). —Chace, 1966: 644, fig. 11f (Hawaiian Is.; synonymy). —Chen, 1980: 139: fig. 22, pl. IV-3 (Paracel Is.). —Dai & Yang, 1991: 510, fig. 261 (Hainan). —Ng & Davie, 2002: 379 (Thailand). —Paulay *et al.*, 2003: 495 (Guam). —Komai *et al.*, 2004: 34 (Japan). —Yeo *et al.*, 2004: 88 (Anambas Is., South China Sea).

*Pachygrapsus longipes* Rathbun, 1893: 247 (Hawaiian Is.). —Rathbun, 1906: 840 (Hawaiian Is.); 1907: 30 (Fakarava Atoll, Tuamotu Archip.); 1911: 242 (Seychelles).

*Pachygrapsus laevis* Borradaile, 1900: 592, pl. 42, fig. 7 (Tuvalu; new synonymy see remarks). —Tesch, 1918: 76 (Key).

#### *Type material*

Presumably lost. According to C. H. Fransen (pers. comm.) the syntypes were probably deposited at Göttingen (ZMG), but are not found there (G. Tröster, pers. comm.), nor are they part of the material that was transferred from Göttingen to Frankfurt (SMF). The Göttingen collection was in poor condition before being transferred to Frankfurt, and a number of types of other species also appear to have been lost (M. Türkay, pers. comm.).

#### *Material Examined*

**Mariana Is. Guam:** Bile Bay, supratidal/intertidal, among rocks, common, coll. G. Paulay, 29 March 1998, 2 M 5.1 x 6.3, 5.6 x 6.8 mm (UF 129).

**Caroline Is. Yap:** Maap I., high intertidal, under rocks and plants debris, coll. G. Paulay, 1 April 2000, 1 ov. F 5.2 x 6.7 mm (UF 3849; Photo GP805).

**Tuvalu. Funafuti:** coll. J. S. Gardiner, 1 ov. F 5.1 x 7.2 mm (UMZC Reg.11.01.1897; holotype of *Pachygrapsus laevis* Borradaile, 1900).

**French Polynesia. Tuamotu Archip.:** Fakarava Atoll, coll. RV *Albatross*, 12 October 1899, 1 F 3.6 x 4.9 mm (USNM 33179). —Rangiroa Atoll, Avatoru Motu, ca. at 1.5 km E of Post Office, at Pension Henri, reef flat, under rocks, 0–1 meter, coll. G. Paulay, 10 January 2001, 1 M 7.0 x 9.0 mm, 2 ov. F 5.4 x 7.0–5.6 x 7.3 mm (UF 1490). —Taiaro Atoll, Taiaro Expedition, intertidal, outer reef, 12–20 February 1994, coll. J. Poupin, 1 ov. F 4.6 x 6.0 mm (MNHN B29264).

**Hawaiian Is.:** Honolulu, coll. RV *Albatross*, 1891, 1 ov. F 6.2 x 8.2 mm (USNM 17320, type of *P. longipes* Rathbun, 1893); Honolulu reef, coll. RV *Albatross*, 6 June 1902, 1 M 9.5 x 11.8 mm (UNSM 29350).

**Clipperton Atoll.** Among rocks at low tide, Jean-Louis Etienne Expedition to Clipperton, coll. J. Poupin, February 2005, 6 M 5.5 x 7.0–9.7 x 11.5 mm, 10 ov. F 4.0 x 6.5–9.5 x 12.0 mm, 1 F 4.5 x 5.5 mm (MNHN B29859); reef at low tide, stn 33, coll. L. Albenga, J. M. Bouchard, 25 January 2005, 5 M 6.0 x 7.0–7.0 x 8.5 mm, 1 ov. F 6.5 x 8.0 mm, 1 F 4.5 x 5.5 mm (MNHN B29858).

#### *Diagnosis*

Small-size species. Carapace with concave lateral margins, markedly convergent posteriorly, without tooth behind exorbital angle (Fig. 10a). Dorsal surface flattened, only weakly convex; protogastric, hepatic regions with thin transverse striae, branchial region with oblique striae; all striae glabrous; mesogastric, cardiac, intestinal regions almost totally smooth. Front 0.6 times width at exorbital angles, anterior margin almost straight (Fig. 10b). Infraorbital margin nearly entire, composed of low granules, outer indentation very low; infraorbital margin forming very obtuse angle with inner margin of exorbital tooth (Fig. 14d).

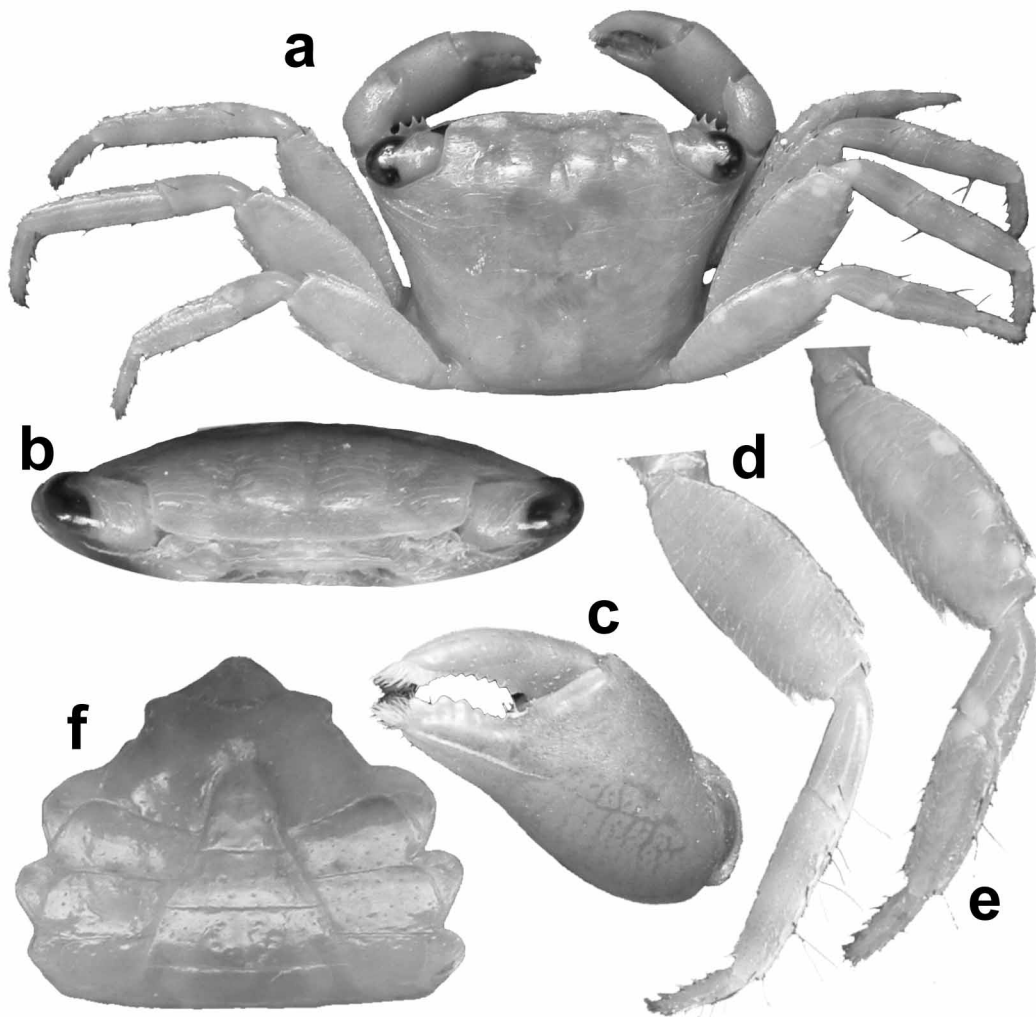
Cheliped merus with 4–5 acute spines at inner distoventral angle. Carpus with sharp inner dorsodistal spine. Outer face of chelae regularly convex; fixed finger with a longitudinal stria extending slightly on outer face of chela; cutting edge with 2–3 large teeth medially and few smaller teeth proximally. Dactyl with 6–8 small teeth over whole length of cutting edge, sometimes indistinct. Tip of fingers spoon-like, with distinctive rows of bristles (Fig. 10c).

Ambulatory legs with scattered long bristles on carpi, propodi, dactyli, but without brush of setae. Upper margins of meri armed with several long mobile spines, lower margins with 1–2 spines (usually 2) at distoventral angles; lower margin of P5 merus smooth, without submedian tubercle (Fig. 10d–e).

Abdominal tergites smooth. Telson of male rounded at tip, longer than sixth somite; telson and sixth somite forming triangle with lateral margins slightly concave (Fig. 10f). G1 slender, petal-like at tip (Fig. 15d; see remarks).

Colour (from Clipperton specimens): brown overall, with darker transverse bands on the ambulatory legs: proximal, median and distal bands on meri (sometimes unclear); proximal and distal bands on carpi and propodi; and median band of variable width on dactyli. Eggs orange red.

Measurements: small size; usual carapace size 5 x 7 mm; greatest size indicated in the literature 9 x 11 mm (Edmondson, 1959; Garth, 1965); specimens examined ranged from: males 5.1 x 6.3–5.6 x 6.8 mm, females 4.6 x 6.0–5.6 x 7.3 mm; smallest ovigerous female 4.6 x 6.0 mm.



**FIGURE 10.** —*Pachygrapsus planifrons* de Man, 1888. Male 7.0 x 9.0 mm, Rangiroa, French Polynesia (UF 1490): a) dorsal view; b) front; c) left chela, outer face; d) right P2; e) right P5; f) abdomen.

### Distribution

**West Indian Ocean to east Pacific islands:** Seychelles; Christmas I., Cocos-Keeling Is.; Thailand, Indonesia; South China Sea (Anambas Is., Hainan I., Xisha or Paracel Is); Japan; Caroline Is.; Mariana Is.; Kiribati; Funafuti; Hawaiian Is.; Tuamotu Archip.; Clipperton.

### Habitat

Common in the high intertidal zone, under rocks and debris.

### Remarks

*Pachygrapsus planifrons* is unique in possessing rows of bristles at the tips of the fingers of the chelae. This character alone is sufficient to distinguish it from all other species of *Pachygrapsus*. It is similar to *P. minutus* in its small size, but the two can be easily separated. The exorbital angle is produced and more spinous in *P. planifrons* than in *P. minutus*, the lateral margins of the carapace are concave in *P. planifrons* but straight in *P. minutus*, the anterior margin of the front is almost straight in *P. planifrons* but sinuous in *P. minutus*, the lower margin of the P5 merus is smooth in *P. planifrons* while having a submedian tubercle in *P. minutus* and the distal end of the G1 has a short vertical gutter-like process in *P. minutus* (Fig. 15c) but a petal-like tip in *P. planifrons* (Fig. 15d).

Chace (1966: 645) indicated that *Pachygrapsus* was in need of revision and figured the gonopods of 8 species in the USNM collection. These figures have been very useful for the present study and some of them are reproduced in Figure 15. Some inconsistencies were found with the figure of the G1 of *P. planifrons* (Chace, 1966: 645, fig. 11f, a male cl 9.5 mm from Honolulu), however. It has a gutter-like tip instead of tulip-like as shown in Figure 15d, even if the G1 illustrated here is from the same specimen as that of Chace, as its size and collection details were the same, and the G1 was already dissected in the jar. We therefore assume that there was a mistake made when Chace's plate was being prepared. The tulip-like shape of the *P. planifrons* G1 was also found in other males examined here, as well as in one illustrated for a Chinese specimen (Chen, 1980: 140, fig. 22-5).

Borradaile (1900: 592, pl. 42, fig. 7) described *P. laevis* from a female collected at Funafuti. The characters described by Borradaile are those of *P. planifrons*, especially the characteristic rows of bristles at the tips of the fingers of the chelae. The type of *P. laevis* (UMZC 11.01.1897) was examined and it can be confirmed that it is a junior synonym of *P. planifrons*.

### ***Pachygrapsus plicatus* (H. Milne Edwards, 1837) (Figures 11a–f, 14e, 15e)**

*Grapsus plicatus* H. Milne Edwards, 1837: 89 [type locality: Hawaiian Is.]. —Krauss, 1843: 43, pl. 3, fig. 1 (Natal).

*Goniograpsus plicatus* —Dana, 1852: 343 (Hawaiian Is.).

- Goniograpsus kraussii* Dana, 1852: 343 (South Africa, Natal; new synonymy, see remarks).  
*Grapsus kraussii* —H. Milne Edwards, 1853: 170 (Natal; see remarks).  
*Pachygrapsus striatus* A. Milne-Edwards, 1873b: 82 (Samoa, Hawaiian Is.; new synonymy, see remarks).  
*Pachygrapsus kraussii* —Stebbing, 1910: 319 (Natal).  
*Pachygrapsus natalensis* Ward, 1934: 25 (Christmas I.). —Tweedie, 1936: 46 (Christmas I., same as Ward).  
*Pachygrapsus spec.* Holthuis, 1953: 32 (Tuamotu Archip.; see remarks).  
*Pachygrapsus plicatus* —Stimpson, 1858: 48 [102] (Ryukyu Is.); 1907: 117 (Ryukyu Is.). —A. Milne-Edwards, 1873a: 292, pl. 15, fig. 1 (New Caledonia). —Kingsley, 1880: 200 (Society Is.; Hawaiian Is.). —Richters, 1880: 140 (Mauritius). —Ortmann, 1894: 708 (Samoa; synonymy). —Rathbun, 1906: 839 (Hawaiian Is.); 1907: 29 (Micronesia, Tuvalu, Tuamotu Archip.); 1911: 241 (Seychelles; Chagos Archipelago). —Tesch, 1918: 77 (Indonesia; synonymy). —Balss, 1934b: 524 (Réunion). —Tweedie, 1947: 32 (Christmas I.; synonymy); 1950b: 130 (Cocos-Keeling Is.). —Barnard, 1950: 117, fig. 22b, 24b (KwaZulu-Natal). —Holthuis, 1953: 32 (Marshall Is., Tuamotu Archip.). —Edmonson, 1959: 171, fig. 10a (Hawaiian Is.). —Forest & Guinot, 1961: 154 (Tuamotu Archip.). —Crosnier, 1965: 27 (Glorieuses Is.). —Chace, 1966: 644, fig. 11g (Hawaiian Is.). —Sakai, 1976: 636, pl. 218, fig. 2 (Ogasawara Is., Japan). —Monteforte, 1984: 172, annex 1, tab. a (Society Is., Tuamotu Archip.); 1987: 9 (Society Is.). —Dai & Yang, 1991: 512 (Xisha or Paracel Is.). —Poupin, 1994: 63, fig. 59, pl. 7f (Tuamotu Archip.). —Fransen *et al.*, 1997: 126 (Indonesia). —Ng *et al.*, 2001: 41 (Taiwan; references). —Davie, 2002: 218 (Catalogue). —Paulay *et al.*, 2003: 495 (Mariana Is.).

#### *Type material*

Two female syntypes (12.0 x 16.5, 15.0 x 19.0 mm) in poor condition (MNHN B3585). The largest female is here designated as the lectotype, the second female the paralectotype.

#### *Material Examined*

**Hawaiian Is.:** Types specimens, coll. M. Freycinet, 2 F 12.0 x 16.5, 15.0 x 19.0 mm (dry collection MNHN B3585; poor condition). Honolulu, Waikiki marine lab., leg. From Smithsonian U.S. Fish Commission, under rock near shore, coll. ‘T. H.’, 2 January 1942, 1 M 11.8 x 15.0 mm (MNHN B24497). Labelled as “*Pachygrapsus striatus* M. Edw., Iles Sandwich”, coll. M. Baillien, 3 M 13.0 x 13.0–14.0 x 16.0 mm (dry collection MNHN B3586; see remarks).

**La Réunion:** “Ruisseau de Saint-Benoit,” leg. G. Petit, 1 M 11.4 x 14.8 mm (MNHN B12896).

**Marshall Is. Arno Atoll:** from boulders and rocks, high on the sea reef boulder rampart, coll. R. W. Hiatt, June–September 1950, 1 F 6.6 x 8.6 mm (UNSM 95009).

**Mariana Is. Saipan:** Garapan pier, reef flat, under rocks, 1 m, coll. J. Stammer, 15 November 1997, 1 F ov. 10.4 x 12.9 mm, 4 F 5.2 x 7.4–6.1 x 8.7 mm (UF 584). **Guam,** Tarague reef flat, coll. T. Rongo, 1 June 1997, 1 M 12.6 x 15.4 mm (UF 130); “Tumon moat” on buoy, coll. G. Paulay, 8 May 1999, 1 M 7.6 x 10.0 mm (UF 138).

**New Caledonia:** “Collection A. M. Edw.” 1 M 9.0 x 11.5 mm (poor condition), 1 M 16.0 x 18.0 mm, 1 F 15.2 x 18.6 mm (poor condition) (dry collection MNHN B3584).

**Western Samoa. Upolu I.:** “Godeffroy Mus., 1888”, 1 M 11.7 x 15.0 mm, 1 ov. F 8.5 x 11.1 mm, MZS (dry collection Cru 1210); 1 F 10.3 x 13.5 mm (dry collection MNHN B3583).

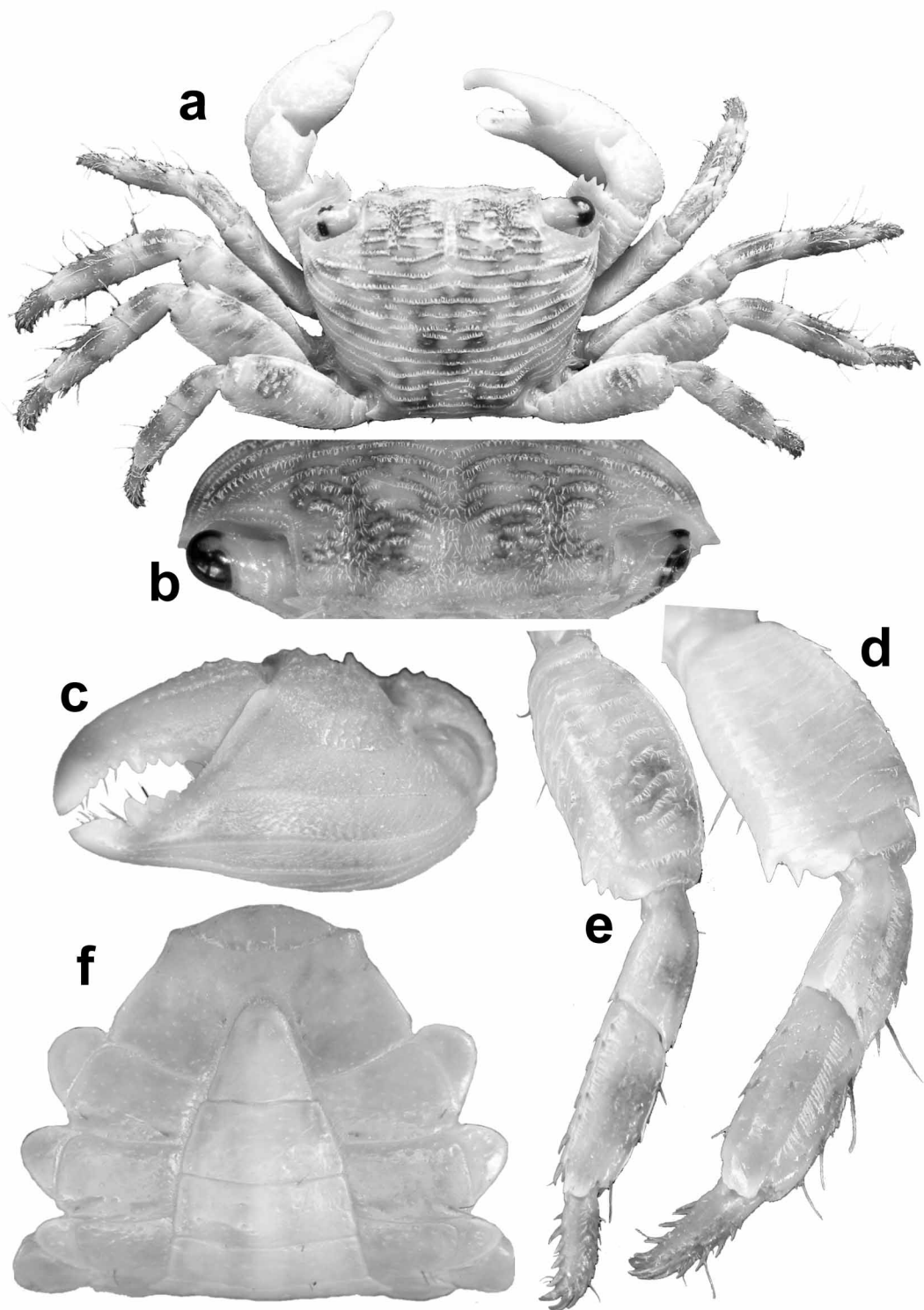
**Niue:** North Alofi, catholic mission, within 5 meters of cliff face or beach inland side of reef flat, exposed rocks surfaces 0–10 cm, coll. Holthuis & Paulay, 30 September 1991, 1 M 2.7 x 3.5 mm (UF 2256).

**French Polynesia. Austral Is.:** Raevavae I., intertidal, RV *Marara* campaign, coll. J. Poupin, 16 March 1995, 1 M juv. 4.3 x 5.7 mm, 1 ov. F 9.6 x 12.7 mm, 3 F juv. 5.0 x 6.3–6.3 x 8.2 mm (MNHN B29274). —**Marquesas Is.:** Nuku Hiva I., intertidal, RV *Marara* campaign, coll. J. Poupin, probably 1996, 1 M 10.7 x 13.5 mm, 1 F 7.8 x 10.8 mm, 1 F juv. 4.5 x 6.2 mm (MNHN B29275). —**Society Is.:** Huahine I., “Fare” harbour, among rocks, RV *Marara* campaign, coll. J. Poupin, 1 M 15.1 x 18.5 mm (MNHN B29277). —Tahiti, intertidal, RV *Marara* campaign, coll. J. Poupin, November 1995, 1 M juv. 3.7 x 5.0 mm (MNHN B29276). —**Tuamotu Archip.:** Makemo Atoll, coll. RV *Albatross*, 24 October 1899, 1 M 5.8 x 8.2 mm (USNM 33180). —Moruroa Atoll, RV *Marara* campaign, coll. J. Poupin, October 1995, 5 M 6.5 x 8.9–9.4 x 12.3 mm, 1 ov. F 15.0 x 19.3 mm, 2 F 6.4 x 9.1, 7.0 x 9.3 mm (MNHN B29278). —Rangiroa Atoll, Avatoru Motu, ca. at 1.5 km E of Post Office, at Pension Henri, reef flat, under rocks, 0–1 m, coll. G. Paulay, 10 January 2001, 1 M 8.2 x 10.7 mm, 1 ov. F 7.7 x 9.9 mm (UF 1491). —Raroia Atoll: Takohe Motu, under stones about high tide line, or little below, coll. J. P. E. Morrison, 21 July 1952, 1 F juv. 5.2 x 7.0 mm (USNM 95110); Ngarumaoa Motu, from outer reef plate, coll. J. P. E. Morrison, 11 July 1952, 1 M (broken) 11.5 x 14.0 mm, 1 ov. F 8.4 x 11.4 mm, 1 juv. 3.9 x 5.6 mm (USNM 95010); Oneroa Motu, from low tide line or just above (wet area) on large reef block at night, coll. J. P. E. Morrison, 5 August 1952, 2 M 12.8 x 15.8, 15.4 x 18.8 mm, 3 ov. F 10.2 x 12.6–14.8 x 18.5 mm, 1 F 11.7 x 15.0 mm (USNM 94883). —Taiaro Atoll, intertidal, outer reef, Taiaro Expedition, coll. J. Poupin, 12–20 February 1994, 3 M 6.0 x 7.9 mm–12.1 x 15.3 mm, 1 ov. F 7.8 x 10.7 mm (MNHN B29279).

### *Diagnosis*

Dorsal surface of carapace convex; entirely covered with coarse transverse striae, each furnished with setae, including cardiac, intestinal regions; lateral margins weakly convergent posteriorly, with no tooth behind exorbital angle (Fig. 11a). Front 0.5 times width at exorbital angles; anterior margin sinuous (Fig. 11b). Infraorbital margin markedly dentate over entire length, with deep outer notch (Fig. 14e).

Merus of cheliped with transverse striae furnished with setae; inner distoventral lobe with 3–4 teeth. Carpus with numerous short striae furnished with setae; inner dorsodistal spine broad at base, distally curved. Outer face of chela regularly convex; lower half with 3–4 main longitudinal striae, without setae, and few additional short oblique striae, near lower margin; upper half tuberculated (Fig. 11c). Cutting edges of fingers with several triangular teeth of unequal size, as illustrated on figure 11c; tip of fingers smooth and spoon-like.



**FIGURE 11.** —*Pachygrapsus plicatus* (H. Milne Edwards, 1837). Male 12.1 x 15.3 mm, Taiaro, French Polynesia (MNHN B29279): a) dorsal view; b) front; c) left chela, outer face; d) right P2; e) right P5; f) abdomen.



Meri of ambulatory legs with transverse striae furnished with setae on outer faces, distoventral angles with 2–3 spines; carpi, propodi with few scattered long bristles on upper margin; P2 propodi with anterodorsal brush of setae, sometimes indistinct on larger males; lower margin of P5 merus without submedian tubercle (Fig. 11d–e).

Abdominal tergites smooth; sixth somite of abdomen plus telson triangular in male (Fig. 11f). Distal process of G1 slender with two large lobes at tip (Fig. 15e).

Colour: carapace white to cream with a pattern of irregular brown patches on carapace as illustrated on figure 11a. Chelipeds with brown to violet hues on meri and carpi, chelae almost totally white to light yellow. Ambulatory legs white to brown, with irregular median bands on meri, carpi and propodi; dactyli brown, paler at base.

Measurements: medium size; carapace of specimens examined ranging from 2.7 x 3.5 mm to 15.1 x 18.5 mm, for males, and 4.5 x 6.2 mm to 15.0 x 19.3 mm, for females; smallest ovigerous female is 8.5 x 11.1 mm.

#### *Distribution*

**Indo-West Pacific from east Africa to Tuamotu Archip.:** East Africa; Glorieuses Is.; Seychelles; La Réunion; Mauritius; Christmas I.; Cocos-Keeling Is.; Indonesia (Java); South China Sea (Xisha or Paracel Is.); Taiwan; Japan; Mariana Is. (Saipan); Micronesia (Kosrae); Marshall Is. (Arno); New Caledonia; Samoa; Niue, Tuvalu; Hawaiian Is.; French Polynesia (Austral Is., Marquesas Is., Tuamotu Archip., Society Is).

#### *Habitat*

Intertidal, on reef flat and under rocks; common and easily collected at night.

#### *Remarks*

*Pachygrapsus plicatus* is morphologically close to *P. corrugatus* (von Martens, 1872), from the west and central Atlantic, and to *P. fakaravensis* Rathbun, 1907, from the west and central Pacific. The three species have in common the carapace shape, which is coarsely striated transversally, and the presence of longitudinal striae on the outer face of the chelae. *Pachygrapsus plicatus* differs from these two species by the lateral margins of its carapace, weakly convergent posteriorly instead of being subparallel, the absence of setae on the striae of the carapace and of the outer face of the chelae, smooth abdominal tergites and different G1, petal-like tip in *P. plicatus* (Fig. 15e) and acicular in *P. corrugatus* and *P. fakaravensis* (Fig. 15a, f).

Krauss (1843: pl. 3, fig. 1, 1a–c) showed a female crab from Natal, South Africa, that he attributed to *Grapsus plicatus* H. Milne Edwards, 1837, which was described from the Hawaiian Is. Although Krauss' figure is of good quality, it seems that the artist exaggerated the spines on the upper and lower margin of the P5 merus. It was this character that led Dana (1852: 343) to believe it was a new species, *Goniograpsus kraussii*, commenting that “from the dentations on the third joint of the posterior legs of Krauss's species on both

margins, we judge that his species must be a different one". Dana's identification was followed by H. Milne Edwards (1853: 170, as *Grapsus kraussii*), and by Stebbing (1910: 319, as *Pachygrapsus kraussii*). All other characters described and figured by Krauss (1843) clearly belong to *P. plicatus*, especially the form of the outer face of the chelae. Furthermore, *P. plicatus* was later recorded from Natal by Barnard (1950), who included an illustration of the characteristic G1. *Pachygrapsus kraussii* (Dana, 1852) is therefore here formally considered a junior synonym of *P. plicatus* (H. Milne Edwards, 1837).

Ortmann (1894: 708) and Tesch (1918: 77) considered *P. striatus* A. Milne-Edwards, 1873, a junior synonym of *P. plicatus*, which was confirmed by the examination of the three male syntypes of *P. striatus* (MNHN B3586). These specimens undoubtedly belong to *P. plicatus* and should not be confused with *P. fakaravensis*. Their carapace is coarsely striated, with lateral margins weakly convergent posteriorly, the outer face of the chelae has three main longitudinal striae without setae, and the abdominal tergites are smooth and without striae. It is not clear why A. Milne-Edwards (1873: 82) alluded to "*Grapsus striatus* Milne Edwards". All earlier work of both H. Milne Edwards and A. Milne-Edwards was examined without finding a reference to this species, so it is assumed that he referred to an unpublished manuscript.

The small specimen from Raroia Atoll that Holthuis (1953: 32) attributed to *Pachygrapsus* spec., (juvenile female, USNM 95110) is clearly identifiable as *P. plicatus*. It had the brush of setae on the P2 merus that is usually present in small specimens of *P. plicatus*, although it tends to disappear on larger specimens, particularly males.

### ***Pachygrapsus propinquus* De Man, 1908 (Figure 12a-c)**

*Pachygrapsus propinquus* De Man, 1908: 216, pl. 18, fig. 2 [type locality: Port Canning, near Calcutta, India]. —Tesch, 1918: 76 (Key).

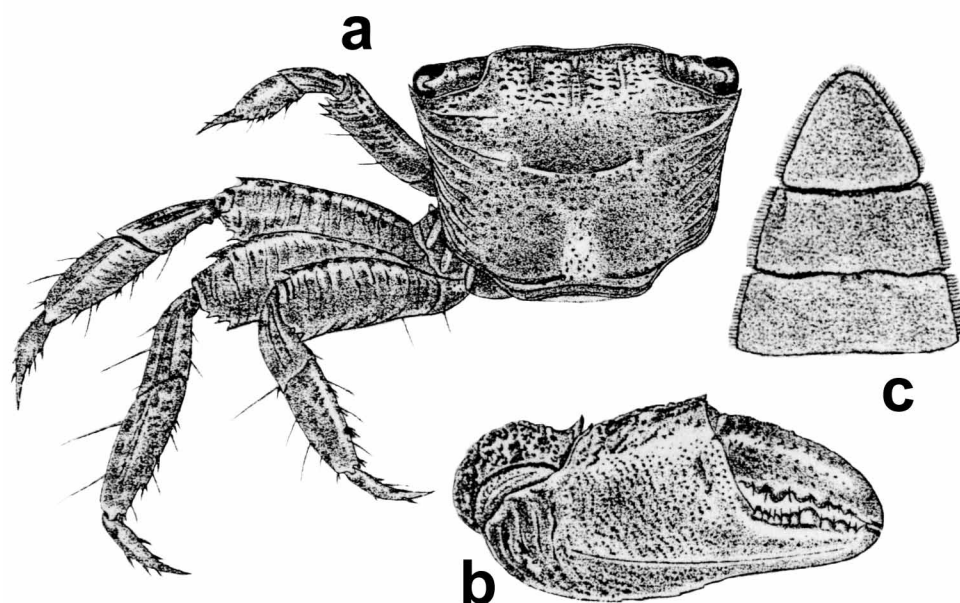
#### *Type material*

Unknown. The types are neither in RMNH (C. Fransen, pers. comm.) nor SMF (M. Türkay, pers. comm.), nor BMNH (P. Clark, pers. comm.), nor ZMA (first author unable to locate it, June 2005). Probably in the Zoological Survey of India, Calcutta.

#### *Diagnosis* (adapted from De Man, 1908)

Carapace 0.75 times longer than wide; lateral margins weakly convergent posteriorly, with no tooth behind exorbital angle (Fig. 12a). Dorsal surface slightly convex with distinct cervical groove; hepatic and branchial regions with glabrous striae; mesogastric, cardiac and intestinal regions smooth. Front about 0.5 times exorbital width, anterior margin sinuous. Infraorbital margin with 3–4 small obtuse teeth, uneven on inner part; outer notch low.

Left chela unknown. Outer face of right chela very finely granular, slightly convex, with conspicuous longitudinal line running from tip of fixed finger to near carpal articulation (Fig. 12b); upper margin with finely granular oblique ridges. Tip of fingers spoon-like, glabrous.



**FIGURE 12.** —*Pachygrapsus propinquus* de Man, 1908. a) dorsal view; b) right chela, outer face; c) abdomen; a, b, female 8.0 x 10.7 mm, c, male 6.25 x 8.3 mm, Port Canning, India (from de Man, 1908, pl. 18 fig. 2).

Ambulatory legs slender with few scattered long bristles on carpi, propodi, dactyli. Meri with transverse ridges on their outer faces; lower margin of P5 merus without submedian tubercle, distoventral angle with 2 spines.

Abdominal tergites smooth. Sixth somite of abdomen plus telson triangular in male. G1 unknown.

Colour (from De Man, 1908: 218): “slate-coloured upper surface of the carapace, and the red-brown legs are mottled with small dark spots.”

Measurements (from De Man, 1908; only two specimens): probably a small-size species (see remarks); carapace 6.25 x 8.3 mm (male), 8.0 x 10.7 mm (female).

#### *Distribution*

**Indian Ocean.** Port Canning, near Calcutta, India.

*Habitat*

Intertidal, brackish water pools.

*Remarks*

De Man (1908) compared his two specimens of *P. propinquus* with one male of *P. minutus*. These two species appear to be closely related, and De Man listed as many similarities as differences. The differences he mentioned, such as “chela less convex” or “ambulatory legs slenderer”, are relative and thus difficult to evaluate. With only two specimens of *P. propinquus* known, it is difficult to see the extent of morphological variation, or to know what size the species may attain. Additional specimens from the type locality must be studied before a proper comparison with *P. minutus* can be made. The shape of the G1 in *P. propinquus* is unknown. Based on De Man’s description, the following characters can be used to separate the two species: the lateral margins of the carapace are weakly convergent posteriorly in *P. propinquus* but strongly convergent in *P. minutus*, the lower margin of the P5 merus is smooth in *P. propinquus* but with 1–2 submedian tubercles in *P. minutus*.

***Pachygrapsus transversus* (Gibbes, 1850) (Figures 13a–e, 14l, 15l, 16)**

*Grapsus transversus* Gibbes, 1850: 181 [type locality: Key West, Florida]

*Goniograpsus innotatus* Dana, 1851: 249; Dana, 1852: 345 (uncertain, probably South American coast)

*Leptograpsus rugulosus* H. Milne Edwards, 1853: 172 (Brazil)

*Metopograpsus dubius* de Saussure, 1858: 445 [29], pl. 2, fig. 16 (St. Thomas, Virgin Is.)

*Metopograpsus miniatus* de Saussure, 1858: 444 [28], pl. 2, fig. 17 (St. Thomas, Virgin Is.)

*Pachygrapsus innotatus* —Stimpson, 1858: 48 [102] (Madeira); 1907: 116 (Madeira).

*Grapsus declivifrons* Heller, 1862: 521 (Brazil).

*Pachygrapsus intermedius* Heller, 1865: 44 (Brazil).

*Pachygrapsus socius* Stimpson, 1871: 114 (Perú, Panamá, San Salvador, Manzanillo, Cabo San Lucas; see remarks).

*Pachygrapsus transversus* —Ortmann, 1894: 709 (Brazil). —Rathbun, 1918: 244 (Cape Cod, Massachusetts; South Carolina; Bahamas; Florida; Texas; México; Cuba; Jamaica; Puerto Rico; St. Thomas; Trinidad; Curaçao; Brazil; Bermuda; Cape Verde Is.; Lower California; Mexico; Costa Rica; Panamá; Galápagos; Perú; part, see remarks, not specimens from Sydney and Easter I., p. 248, which are *P. laevimanus*); 1921: 444, pl. 40, fig. 2-3 (Congo); 1933: 88 (Puerto Rico). —Tesch, 1918: 76 (Key). —Bouvier, 1940: 290 (Mediterranean). —Garth, 1946: 507, pl. 87 fig. 2 (Galápagos; differences with *P. crassipes*); 1992: 4 (Revillagigedo Is.). —Capart, 1951: 186, fig. 73, pl. 3, fig. 20 (West Africa). —Monod, 1956: 415, fig. 568, 570, 572, 573 (West Africa). —Holthuis & Gottlieb, 1958: 100 (Mediterranean coast of Israel). —Zariquiez Álvarez, 1968: 425, fig. 140c, 141a (Spain). —Chace & Hobbs, 1969: 169 (West Indies; references, distribution). —Christiansen, 1969: 92, fig. 38 (Denmark). —Manning & Holthuis, 1981: 234 (Nigeria, Canary Is., Morocco, Senegal, Liberia, Cameroon; synonymy, references, distribution). —Williams, 1984: 459 (from “Cape Lookout, N.C. to Montevideo, Uruguay”; references, distribution). —Falciai & Minervini, 1992: 234. —González Pérez, 1995: 223, photo 165 (Canary Is.). —Hendrickx, 1995: 140 (references, east Pacific distribution; from California (unknown locality), USA, and Cedros I., west coast of Baja California, Mexico,

south to San Lorenzo I., Perú, Revillagigedo, and Galápagos Is.). —Melo, 1996: 454 (Brazil); 1998: 499 (Brazil). —Cuesta & Schubart, 1998: 1499 (Pacific and Atlantic coasts of Panamá, Florida, Jamaica, Antigua, Puerto Rico, Grenada, Curaçao, Spain; morphometry and DNA sequences). —Flores & Negreiros-Fransozo, 1999: 1051 (Brazil; secondary sexual characters and allometry). —d'Udekem d'Acoz, 1999: 256 (references, distribution, ecology). —Hickman & Zimmerman, 2000: 126, photograph (Galápagos).

#### *Type material*

Type not extant, according to Rathbun (1918: 244).

#### *Material examined*

**Mediterranean Sea. Egypt:** Port Said, coll. H. C. Kellers, July 1922, 1 M 21.6 x 26.3 mm, 1 F 15.1 x 18.9 mm (USNM 57443).

**East Atlantic. Senegal:** Dakar, littoral zone, coll. D. E. Harvey, 2 August 1966, 3 M 4.7 x 6.6–10.8 x 14.2 mm, 3 ov. F 9.2 x 12.2–10.9 x 14.1 mm, 3 F 5.5 x 7.6–8.3 x 10.8 mm, 1 juv. (USNM 125805).

**West Atlantic. Florida:** Tortugas, coll. W. L. Schmitt, July 1930, 1 M 11.2 x 14.4 mm (USNM 71091). —**French Guiana,** coll. F. Geay 1906, 1 M 17.5 x 22.5 mm (MNHN B16013; plus 3 other specimens not examined). —**Brazil,** stony beach south of hotel, Villa Bella, São Sebastiao I., coll. W. L. Schmitt, 21 September 1925, 1 M 8.4 x 10.5, 1 F 8.3 x 11.4 mm (USNM 70955). Abrolhos Is., coll. RV *Albatross*, 27 December 1887, 3 M 6.0 x 8.1–15.0–19.5, 1 F 11.7 x 15.5 mm (USNM 22095).

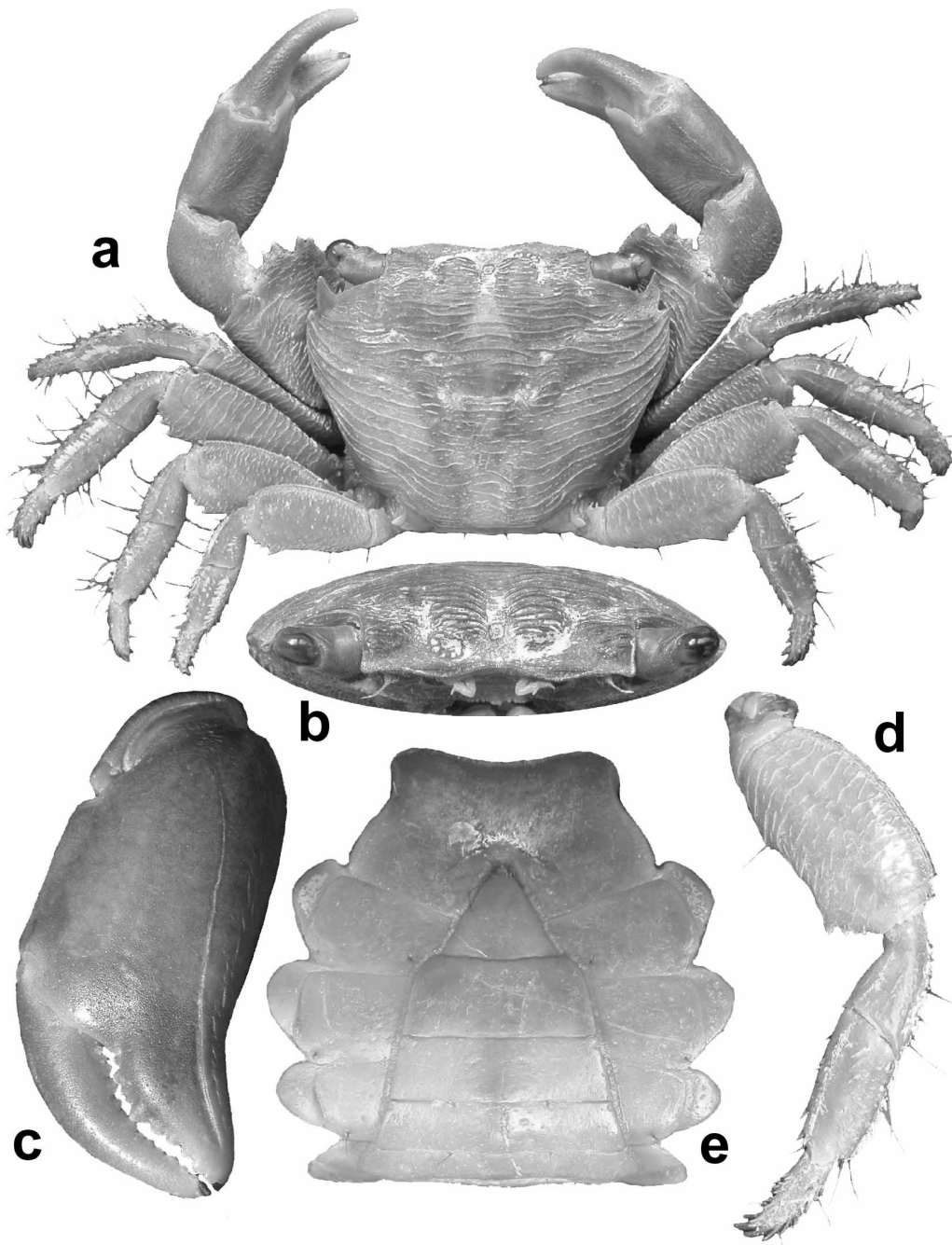
**East Pacific. Costa Rica:** Puntarenas, coll. J. F. Tristan, February 1905, 1 F 9.0 x 12.6 mm (USNM 32363). **Perú:** Praitá, first point of rocks N. of railway station, coll. W. L. Schmitt, 6 October 1926, 4 M 12.2 x 15.2–14.0 x 17.5 mm, 2 F 8.8 x 11.5, 12.0–15.5 mm, 1 ov. F 9.7 x 12.7 mm, 2 juv. (USNM 70963).

**Clipperton Atoll.** Beach, Jean-Louis Etienne Expedition to Clipperton, stn 11, coll. L. Albenga, J. M. Bouchard, 18 January 2005, 1 M 10.0 x 12.0 mm, 2 F 6.5 x 8.0 mm, 8.5 x 11 mm (MNHN B29857).

#### *Diagnosis*

Carapace weakly convex, coarsely striated on gastric, hepatic and branchial regions; striae glabrous or only with short setae; cardiac, intestinal regions with shorter striae; lateral margins convergent posteriorly (more pronounced on the smallest specimens), with tooth behind exorbital angle (Fig. 13a). Front 0.5 times (to 0.6 on larger specimens) exorbital width; anterior margin sinuous (Fig. 13b). Infraorbital margin denticulated over entire length; with deep outer notch (Fig. 14l).

Outer face of palm smooth, regularly convex; with marked longitudinal stria running near lower margin from tip of finger to near carpal articulation; upper margin of palm smooth or with faint carina and few oblique lines on inner face in larger specimens; cutting edges of fingers narrowly gaping with large triangular teeth; tip of fingers corneous, spoon-like, glabrous (Fig. 13c).



**FIGURE 13.** —*Pachygrapsus transversus* (Gibbes, 1850). Male 17 x 22.5 mm, French Guiana (MNHN B16013): a) dorsal view; b) front; c) left chela outer face, d) right P5, e) male abdomen.

Ambulatory legs with brush of setae on P2 propodi that tends to disappear in larger males (see remarks); lower margin of P5 merus smooth or slightly incised by oblique striae of outer face; submedian tubercle usually absent, sometimes present on smallest specimens (6 x 8 mm); distoventral angle with 3–4 spines (Fig. 13d).

Abdominal tergites smooth. Sixth somite of male abdomen subrectangular, not forming a triangle with telson (Fig. 13e). G1 with elongated, petal-like tip (Fig. 15l).

Colour (from photographs): carapace cream to light brown with striae dark brown; cardiac and intestinal regions with a pattern of dark brown patches, symmetrical to longitudinal axis. Chelipeds dark brown to pink with paler areas on articulations and at tip of fingers. Ambulatory legs with dark brown patches on meri, carpi, and propodi, more or less arranged in bands on propodi; dactyli dark brown.

Measurements: large size; cw greater than 20 mm common; carapace of specimens examined ranging from 4.7 x 6.6–21.6 x 26.3 mm, smallest ovigerous female 9.2 x 12.2 mm.

#### *Distribution*

**East Pacific.** From Lower California to Perú, including the oceanic island groups of Revillagigedo, Clipperton, and the Galápagos. **West Atlantic.** From Cap Cod to Montevideo, including the Caribbean and Bermuda. **East Atlantic.** From South Portugal to Namibia, including Madeira, Canary Is., and Cape Verde Is. **Mediterranean.** From Alboran Sea to the Levant basin. There is one record from Denmark. According to Christiansen (1969), “in Copenhagen about 20 living specimens were found on a ship coming from the Bermudas.”

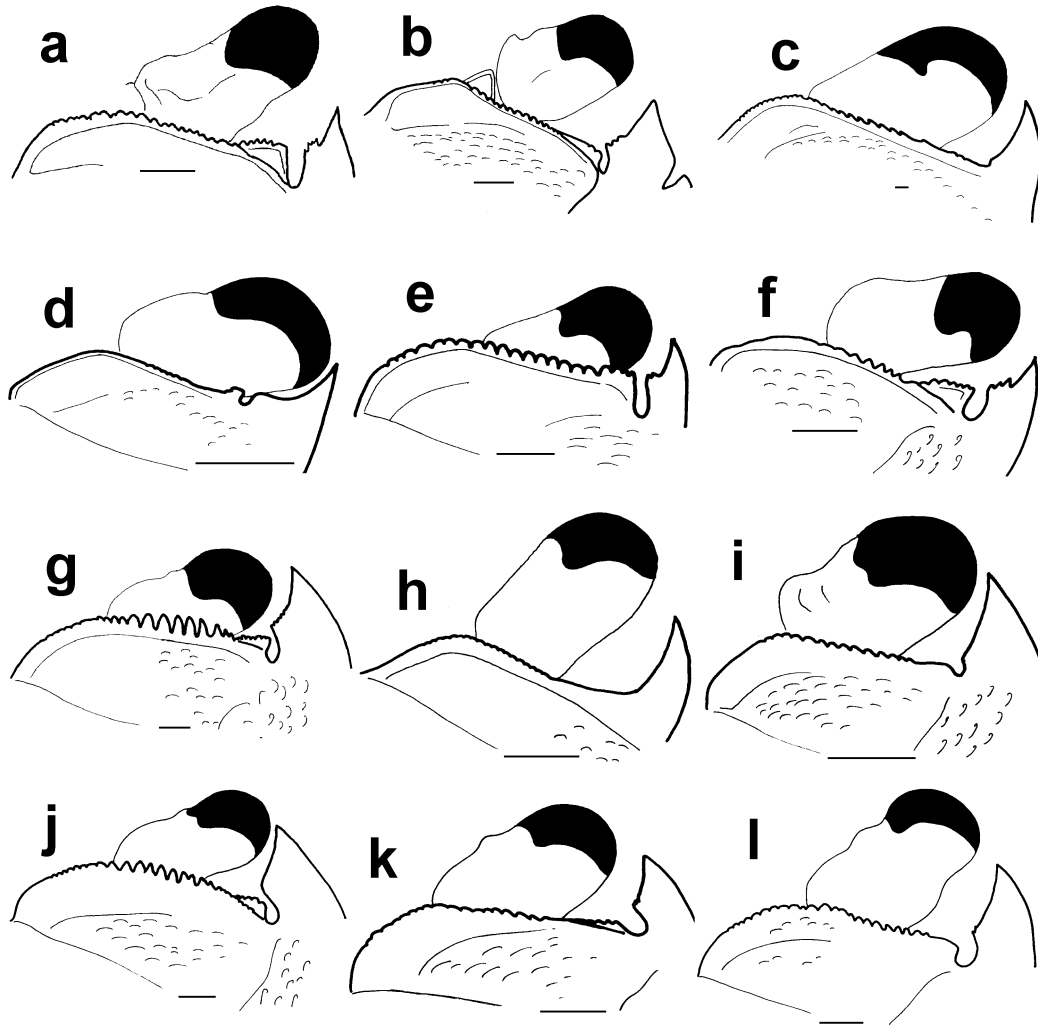
*Pachygrapsus transversus* is a warm-water species but with a few occasional records at high latitudes (Fig. 16): Denmark to Namibia (see d’Udekem d’Acoz, 1999: 256); Cap Cod (Rathbun, 1914) to Montevideo (William, 1984). Williams (1984: 459) indicates that this species “has been carried to higher latitudes than it normally inhabits by transport on ships’ bottoms, and ... the range may have been greatly extended by commerce in modern times”.

#### *Habitat*

Intertidal on rocky shores; also recorded on sandy shores and mangroves (see d’Udekem d’Acoz, 1999: 256).

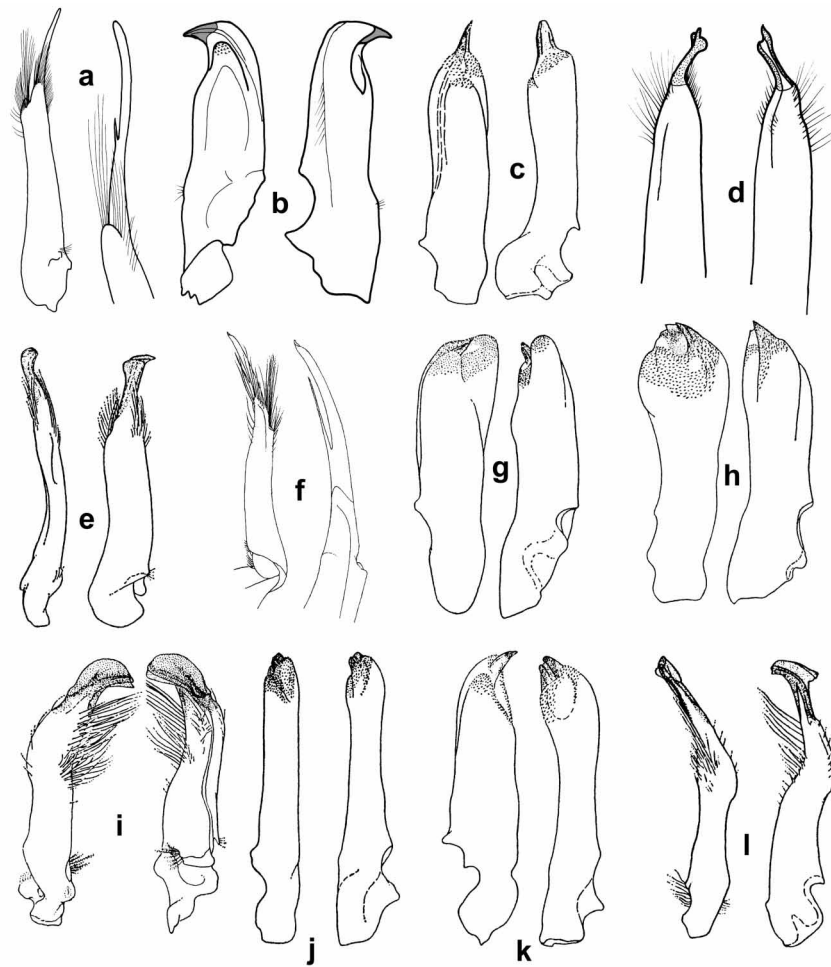
#### *Remarks*

Some characters used to identify this species vary according to size and/or sex. The lateral margin of the carapace is only weakly convergent posteriorly in large specimens, but more strongly convergent in small specimens. The striae on the cardiac and intestinal regions also tend to disappear on the smallest specimens. The front is 0.6 times the exorbital width on larger specimens but 0.5 on smaller crabs. The upper margin of the palm has a faint carina and oblique lines that tend to disappear on larger specimens. The brush of setae on P2 propodi is noticeable on small specimens and females but absent on large males. The lower margin of the P5 merus has a submedian tubercle only in small specimens.



**FIGURE 14.** —Infra-orbital margin: a) *Pachygrapsus fakaravensis* Rathbun (1907), ov. female 15.0 x 16.5 mm, Taiaro, French Polynesia (MNHN B25782); b) *Pachygrapsus laevimanus* Stimpson, 1858, neotype male 18.0 x 21.7 mm, Sydney, Australia (AM P7478); c) *Pachygrapsus minutus* A. Milne-Edwards, 1873, male 5.2 x 7.0 mm, Moruroa, French Polynesia (MNHN B29273); d) *Pachygrapsus planifrons* de Man, 1888, male 7.0 x 9.0 mm, Rangiroa, French Polynesia (UF 1490); e) *Pachygrapsus plicatus* (H. Milne Edwards, 1837), male 12.1 x 15.3 mm, Taiaro, French Polynesia (MNHN B29279); f) *Pachygrapsus corrugatus* (von Martens, 1872) ov. female 13.6 x 15.2 mm, Virgin Is. (USNM 72340); g) *Pachygrapsus crassipes* Randall, 1840, male 31.9 x 36.6 mm, Sagami Bay, Japan (NSMT Cr7516); h) *Pachygrapsus gracilis* (de Saussure, 1858), ov. female 8.5 x 11 mm, Angola (MNHN B12903); i) *Pachygrapsus loveridgei* Chace, 1966, male 8.1 x 10 mm, St. Helena I. (MNHN B17836); j) *Pachygrapsus marmoratus* (Fabricius, 1787), female 12.7 x 14.3 mm, Préfailles, France (MNHN B22654); k) *Pachygrapsus maurus* (Lucas, 1846), female 12.7 x 14.3 mm, Banyuls, France (MNHN B12933); l) *Pachygrapsus transversus* (Gibbes, 1850), male 17.0 x 22.5 mm, French Guiana (MNHN B16013). Scale bar 1 mm.

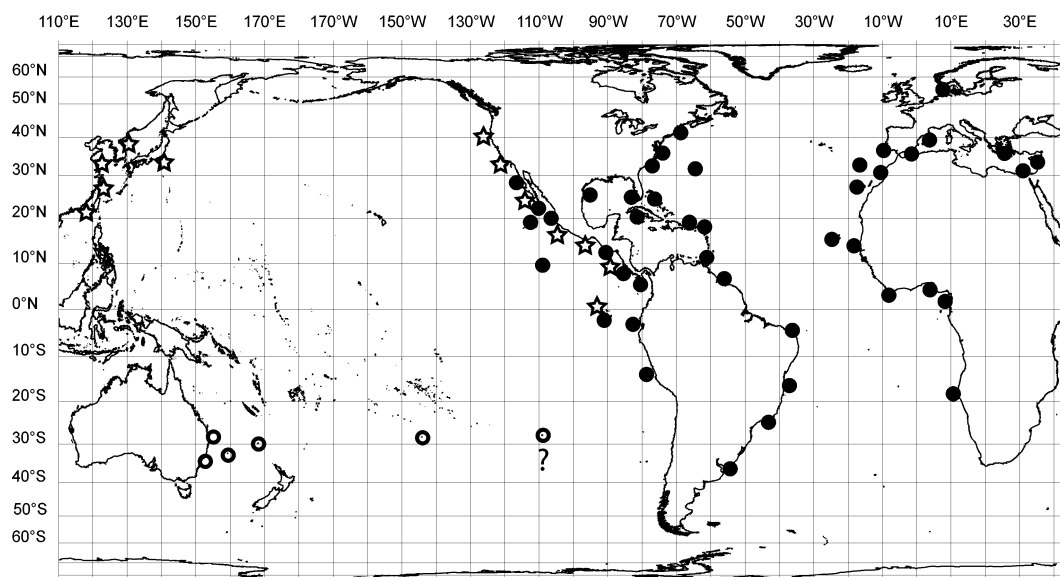




**FIGURE 15.** —Male gonopods: a) *Pachygrapsus fakaravensis* Rathbun (1907), holotype 18.0 x 19.4 mm, Fakarava, French Polynesia (USNM 32844), right G1, abdominal face (left) and detail of terminal portion, sternal face (right); b) *Pachygrapsus laevimanus* Stimpson, 1858, neotype 18.0 x 21.7 mm, Sydney, Australia (AM P7478), left G1, abdominal (left) and sternal face (right), setae omitted; c) *Pachygrapsus minutus* A. Milne-Edwards, 1873, cl 8.2 mm, Caroline Is., lateral (left) and abdominal face (right), setae omitted; d) *Pachygrapsus planifrons* de Man, 1888, 9.5 x 11.8 mm, Hawaiian Is. (USNM 29350), right G1, abdominal (left) and sternal face (right); e) *Pachygrapsus plicatus* (H. Milne Edwards, 1837), cl 11.7 mm, Hawaiian Is., lateral (left) and abdominal face (right); f) *Pachygrapsus corrugatus* (von Martens, 1872), cl 8.5 mm, Ascension I., left G1 abdominal face (left) and detail of terminal portion, setae omitted (right); g) *Pachygrapsus crassipes* Randall, 1840, cl 35.6 mm, California, lateral (left) and abdominal face (right) setae omitted; h) *Pachygrapsus gracilis* (de Saussure, 1858), cl 8.7 mm, Virgin Is., lateral (left) and abdominal face (right), setae omitted; i) *Pachygrapsus loveridgei* Chace, 1966, holotype 10.3 x 13.1 mm, St. Helena I. (USNM 112457), left G1, abdominal (left) and sternal face (right); j) *Pachygrapsus marmoratus* (Fabricius, 1787), cl 30.5 mm, Gibraltar, lateral (left) and abdominal face (right), setae omitted; k) *Pachygrapsus maurus* (Lucas, 1846), cl 8.5 mm, Canary Is., lateral (left) and abdominal face (right) setae omitted; l) *Pachygrapsus transversus* (Gibbes, 1850), cl 11.1 mm, Key West, Florida, lateral (left) and abdominal face (right), setae omitted. (c, e, g–l, from Chace, 1966, fig. 10–11; f, from Manning & Chace, 1990, fig. 43). Approximate magnification x 6 (x 12 for detail of terminal portion).

*Pachygrapsus transversus* is morphologically close to *P. laevimanus*, and has been often confused with the former. The differences between the two are discussed under *P. laevimanus*.

Cuesta & Schubart (1998) studied the morphological and molecular variation of *P. transversus* from east, west Atlantic, and east Pacific populations. Their results suggest sufficient differentiation among these three populations that taxonomic separation can be considered. C. Schubart (pers. comm.) has indicated that a taxonomic revision is currently in progress, with the reinstatement of *P. socius* Stimpson, 1871 from the east Pacific, based on colour pattern, larval and adult morphometry, and DNA analysis.



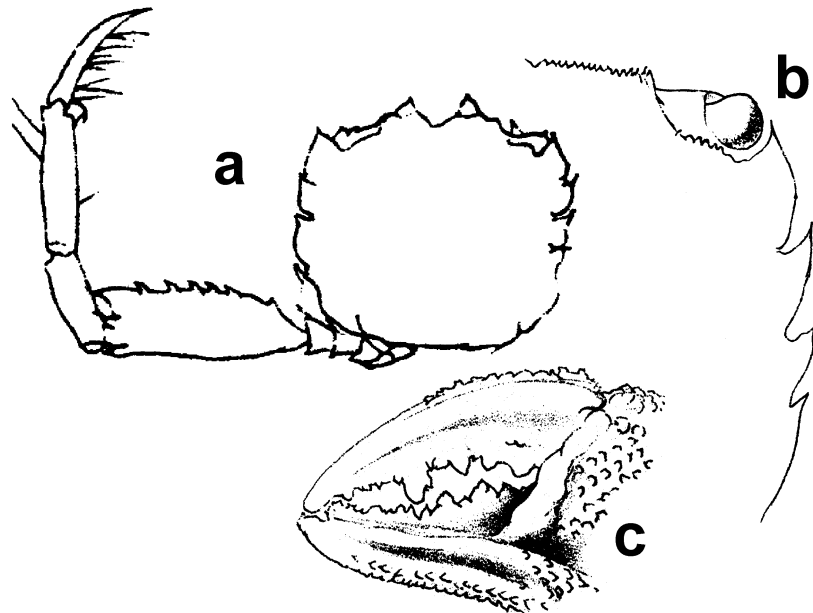
**FIGURE 16.** —Geographic distribution of: a) *Pachygrapsus crassipes* Randall, 1840 (Stars); b) *Pachygrapsus transversus* (Gibbes, 1850) (full dots); and c) *P. laevimanus* Stimpson, 1858 (empty dots). a–b, mostly from literature; c) from collections examined during this study. Occurrence of *P. laevimanus* at Easter I. uncertain (?) and must be confirmed by examination of G1 (see text).

## Discussion

*Pachygrapsus* now consists of twelve distinct species. An additional species, *P. propinquus*, may also be included if it is shown to be distinct from *P. minutus*. Three species have been shown to be synonyms of others: *P. striatus* A. Milne-Edwards, 1873 and *P. kraussii* (Dana, 1852), of *P. plicatus* (H. Milne Edwards, 1837) and *P. laevis* Borradaile, 1900 of *P. planifrons* De Man, 1888. The status of *P. polydous* Stebbing, 1921 remains questionable (see below).

*Remarks on Pachygrapsus polyodous* Stebbing, 1921 (Fig. 17a–b)

*Pachygrapsus polyodous* Stebbing, 1921, is known only from the holotype male (18 x 22 mm), which was collected at 91.5 m (50 ft) off the Umhlangakulu River, KwaZulu-Natal, South Africa. Stebbing (1921: 458) placed this species in *Pachygrapsus* but had to modify the generic diagnosis to include species having three teeth behind the exorbital angles as a diagnostic character. Barnard (1950: 118) included *P. polyodous* in *Pachygrapsus* but stated that “only one male specimen was captured. It has not been returned to the South African Museum, so I am unable to check Stebbing’s description or give further details”. Stebbing’s South African collection was largely donated to the Natural History Museum, London, but the holotype of *P. polyodous* is not found there and is probably lost (P. F. Clark, pers. comm.).



**FIGURE 17.** —*Pachygrapsus polyodous* Stebbing, 1921. Holotype male 18 x 22 mm, from Stebbing (1921, pl. 16): a) carapace and P5; b) detail of lateral margin of carapace; c) right chela, terminal portion, inner face.

From the description and illustrations of Stebbing (1921), we conclude that *P. polyodous* (Fig. 17) is morphologically distinct from all the other species of *Pachygrapsus*. It differs markedly by the subquadrate shape of the carapace (Fig. 17a), the presence of three teeth on its lateral margins (Fig. 17b), the fine spinulation of the frontal lobes and supraorbital margins (Fig. 17b), the irregular cutting margin of the cheliped dactylus and granular

palm (Fig. 17c), the “strikingly dentate carinae” on the meri of the chelipeds, P2 and P5 that are shorter than the P3–P4, the presence of spines on the upper margin of the meri of the ambulatory legs, and its subtidal habitat. *Pachygrapsus* as defined here, is otherwise homogenous, and in our opinion *P. polydous* cannot be monophyletic with the other members of this genus and therefore must be excluded. We provisionally place it in *Euchi-rograpsus* H. Milne Edwards, 1853 (Plagusiidae), a subtidal genus that has similar antero-lateral carapace armature, and with which it seems much more likely to be related. This placement is still problematic because *P. polydous* has spines on the upper margins of the meri of the ambulatory legs, and this is atypical of all known species of *Euchi-rograpsus*, although often present in other Plagusiidae. Its taxonomic status will remain in doubt until additional specimens are available.

#### *Biogeography*

Six species of *Pachygrapsus* are Indo-West Pacific in their distribution, five Atlantic, and only one, *P. transversus*, occurs in both the Atlantic and the east Pacific. *Pachygrapsus minutus*, *P. planifrons*, and *P. plicatus* are widespread Indo-West Pacific species; *P. minutus* and *P. planifrons* are also found as far as the east Pacific islands of Clipperton and the Revillagigedo group. Three species appear restricted to the Pacific: *P. crassipes* in the east and northwest Pacific (Fig. 16), *P. fakaravensis* in the northwest and central Pacific (Hawaiian Is. and French Polynesia), and *P. laevimanus* in the southwest and south central Pacific and possibly Easter I. in the east Pacific (Fig. 16).

*Pachygrapsus gracilis* is the only Atlantic species of *Pachygrapsus* to occur on both the east and west coasts. *Pachygrapsus marmoratus* and *P. maurus* are both found in the Azores, Madeira, Canary Is., and the Mediterranean. *P. marmoratus* has also been reported on the west European coast from France to Portugal and in the Black Sea. *Pachygrapsus corrugatus* is found in the west and central Atlantic (St Paul’s Rocks and Ascension I.) and *P. loveridgei* is restricted to the central Atlantic (Ascension and St. Helena islands).

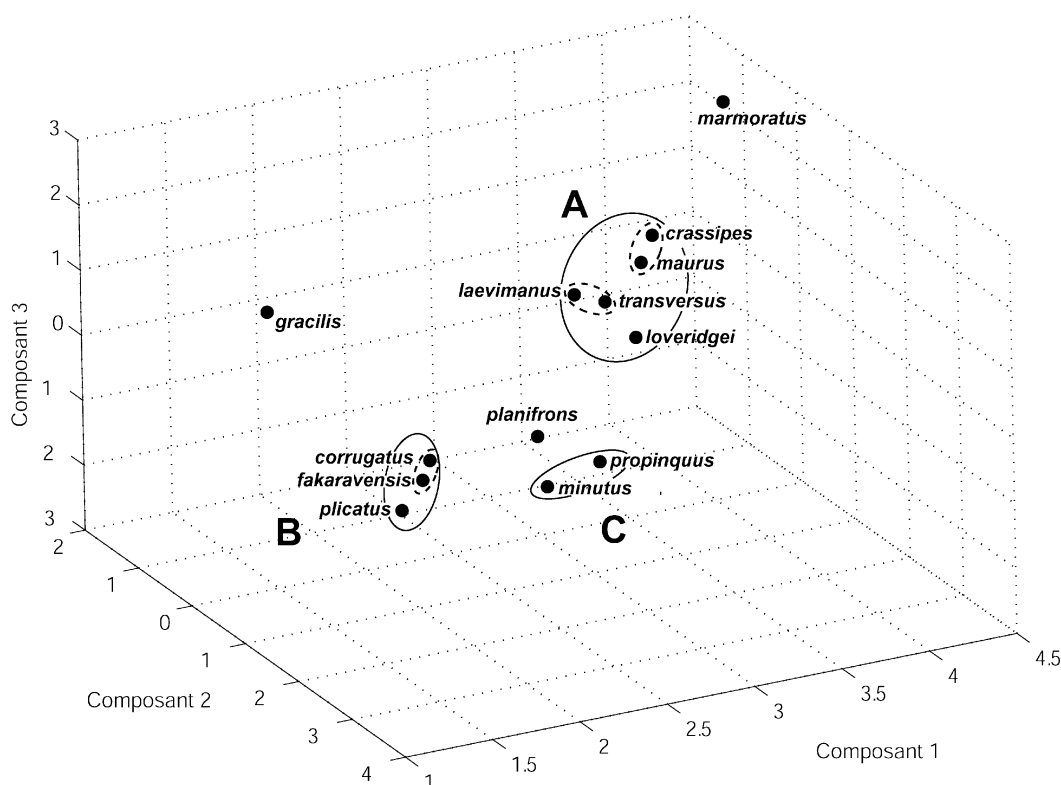
*Pachygrapsus transversus* has an unusually wide geographic distribution, being found in the Mediterranean, the east and west Atlantic, and the east Pacific, including the oceanic islands of Revillagigedo, Clipperton Atoll, and the Galápagos (Fig. 16). It is also reported at uncommonly high latitudes (to 55°N and 35°S), possibly because of transport by commercial shipping.

#### *Morphology*

No rigorous attention was paid to colour pattern because most of the specimens examined had been long preserved and all colour had faded. Colour pattern was retained in two species, however, and this was useful as an additional aid in their identification. *Pachygrapsus gracilis* has unique small spots on the carapace and legs (Fig. 4a) and *P. maurus* has a characteristic marbled colour pattern on the carapace that is longitudinally symmetrical (Fig. 8a) (see Zariquiey Álvarez, 1968, fig. 140b and d’Udekem d’Acoz, 2005).

All species can be confidently separated based on the shape of their G1 (Fig. 15), but identification is sometimes difficult in females and juveniles. Confusion or difficulty in identification often occurs between the following pairs of species: *P. transversus*/*P. laevimanus*, *P. plicatus*/*P. fakaravensis*, *P. transversus*/*P. gracilis*, *P. minutus*/small specimens of *P. plicatus*, and *P. crassipes*/young females of *P. maurus*.

A suite of sixteen morphological characters (see Appendix) were scored into the DELTA Editor Software system (Dallwitz *et al.*, 1999), and then used to generate a key to species using Intkey (Dallwitz *et al.*, 2000). This data set was also the basis for a morphological relationships analysis. A correct determination of *Pachygrapsus* species is possible in most cases by using these characters although juveniles, females, or incomplete specimens may not be identifiable.



**FIGURE 18.** —Principal Component Analysis (PCA) on *Pachygrapsus* species using 15 morphological characters. Three complexes of species are identified: A, *P. crassipes* Randall, 1840, *P. laevimanus* Stimpson, 1858, *P. loveridgei* Chace, 1966, *P. maurus* (Lucas, 1846), *P. transversus* (Gibbes, 1850), with *P. laevimanus*/*P. transversus* and *P. crassipes*/*P. maurus* as subgroups; B, *P. corrugatus* (von Martens, 1872), *P. fakaravensis* Rathbun, 1907, *P. plicatus* (H. Milne Edwards, 1837), with *P. corrugatus*/*P. fakaravensis* as subgroup; and C, *P. minutus* A. Milne-Edwards, 1873, *P. propinquus* de Man, 1908. Three species are isolated: *P. marmoratus* (Fabricius, 1787), *P. planifrons* de Man, 1888, and *P. gracilis* (de Saussure, 1858).

*Morphological Relationships*

The DELTA data matrix was exported to MATLAB® to perform a PCA analysis in an attempt to graphically show affinities between the *Pachygrapsus* species. The distal appearance of the G1 (character 2) was excluded from this analysis because the states identified have been created arbitrarily for use in the key only. They should not be used to evaluate the affinities between species because the shape of the G1 is basically distinct for each species (as many states as species), and therefore does not usefully contribute to the PCA analysis.

The result of the analysis is presented in Figure 18. Three complexes of species have been identified: A, includes species that cluster with the type species of the genus (*P. crassipes*, *P. laevimanus*, *P. loveridgei*, *P. maurus*, *P. transversus*), and includes two subgroups, *P. laevimanus*/*P. transversus* and *P. crassipes*/*P. maurus*; B, includes *P. corrugatus*, *P. fakaravensis*, and *P. plicatus*, with *P. corrugatus*/*P. fakaravensis* as a distinct subgroup; C, includes two species that are potential synonyms, *P. minutus* and *P. propinquus*. *Pachygrapsus planifrons* is isolated but morphologically close to that group. Two species, *P. marmoratus* and *P. gracilis*, are isolated from each other and from all other groups.

**KEY TO SPECIES OF *Pachygrapsus***

1. Lateral margins of carapace with 2 teeth behind exorbital angle. *West Atlantic, Mediterranean, Black Sea*..... ***Pachygrapsus marmoratus***
  - Lateral margins of carapace with 1 tooth behind exorbital angle..... 2
  - Lateral margins of carapace without tooth behind exorbital angle..... 7
2. Anterior margin of front straight (Fig. 4b); upper margin of dactyl of chela minutely tuberculated throughout (Fig. 4c); lateral margins of carapace strongly convergent posteriorly; carapace and ambulatory legs with numerous small spots. *East and west Atlantic*..... ***Pachygrapsus gracilis***
  - Anterior margin of front sinuous; upper margin of dactyl of chela smooth; lateral margins of carapace faintly convergent posteriorly; carapace, ambulatory legs without spots 3
- 3(2). Carapace markedly convex, cl usually less than 12 mm; infraorbital margin feebly denticulated with low outer notch (Fig. 14i); lower margin of P5 merus with submedian tubercle; G1 with sickle-like tip (Fig. 15i). *Central Atlantic (St. Helena and Ascension islands)*..... ***Pachygrapsus loveridgei***
  - Carapace feebly convex, cl usually more than 12 mm; infraorbital margin markedly denticulated with deep outer notch; lower margin of P5 merus without submedian tubercle; G1 without sickle-like tip 4
- 4(3). P5 merus with spines at distoventral angle (Fig. 5e); brush of setae often present on P2 or P3 propodi 5
  - P5 merus without spines at distoventral angle (Fig. 2d); no brush of setae on P2 or

- P3 propodi..... 6
- 5(4). Distal process of G1 petal-like (Fig. 15l); P2 propodus with brush of setae (sometimes absent on large males). *Mediterranean, west and east Atlantic; east Pacific ...*  
..... ***Pachygrapsus transversus***
- Distal process of G1 bluntly rounded, with horizontal corneous process (Fig. 14b); P3 propodus usually with brush of setae (Fig. 5d). *West and central south Pacific....*  
..... ***Pachygrapsus laevimanus***
- 6(4). Medium-size species (cl 10–20 mm); anterior margin of front distally angular (Fig. 8b); infraorbital margin slightly denticulated with outer notch obliquely oriented (Fig. 14k); carapace with a marbled colour pattern (Fig. 8a); *Azores, Madeira and Canary Is.; Mediterranean ...*  
..... ***Pachygrapsus maurus***
- Large-size species (cl often more than 20 mm); anterior margin of front with 2 lobules distally (Fig. 2b); infraorbital margin strongly denticulated with deep outer notch, not obliquely oriented (Fig. 14g); carapace green or black, without noticeable marble pattern. *East and northwest Pacific ...*  
..... ***Pachygrapsus crassipes***
- 7(1). Fingers of chelae with rows of setae at tip (Fig. 10c); carapace flattened, almost smooth, with only thin striae on protogastric, hepatic, and branchial regions (Fig. 10a); anterior margin of front almost straight (Fig. 10b); *Indo-West Pacific and Clipperton I. ....*  
..... ***Pachygrapsus planifrons***
- Fingers of chelae without rows of setae at tip; carapace convex, noticeably striated; anterior margin of front sinuous..... 8
- 8(7) Carapace coarsely striated overall, striae with abundant setae (Fig. 3a); outer face of chela with longitudinal striae; medium-size species (cl 10–20 mm)..... 9
- Carapace with thin and glabrous striae (Fig. 9a); outer face of chela smooth, with single stria near lower margin; small-size species (cl usually less than 10 mm)..... 11
- 9(8). Lateral margins of carapace faintly convergent posteriorly (Fig. 11a); abdominal tergites smooth (Fig. 11f); outer face of chela with glabrous longitudinal striae (Fig. 11c); distal process of G1 petal-like (Fig. 15e). *Indo-West Pacific ...*  
..... ***Pachygrapsus plicatus***
- Lateral margins of carapace subparallel (Fig. 3a); abdominal tergites with striae (Fig. 3e–f); outer face of chela with setiferous, longitudinal striae (Fig. 3c); distal process of G1 acicular (Fig. 15a–f) 10
- 10(9). Striae on abdominal tergites numerous, and setiferous (Fig. 3e, f). *Northwest and central Pacific ...*  
..... ***Pachygrapsus fakaravensis***
- Striae on abdominal tergites scarce, with only few setae (Fig. 1d). *West and central Atlantic ...*  
..... ***Pachygrapsus corrugatus***
- 11(8). Lateral margins of carapace strongly convergent posteriorly (Fig. 9a); P5 merus with submedian tubercle on lower margin (Fig. 9d). *Indo-West Pacific, Clipperton I., and Revillagigedo Is. ....*  
..... ***Pachygrapsus minutus***
- Lateral margins of carapace faintly convergent posteriorly; P5 merus without sub-

median tubercle on lower margin. *West Indian Ocean* .... *Pachygrapsus propinquus* (status uncertain; potential junior synonym of *P. minutus*)

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Many contributed to this review. Particularly important was access to collections and libraries at MNHN and USNM, which was possible thanks to the help of R. Cleva and D. Guinot (MNHN) and R. Lemaitre (USNM), who obtained travel support for the first author through the Smithsonian's Rathbun Fund.

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## Appendix

The characters listed below have been arbitrarily weighted (W), according to their usefulness in separating species from W10 (good) to W0 (poor).

- 1) Number of teeth behind exorbital angle (W10). 1 – no tooth (*P. fakaravensis*, *P. corrugatus*, *P. plicatus*, *P. minutus*, *P. propinquus*, *P. planifrons*); 2 – one tooth (*P. crassipes*, *P. gracilis*, *P. laevimanus*, *P. loveridgei*, *P. maurus*, *P. transversus*); 3 – two teeth (*P. marmoratus*).
- 2) Distal view of G1 (W10). Available for males only and unknown for *Pachygrapsus propinquus*. Six states arbitrarily identified only for the key: tip of G1: 1 – petal-like (*P. planifrons*, *P. plicatus*, *P. transversus*); 2 – sickle-like (*P. loveridgei*); 3 – acicular (*P. fakaravensis*, *P. corrugatus*); 4 – bluntly rounded with short corneous process (*P. crassipes*, *P. gracilis*, *P. marmoratus*, *P. maurus*); 5 – bluntly rounded with horizontal corneous process (*P. laevimanus*); 6 – rounded with short vertical gutter-like process (*P. minutus*).
- 3) Presence of rows of setae at tips of fingers of chelae (W9). Two states: 1 – present (*P. planifrons*); 2 – absent (all other species).
- 4) Striation of the carapace (W8). Three states: carapace is: 1 – coarsely striated with setiferous striae (*P. corrugatus*, *P. fakaravensis*, *P. plicatus*); 2 – striated at least on gastric and branchial region, striae smooth or furnished only with sparse setae (*P. crassipes*, *P. gracilis*, *P. laevimanus*, *P. loveridgei*, *P. minutus*, *P. maurus*, *P. marmoratus*, *P. propinquus*); 3 – almost smooth, with at most thin striae behind exorbital angle (*P. planifrons*). State 2 is heterogeneous: species such as *P. transversus* have the carapace striated overall (Fig. 13a); other species, such as *P. gracilis*, *P. loveridgei*, *P. minutus* (Fig. 4a, 6a, 9a) have only few striae on cardiac and intestinal regions.
- 5) Abdominal tergites (W8). Three states: abdominal tergites have: 1 – numerous setiferous striae (*P. fakaravensis*); 2 – scarce striae, feebly setiferous (*P. corrugatus*); 3 – no striae (all other species).
- 6) Upper margin of dactyli of chela (W8). Three states: upper margin can be: 1 – minutely denticulated overall (*P. gracilis*); 2 – with 1–2 tuberculated carinae on proximal half (*P. corrugatus*, *P. fakaravensis*, *P. plicatus*); 3 – smooth (remaining taxa). State 3 is applied to *P. marmoratus* but the upper margin of the dactyl of the larger specimens can have few tubercles proximally.
- 7) Anterior margin of front (W7). Two states: anterior margin is: 1 – straight (*P. gracilis*, *P. planifrons*, *P. marmoratus*); 2 – sinuous (all other species). State 1 is somewhat heterogeneous: in *Pachygrapsus gracilis* the front is straight overall (Fig. 4b); in *P. marmoratus* and *P. planifrons* it is slightly curved near outer angles (Fig. 7b, 10b).
- 8) Distoventral angle of P5 merus (W7). Two states: distoventral angle is: 1 – spinous (*P. gracilis*, *P. laevimanus*, *P. loveridgei*, *P. minutus*, *P. planifrons*, *P. plicatus*, *P. propinquus*, *P. transversus*); 2 – rounded or only with low indentations (*P. corrugatus*, *P. crassipes*, *P. fakaravensis*, *P. marmoratus*, *P. maurus*).
- 9) Outer face of chelae (W6). Four states: outer face of chelae is: 1 – smooth, with at



- most a faint stria on fixed finger and/or palm, near lower margin (*P. crassipes*, *P. gracilis*, *P. laevimanus*, *P. marmoratus*, *P. maurus*, *P. planifrons*); 2 – with a single noticeable stria near lower margin, from tip of finger to near carpal articulation (*P. loveridgei*, *P. minutus*, *P. propinquus*, *P. transversus*); 3 – with several setiferous longitudinal striae (*P. corrugatus*, *P. fakaravensis*); 4 – with several glabrous longitudinal striae (*P. plicatus*). Distinction between states 1 and 2 is sometimes difficult. For example, state 2 applies to *Pachygrapsus minutus* (Fig. 9c) but the longitudinal stria near lower margin becomes unnoticeable on the smallest specimens examined. Conversely, state 1 applies to *P. crassipes* and *P. laevimanus* (Fig. 2c, 5c) but a faint stria is sometimes present near lower margin on the smallest specimens.
- 10) Size (W6). Three states: carapace size is: 1 – small, cl usually less than 10 mm (*P. gracilis*, *P. loveridgei*, *P. minutus*, *P. planifrons*, *P. propinquus*); 2 – medium, cl 10–20 mm (*P. corrugatus*, *P. fakaravensis*, *P. laevimanus*, *P. maurus*, *P. plicatus*); 3 – large, cl often more than 20 mm and up to 40 mm (*P. crassipes*, *P. marmoratus*, *P. transversus*). This character is difficult to evaluate when only few specimens are available; state 1 applies to *Pachygrapsus gracilis* and *P. loveridgei*, but maximum cl can be 12 mm for these species.
  - 11) Direction of lateral margins of the carapace (W6). Lateral margins can be: 1 – subparallel (*P. corrugatus*, *P. fakaravensis*, *P. marmoratus*); 2 – faintly convergent posteriorly (*P. crassipes*, *P. laevimanus*, *P. loveridgei*, *P. maurus*, *P. transversus*, *P. plicatus*, *P. propinquus*); 3 – strongly convergent posteriorly (*P. gracilis*, *P. minutus*, *P. planifrons*). State 1 is easy to differentiate, but distinction between states 2 and 3 is more difficult. For example, the posterior convergence is more pronounced on small specimens of *P. transversus* and in this case state 3 could be applied instead of state 2.
  - 12) Infraorbital margin (W6). Two states: infraorbital margin is: 1 – smooth or feebly denticulated (*P. gracilis*, *P. loveridgei*, *P. minutus*, *P. planifrons*, and possibly *P. propinquus*); 2 – obviously denticulated (all other species).
  - 13) Outer notch of infraorbital margin (W5). Three states: outer notch of infraorbital margin is: 1 – absent (*P. gracilis*, *P. minutus*); 2 – low (*P. loveridgei*, *P. planifrons*, *P. propinquus*); 3 – deep (all other species).
  - 14) Brush of setae on anterodorsal surface of the P2 or P3 propodi (W4). Three states: brush of setae is: 1 – absent (*P. corrugatus*, *P. crassipes*, *P. fakaravensis*, *P. gracilis*, *P. marmoratus*, *P. maurus*, *P. planifrons*, and possibly *P. propinquus*); 2 – present on P2 propodi (*P. loveridgei*, *P. minutus*, *P. plicatus*, *P. transversus*); 3 – present on P3 propodus (*P. laevimanus*). Important as it can be in species such as *Pachygrapsus laevimanus*, this character is often difficult to use. State 1 applies to *Pachygrapsus maurus* and *P. marmoratus* with hesitation because in juveniles a faint brush of setae is present on the P2 propodi (and sometimes P3). Conversely, the brush of setae tends to disappear in larger males of *P. laevimanus*, *P. loveridgei*, *P. minutus*, and *P. plicatus*. The development of this brush appears therefore to be sex and size related and it must be

used with caution.

- 15) Presence of a submedian tubercle on the lower margin of P5 merus (W4). Two states: submedian tubercle is: 1 – present (*P. gracilis*, *P. loveridgei*, *P. minutus*); 2 – absent (all other species). Presence of this tubercle is characteristic of the small-size species, such as *Pachygrapsus minutus* (Fig. 9d). It is not a very good character because it is size related. The tubercle is sometimes present in juveniles of species that lack this formation in the adults (e.g. *P. transversus*), and it tends to disappear in larger specimens of species that usually have it (e.g. *P. loveridgei*).
- 16) Distal view of male abdomen (W2). Two states: distal part of male abdomen (sixth somite and telson) is: 1 – not triangular (*P. gracilis*, *P. loveridgei*, *P. transversus*); 2 – triangular (all other species). State 1 is obvious only in *P. loveridgei* (Fig. 6e). This character is sometimes difficult to evaluate because it is size related.