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Monograph



# ZOOTAXA



# **Revision of the family Euryplacidae Stimpson, 1871** (Crustacea: Decapoda: Brachyura: Goneplacoidea)

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# Abstract

The family Euryplacidae Stimpson, 1871, traditionally included in the Goneplacidae MacLeay, 1838, is revised based on the examination of the type material of many of its species as well as unidentified and previously identified material from around the world. The revised family now consists of 31 species (including five that are described as new) belonging to 13 genera (including four that are described as new): Eucrate De Haan, 1835, with eight species, of which one is new; Euryplax Stimpson, 1859, with two species; Frevillea A. Milne-Edwards, 1880, with three species; Henicoplax n. gen., with five species of which three are new; *Heteroplax* Stimpson, 1858, monotypic; *Machaerus* Leach, 1818, with two species; Nancyplax Lemaitre, García-Gómez, von Sternberg & Campos, 2001, monotypic; Platyozius Borradaile, 1902, monotypic; Psopheticoides Sakai, 1969, monotypic; Systroplax n. gen., monotypic; Trissoplax n. gen., with two species, of which one is new; Trizocarcinus Rathbun, 1914, with two species; Villoplax n. gen., monotypic; and Xenocrate Ng & Castro, 2007, monotypic. The genus Platyozius and Eucrate formosensis Sakai, 1974, are removed from the synonymy of Eucrate and E. alcocki Serène, in Serène & Lohavanijaya, 1973, respectively. Neotypes are selected for Heteroplax dentata Stimpson, 1858, and Pilumnoplax sulcatifrons Stimpson, 1858, two species described from Hong Kong that have a confusing taxonomic history. A neotype is also selected for Euryplax nitida Stimpson, 1859, described from the Florida Keys. Seven nominal species described by other authors were found to be junior subjective synonyms for other species: Eucrate affinis Haswell, 1882, E. costata Yang & Sun 1979, E. haswelli Campbell 1969, and Pseudorhombila sulcatifrons var. australiensis Miers, 1884, of Trissoplax dentata (Stimpson, 1858); Galene laevimanus (Lucas, in Jacquinot & Lucas, 1853) of Eucrate dorsalis (White, 1849); Heteroplax nagasakiensis Sakai, 1934, of H. transversa Stimpson, 1858; and Pilumnoplax sulcatifrons Stimpson, 1858, of Eucrate crenata (De Haan, 1835). Eight euryplacid genera are exclusively found in the Indo-West Pacific region (except one species introduced in the Mediterranean), one is exclusive to each the Eastern Atlantic and Tropical Eastern Pacific regions, three to the Western Atlantic region, and one genus has both Western Atlantic and Tropical Eastern Pacific species.

**Key words**: Decapoda, Crustacea, Brachyura, Goneplacoidea, Euryplacidae, new genera, new species, revision, *Eucrate*, *Euryplax*, *Frevillea*, *Henicoplax* n. gen., *Heteroplax*, *Machaerus*, *Nancyplax*, *Platyozius*, *Psopheticoides*, *Systroplax* n. gen., *Trissoplax* n. gen., *Trissoplax* n. gen., *Xenocrate* 

# Introduction

Euryplacid crabs have long been grouped as a subfamily of the family Goneplacidae MacLeay, 1838, a taxon that proved to be polyphyletic (see Ng & Manuel-Santos 2007; Castro 2007; Ng *et al.* 2008). The Euryplacidae *sensu lato* is a relatively homogeneous and well-defined taxon that together with other families is grouped in the superfamily Goneplacoidea, a taxon that, however, may ultimately prove to be polyphyletic (Ng *et al.* 2008; Castro *et al.* 2010) as phylogenetic relationships at the superfamily level are still relatively poorly understood.

Although the genera now recognised as members of the Euryplacidae were traditionally included in the Goneplacidae, some of the unique characters they share have long been recognized. Miers (1886: 222), who proposed grouping goneplacid genera based on the morphology of the male sternum, placed the euryplacid genera among those where the last somite of the sternum is for the most part concealed by the closed abdomen in contrast to those where the last somite of the sternum remains exposed by the closed abdomen. A separate subfamily within the Goneplacidae *sensu lato*, the Euryplacinae, was established by Stimpson (1871: 150), who noted the "verges [penises] lodged in covered or closed canals" in *Euryplax nitida* but he did not provide a diagnosis to the subfamily.

Similarities in the general morphology of the carapace in taxa once included in the polyphyletic Goneplacidae *sensu lato*, led some of the euryplacid genera to be grouped with unrelated genera, some now included in separate families. Alcock (1900: 292), for instance, included *Eucrate* De Haan, 1835, *Frevillea* A. Milne-Edwards, 1880 (as *Freyvillea* [sic]) and *Heteroplax* Stimpson, 1858, together with goneplacid genera such as *Carcinoplax* H. Milne Edwards, 1852, and *Psopheticus* Wood-Mason, 1892, in the subfamily Pseudorhombilinae Alcock, 1900, of Goneplacidae *sensu lato*, whereas *Euryplax* Stimpson, 1859, was attached to the Prionoplacinae Alcock, 1900, now a junior synonym of Eucratopsinae Stimpson, 1871, in the Panopeidae Ortmann, 1893 (see Ng *et. al.* 2008).

Euryplacids were not studied in detail as a group until Guinot's extensive studies (1969a–c, 1971), who also referred to the euryplacine genera as the *lignée euryplacyenne* of the Goneplacidae *sensu lato* (1969b: 507) and as *Goneplacidae euryplaciens* (Guinot 1971: 1080). Her work moved away from the use of the morphology of the carapace as an important character and concentrated instead on the morphology of the sternum, abdomen, and the male external reproductive structures, an approach we follow here.

The Euryplacinae continued to be included in the Goneplacidae (i.e. Davie 2002; Karasawa & Kato 2003a, b) although d'Udekem d'Acoz (1999: 241) had raised the taxon to a family status, a position previously suggested by Guinot (1969b) (see Castro 2007: 612). Števčić (2005), Karasawa & Schweitzer (2006), and Ng & Manuel-Santos (2007) recognised its familial status. Števčić (2005) placed the family in the superfamily Euryplacoidea without explanation and without including a list of genera other than the type genus, *Euryplax*. Ng & Castro (2007: 44) provisionally included 12 genera in the family, whereas Ng *et al.* (2008: 78) restricted the family to 10 genera, referring three monotypic genera to other families: *Chasmophora* Rathbun, 1914, to the Panopeidae Ortmann, 1893, *Eucratodes* A. Milne-Edwards, 1880, to Xanthidae MacLeay, 1838, and *Trapezioplax* Guinot, 1969, to Pseudorhombilidae Alcock, 1900. The placement of one genus, *Sotoplax* Guinot, 1984, which Guinot (1984) had originally placed with doubt in the Euryplacidae, was also questioned by Ng *et al.* (2008). It has been transferred to its own family (Castro *et al.* 2010).

The present revision of the Euryplacidae has allowed us to examine the type material of most species and particularly investigate the status of several species that have been problematic for a long time. Of particular significance are three species (*Heteroplax dentata*, *H. transversa* and *Pilumnoplax sulcatifrons*) that were described by Stimpson (1858) from material collected in Hong Kong, whose identitities have been ambiguous or contentious for a long time owing to their short descriptions without illustrations and the loss of the type material.

# **Terminology and Presentation**

Morphological terms essentially follow the terminology used by Castro (2007). The "outer orbital tooth" is used for a tooth connected to each of the orbits instead of the "first anterolateral tooth" of some authors, with the teeth behind the orbital margin referred to as "anterolateral teeth". Pereopods are referred to by the abbreviations P1 (chelipeds) and P2 to P5 (ambulatory legs); the first and second pairs of male pleopods by G1 and G2, respectively. Following general usage, the exposed terminal portion of the vas deferens that delivers sperm to the G1 has been referred to as "penis" although it does not truly function as the copulatory organ. A sclerotised extension of the sternum covering of the vulva is referred to as "sternal vulvar cover" instead of "operculum". The term "median groove" is used for the longitudinal groove across the median portion of the thoracic sternites 7 and 8 instead of the more commonly used "median line" (see Guinot 1979; Guinot & Quenette 2005; Secretan 1998; Sternberg & Cumberlidge 2003) to emphasize it as a tri-dimensional rather than a bi-dimensional structure. Carapace length (cl) was measured along the median portion of the carapace from the middle of the front to the middle of the posterior border of the carapace; carapace width (cw) across the widest breadth of the carapace, in most cases between the longest anterolateral teeth but between the outer orbital teeth in a few species. The type material examined was re-measured. The supraorbital width of each orbit was measured from the outer angle of the frontal margin to the tip of the outer orbital tooth; the length of each eye peduncle was measured dorsally from the proximal edge of the peduncle to the margin of the cornea immediately posterior to the thin extension of the peduncle; the length of the cornea dorsally from its proximal edge posterior to the thin extension of the peduncle to its distal margin; frontal width between the outer edges of the frontal margin. The total length of the merus of the fifth percopods (P5) was measured along the dorsal margin, width across the median portion of the article. Unless missing, right perceptds were used in the measurements. In their descriptions, paired appendages and structures, including G1, G2, and the vulvae, are referred to in the singular for simplicity. Genera and species are arranged in alphabetical order.

A complete diagnosis is given for the family and all genera. The diagnoses for species, however, are more concise and consist only of the most important characters separating each species from their congeners.

The material examined and depository institutions are abbreviated as follow: Academia Sinica, Taipei, Taiwan (ASIZ); Beijing Museum of Natural History, China (BMNH); Florida Museum of Natural History, Gainesville, Florida (UF); Institute Oceanographique, Nhatrang, Viet Nam (ION); Kanagawa Prefectural Museum of Natural History, Odawara, Japan (KPM); Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts (MCZ); Muséum national d'Histoire naturelle, Paris (MNHN); Carcinological Reference Collection, National Museum of the Philippines, Manila (NMCR); The Natural History Museum, London, (NHM); Natural History Museum and Institute, Chiba, Japan (CBM-ZC); Natural History Museum of Los Angeles County, California (LACM); Naturalis (formerly Nationaal Natuurhistorisch Museum), Leiden, The Netherlands (RMNH); Peabody Museum of Natural History, Yale University (YPM); Swire Institute of Marine Science, Hong Kong (SWIMS); University Museum of Zoology, University of Cambridge, Cambridge, U. K. (UMZC); United States National Museum, Smithsonian Institution, Washington, D.C. (USNM); Zoologisk Museum, Københavns Universitet, Copenhagen (ZMUC); Zoological Reference Collection, Raffles Museum of Biodiversity Research, National University of Singapore (ZRC).

#### **Taxonomic Account**

# Superfamily GONEPLACOIDEA MacLeay, 1838 Family EURYPLACIDAE Stimpson, 1871

Euryplacinae Stimpson, 1871: 150. — Guinot 1969b: 507 [discussion]; 1971: 1080 [in list, list of genera and species]. —
Serène & Lohavanijaya 1973: 70. — Williams 1984: 431 [in key], 431 [diagnosis]. — Davie, 2002: 192 198. —
Karasawa & Kato, 2003a: 147, 151 [in list]; 2003b: 130 [in list], 137 [in list], 138 [diagnosis].

Euryplacidae — d'Udekem d'Acoz (1999): 241. — Števčić 2005: 71. — Karasawa & Schweitzer 2006: 41, 55, 57 [diagnosis]. — Castro 2007: 612, 613, 617, 619. — Ng & Castro 2007: 43 [discussion, diagnosis]. — Ng *et al.* 2008: 78 [discussion]. — De Grave *et al.* 2009: 33 [in list]. — Castro *et al.* 2010: table 1 [discussion].

Euryplacoidea — Števčić 2005: 71.

Diagnosis. Carapace transversely rectangular, trapezoidal, quadrate, or suboctagonal; dorsal surface smooth, without well defined regions, or with variously developed setose grooves, depressions, ridges; anterolateral borders arched, nearly straight, or straight, with 1–3 teeth posterior to outer orbital tooth. Orbits short to long, eye peduncles short to moderately long. Basal antennal article typically immobile (mobile or slightly mobile in some species, small individuals of many other species). Orbital hiatus almost always closed by basal antennal article excluding antennal flagellum from orbit (basal antennal article does not fill orbital hiatus in Frevillea [Fig. 19B; Guinot 1969b: fig. 40]). Anterior border of endostome well demarcated from buccal cavern, ridges faint but clearly defined. Third maxillipeds completely closing buccal cavern; anteroexternal margin of merus angular or ariculiform. Usually no visible stridulating mechanism (but present in *Nancyplax* Lemaitre, García-Gómez, von Sternberg & Campos, 2001, and Trizocarcinus Rathbun, 1914). Thoracic sternum with suture 2/3 complete, convex or straight; 4/5, 6/7, 7/8 interrupted, 5/6 complete (interrupted in *Nancyplax* [Fig. 31F, G], Systroplax n. gen. [Fig. 37G], Xenocrate Ng & Castro, 2007 [Fig. 49G, H]); median groove on thoracic sternites 7, 8 (e.g. Figs. 11F; 17G). Sterno-abdominal cavity of male deep, long, reaching anterior margin of sternite 4 (3/4 suture scar) (e.g. Figs. 3C; 16D). Male abdomen typically narrow, slender (T-shaped), lateral margins of somites 4-6 abruptly narrowing from somite 3 to narrow telson (Fig. 1C, D), but width of abdomen varying in remaining genera from moderately wide but not triangular (Euryplax, Frevillia, Machaerus Leach, 1818; Fig. 1B) to clearly triangular (Nancyplax, Trizocarcinus, Villoplax n. gen.; Fig. 1A); telson slender, much longer than wide (wider than long in Nancyplax; Fig. 32G); somite 6 much longer than wide, somite 5 as long as wide. Press-button of male abdominal-locking mechanism as tubercle near thoracic suture 4/5 (e.g. Figs. 11E; 17D) (present also in females of 7 genera where pre-adult females are known). Sternite 8 of male almost always completely covered by abdominal somites 2, 3 when abdomen closed but small portion exposed in some species. G1 long, slender, slightly curved or straight, slender part gradually tapering distally, varying number of small denticles along distal portion, acuminate apex (e.g. Figs. 11E; 14A, B, D, E) (arrowhead-shaped in Psopheticoides Sakai, 1969; Fig. 38D, E). G2 short (less than 1/3 length of G1), apex with 2 unequal acute or obtuse processes (e.g. Fig. 14C, F) Male genital opening (male gonopore) large, opening just anterior to the coxo-sternal condyle of P5 coxa (e.g. Figs. 30F; 31F). Clear coxo-sternal disposition, with long penis protected by concavity (sometimes called "tube") along posterior portion of thoracic sternite 7 at the level of thoracic suture 7/8 (sometimes extending to thoracic sternite 8), prolongation of episternite 7, transversely wide abdominal somite 3 (close proximity or near overlapping of episternite 7 with sternite 8 over penis in Euryplax but never forming close channel; Fig. 16E). Female abdomen relatively narrow, not covering outer portions of thoracic sternum, with 6 freely-mobile somites, large portions left exposed by abdominal somites 2, 3 of closed abdomen (e.g. Figs. 25F; 26D). Vulva ovoid, rounded, or elongated, extending across anterior third of sternite 6 relatively close to median axis of thorax (e.g. Figs. 3G; 19H); covered by soft membrane, sternal vulvar cover generally absent (present in Psopheticoides Sakai, 1969, Trissoplax n. gen. [Figs. 36G; 41G]); margins typically thick, often elevated.

# Type genus. *Euryplax* Stimpson, 1859

**Extant genera included.** *Eucrate* De Haan, 1835; *Euryplax* Stimpson, 1859; *Frevillea* A. Milne-Edwards, 1880; *Heteroplax* Stimpson, 1858; *Henicoplax* **n. gen.**; *Machaerus* Leach, 1818; *Nancyplax* Lemai-tre, García-Gómez, von Sternberg & Campos, 2001; *Platyozius* Borradaile, 1902; *Psopheticoides* Sakai, 1969; *Systroplax* **n. gen.**; *Trizocarcinus* Rathbun, 1914; *Xenocrate* Ng & Castro, 2007; *Villoplax* **n. gen**.

**Fossil genera included** (*fide* De Grave *et al.* 2009: 33). *Chirinocarcinus* Karasawa & Schweitzer, 2004; *Chlinocephalus* Ristori, 1886; *Corallicarcinus* Müller & Collins, 1991; *Orbitoplax* Tucker & Feldmann, 1990; *Paleopsopheticus* Hu & Tao, 1996; *Simonellia* Vinassa de Regny, 1897; *Stoaplax* Vega, Cosma, Coutiño, Feldmann, Nyborg, Schweitzer & Waugh, 2001; *Viaplax* Karasawa & Kato, 2003.

**Remarks.** The characters that are diagnostic of the Euryplacidae (see Guinot 1969b: 507, as Euryplacinae; Števčić 2005: 71; Karasawa & Schweitzer 2006: 57; Castro 2007: 617; Ng & Castro 2007: 43) are for the most part relatively homogeneous. One notable exception is the relative width of the male abdomen. In most species, the male abdomen is narrow, slender, and T-shaped, with the lateral margins of somites 4–6 abruptly narrowing from somite 3 (Fig. 1C, D). The width of the abdomen nevertheless varies almost as a continuum

from narrow to wide among euryplacid genera, being comparatively wider, triangular, and thus not T-shaped, in *Nancyplax* (Fig. 32G), *Trizocarcinus* (Figs. 1A; 46C, I), and *Villoplax* **n. gen.** (Fig. 48D), whereas it is intermediate in shape in *Euryplax* (Figs. 16D, F; 17E, F), *Frevillea* (Fig. 19D), and *Machaerus* (Figs. 1B; 29B).



**FIGURE 1.** Variation in the shape of the male abdomen among the genera of Euryplacidae. A, *Trizocarcinus dentatus* (Rathbun, 1893); male (14.7 mm  $\times$  20.2 mm) (MNHN-B20990), Mexico, Gulf of California; B, *Machaerus oxyacanthus* (Monod, 1956), male (19.0 mm  $\times$  30.3 mm) (MNHN-B10242), Sierra Leone; C, *Systroplax angusta* (Rathbun, 1914), male (32.3 mm  $\times$  37.2 mm) (MNHN-B29377), Fiji; D, *Eucrate solaris* Yang & Sun, 1979, male (23.3 mm  $\times$  28.1 mm) (ZRC 2008.1333), Philippines, Bohol, Panglao. Abbreviations: a3 = abdominal somite 3.

The slender, T-shaped abdomen of most euryplacids (20 species assigned to eight genera) is found only in species restricted to the Indo-West Pacific region (which includes one species introduced to the Mediterranean Sea), whereas the wider abdomen, either triangular or intermediate between slender and triangular, is present

in nine species (six genera) that are restricted to the tropical and subtropical Atlantic and Eastern Pacific. Of the four species having a clearly triangular abdomen (*Nancyplax*, *Trizocarcinus*, and *Villoplax* **n. gen.**), two are Western Atlantic and two Tropical Eastern Pacific in distribution. Among intermediate shapes, one species of *Euryplax* and three of *Frevillea* are restricted to the Western Atlantic, one of *Euryplax* to the Tropical Eastern Pacific, and two of *Machaerus* to the Eastern Atlantic.

Genera having a male abdomen that is triangular or that is intermediate between slender and triangular nevertheless share with euryplacids having a slender abdomen the narrow and deep sterno-abdominal cavity and long and slender G1, characters found in all members of the Euryplacidae.

Another difference between Indo-West Pacific species and those in the tropical and subtropical Atlantic and Eastern Pacific is that in most Indo-West Pacific species the thoracic sternite 8 of the male is completely or almost completely covered by the closed abdomen (e.g. Figs. 3F; 36F) whereas in the second group a small portion is exposed, even if somite 2 is transversely longer than somite 3 (e.g. Figs. 16F; 30G; 44G). There are exceptions, however. In two Western Hemisphere genera, *Frevillea* and *Villoplax* **n. gen.**, thoracic sternite 8 is covered by the abdomen, whereas in some species of the Indo-West Pacific genera *Henicoplax* **n. gen.** and *Trissoplax* **n. gen.**, a small portion of sternite 8 is exposed on each side. This is particularly evident in *Henicoplax* **eriochir n. sp.**, where a relatively large portion of sternite 8 is exposed (Fig. 21C).

There are no clear-cut morphological differences between Indo-West Pacific euryplacids and those found in the tropical Atlantic and Eastern Pacific, and therefore no evidence supporting a hypothesis that the two groups represent different lineages corresponding to subfamilies of the Euryplacidae.

The male genital opening, or gonopore, is large and coxal as in other members of the Goneplacoidea (Castro *et al.* 2010), being located immediately above the coxo-sternal condyle of the P5 coxa (Figs. 30F; 31F; 32A, C).

Although the long penis emerges from the P5 coxa, it shows a coxo-sternal condition, as named by Guinot (1978: 244), because it is protected by a concavity on thoracic sternite 7 (sometimes also on thoracic sternite 8), a modification that has sometimes been referred to as a penial "groove" or "tube". The emergence of the penis onto the sternum has led some to interpret the male gonopore as functionally sternal by some workers, e.g. Davie (2002: 198), who commented that it was "clearly sternal with penis free but lying in more or less well-developed groove; becoming sternal with penis sheathed and/or protected proximally by a covered groove; or sternal, with penis lying in closed canal". There can be no doubt that the gonopore is coxal in all goneplacoids, but with the emergence of the penis showing various trends from a coxal to a sternal position among several families of the Goneplacoidea (see Castro *et al.* 2010; Guinot *et al.* in prep.).

Protection of the penis in the Euryplacidae may also be provided by various modalities of the overlapping of thoracic somite 7 (often together with an expansion of episternite 7) and sternite 8. This is particularly well developed in *Euryplax* (see Remarks for *Euryplax* below) but it can also be observed in *Heteroplax*.

The various genera treated here also appear to show an interesting pattern in the adult carapace size in relation to how far the sterno-abdominal cavity reaches thoracic suture 2/3. The anterior edge of the sterno-abdominal cavity and the tip of the male telson are approximately between thoracic sternites 3 and 4 in most euryplacid genera. In *Henicoplax* **n. gen.**, in which the adult sizes of its members are relatively small (less than 10 mm carapace width), the anterior edge of the sterno-abdominal cavity and the tip of the male telson reaches relatively close to the thoracic suture 2/3 (Figs. 21B; 22B; 25B). In one of the smallest species, *H. trachydactylus* **n. sp.**, the cavity and telson almost reaches thoracic suture 2/3 (Fig. 26B). This pattern is also probably correlated with the relative width of the carapace: species of *Henicoplax* **n. gen.** tend to have relatively wider carapaces than in other genera. In large-size species of euryplacids in which the carapace is also relatively broad (*Heteroplax sensu stricto*), the sterno-abdominal cavity is not substantially displaced anteriorly (Fig. 28C, D).

*Carcinoplax microphthalmus* Guinot & Richer de Forges, 1981, which Castro (2007: 623) referred to as having affinities to the Euryplacidae, is not a member of the family. It belongs instead in the Progeryonidae Števčić, 2005, as *Rhadinoplax microphthalmus* (Guinot & Richer de Forges, 1981) (see Castro & Ng 2008). The identity of *Galene panopeoides* White, 1847, a *nomen nudum* listed under *incertae sedis* in the Euryplacidae (Ng *et al.* 2008: 79), remains unknown.

# Key to genera of Euryplacidae

| 1.  | Male abdomen clearly narrow, slender, T-shaped (Fig. 1C, D); Indo-West Pacific distribution (but one species intro-                                    |
|-----|--|
|     | duced in the Mediterranean Sea)  |
| _   | Male abdomen clearly triangular (Fig. 1A, B) or proportionally wide, not slender, T-shaped; tropical and subtropical                                   |
|     | Atlantic and Eastern Pacific distribution  |
| 2.  | Orbits, eye peduncles short, eye peduncles as short as or slightly longer than corneas   |
| _   | Orbits, eye peduncles long, eye peduncles much longer than corneas   |
| 3.  | Corneas reniform, dorsoventrally flattened (Fig. 36B); G1 with arrowhead-shaped apex (Fig. 38D, E)   |
|     | Psopheticoides   |
| _   | Corneas spherical, not dorsoventrally flattened (e.g. Figs. 3B; 16C); G1 with acuminate apex (e.g. Figs. 14A; 20A,                                     |
|     | D)   |
| 4.  | Sulcus posterior to orbits extending along anterior border of carapace between anterolateral borders (Fig. 34E)  |
| _   | No sulcus extending along anterior border of carapace between anterolateral borders (if sulcus present it is short, not                                |
|     | extending between anterolateral borders)   |
| 5.  | P5 dactylus, propodus proportionally slender (e.g. Fig. 2), with only scattered setae; conspicuous tomentum on che-<br>lineds                          |
| _   | P5 dactylus propodus proportionally wide with many long setae (Figs 37A: 49A): no conspicuous tomentum on  |
|     | chelipeds  |
| 6.  | Each side of carapace with two short, inconspicuous anterolateral teeth (Figs. 37A, B; 38I, J) Systroplax n. gen.                                      |
| -   | Each side of carapace with two acute, conspicuous anterolateral teeth (Fig. 49A, B)  |
| 7.  | One short anterolateral tooth posterior to outer orbital tooth on each side of carapace (e.g. Figs. 21A; 23A), trans-                                  |
|     | verse depression (postorbital ridge) posterior to each orbit (except in one species)   |
| -   | Two or three anterolateral teeth posterior to outer orbital tooth on each side of carapace, carapace without transverse                                |
|     | depression posterior to orbits   |
| 8.  | First anterolateral tooth minute, inconspicuous, leaving wide, straight margin between outer orbital tooth and second                                  |
|     | (largest) anterolateral tooth (Fig. 28A, D), thus having only two large anterolateral teeth posterior to outer orbital                                 |
|     | tooth on each side of carapace   |
| -   | First anterolateral tooth large, conspicuous, thus having three large anterolateral teeth posterior to outer orbital tooth<br>on each side of carapace |
| 9   | Anteroexternal margin of third maxillineds auriculiform (Fig. 41A) Trissonlax <b>n</b> . gen.  |
| _   | Anteroexternal margin of third maxillineds angular (Figs. 29D: 30C) Machaerus  |
| 10  | Outer orbital tooth short inconspicuous (Fig. 31A–C)   |
| -   | Outer orbital tooth conspicuous (115, 5111 C)  |
| 11  | Conspicuous (abundant long) tomentum on merus carpus propodus of cheliped (e.g. Figs $4/4$ D: $484$ C) 12  |
|     | Short tomentum on chelipeds, never long, abundant throughout cheliped  |
| 12  | Two anterolateral teeth posterior to outer orbital tooth on each side of carapace (Figs $M\Delta \cdot A5\Delta$ ) . Trizocarcinus                     |
| 12. | Note anterolateral tooth posterior to outer orbital tooth on each side of carapace (Figs. $474$ , $454$ ) $1120carcmas$                                |
| _   | Willowlar n gen  |
| 13  | Two broad short anterolateral teeth posterior to outer orbital tooth on each side of carapace (e.g. Figs. 16A: 17A):                                   |
| 13. | corneas spherical (e.g. Fig. 16C)  |
|     | Concess spherical (e.g. Fig. 100)  |
| _   | form dorsoventrally flattened (Fig. 10A B)   |
|     | Torini, dorsovenitariy naueneu (Fig. 17A, D)   |

# Genus Eucrate De Haan, 1835

*Cancer (Eucrate)* De Haan, 1835: 36 (type species *Cancer (Eucrate) crenatus* De Haan, 1835, by monotypy; gender feminine) [Opinion 85, Direction 37].

Cancer (Galene) — White, 1849: 144.

*Pilumnoplax* Stimpson, 1858: 93 (39); 1907: 90 (type species *Pilumnoplax sulcatifrons* Stimpson, 1858, subsequent designation by Rathbun, 1918; gender feminine).

*Eucrate* — Haswell 1882b: 86 [diagnosis]. — De Man 1887: 88 [discussion]. — Alcock 1900: 292 [in list], 298 [in key], 298. — Tesch 1918: 157. — Stebbing 1920a: 238; 1920b: 268. — Barnard 1950: 282 [in key], 295. — Balss 1922a:

137; 1957: 1656. — Sakai 1939: 555 [in key], 561; 1976: 523 [in key], 535. — Campbell 1969: 117. — Guinot 1969b: 508 [discussion]; 1971: 1080 [list of species]. — Serène & Lohavanijaya 1973: 70 [list of species]. — Takeda & Shimazaki 1974: 60 [discussion]. — Tirmizi & Ghani 1996: 76 [diagnosis]. — Davie, 2002: 198 [diagnosis]. — Karasawa & Kato 2003a: 151 [in list]; 2003b: 130 [in list], 139 [in list]. — Ng & Castro 2007: 44 [in list], 45 [discussion]. Ng *et al.* 2008: 78, 79 [in list]. — De Grave *et al.* 2009: 33 [in list].

**Diagnosis.** Carapace (e. g. Figs. 2; 3A) trapezoidal, almost as wide as long, dorsal surface smooth without clear indication of regions or with variously developed setose grooves, depressions (median frontal notch, shallow depression posterior to each orbit extending laterally to anterolateral teeth), convex; anterolateral borders arched; front wide, straight, lamelliforn or truncate, typically with median notch (Fig. 3B–D; absent or inconspicuous in E. alcocki, E. formosensis). Two or 3 typically low teeth (second may be acute, dorsally salient) posterior to rounded or triangular outer orbital tooth. Short (shorter than front), wide, spherical orbits (Fig. 3B); 2 notches on thick supraorbital border; short median lobe, outer notch on thick suborbital border (Fig. 3C, D); eye peduncles short, as long as or slightly longer than corneas (Fig. 3B); large, spherical corneas. Basal antennal article immobile, with disto-lateral process so that orbital hiatus is closed excluding antennal flagellum from orbit (Fig. 3B–D; Campbell 1969: fig. 1C). Anteroexternal margin of third maxilliped merus angular or auriculiform. Cheliped fingers moderately stout, slightly longer than swollen propodus, dark or light in colour; carpus with tooth on inner margin; dense, short tomentum on anterior margin of carpus in most species. Dorsal margins of ambulatory legs (P2-P5; Fig. 3A) meri, carpi, propodi unarmed (granular in some species), dactyli slender, smooth, setose; P5 propodus slender, dactylus long, slender, with shallow longitudinal depression, fringed with scattered, long setae. Thoracic sternum wide (Fig. 3C, G); thoracic suture 2/3 complete, convex, close to anterior margin of sternum (Fig. 3C); 3/4 deep, short, interrupted; 4/5, 6/7, 7/8 interrupted, 5/6 complete (Figs. 3G; 11F); median groove on thoracic sternites 7, 8 (Fig. 3G). Sterno-abdominal cavity of male deep, nearly reaching anterior margin of sternite 4 (Fig. 11E). Press-button of male abdominal-locking mechanism (Fig. 11E) as tubercle near thoracic suture 4/5 (small tubercle present in pre-adult females). Male abdomen (Fig. 3C) narrow, slender (T-shaped), lateral margins of somites 4-6 abruptly narrowing from somite 3 to transversely narrow, pointed telson; somite 3 reaching inner margins of P5 coxae (Fig. 3F); no portions of thoracic 8 exposed by closed abdomen, somite 2 transversely almost as long as somite 3. G1 long, slender, sinuous (straight in E. tripunctata Campbell, 1969; Fig. 15J), acuminate apex, with small denticles (e.g. Figs. 11E; 14A, B, D, E); G2 less than one-third of G1, apex with 2 unequal acute or obtuse processes (e.g. Fig. 14C, F). Male genital opening (gonopore) coxal (Guinot 1969b: fig. 35); coxo-sternal disposition of long penis, protected by concave posterior portion of thoracic sternite 7 (Fig. 11E). Vulva (Fig. 3G) ovoid, extending across anterior portion of sternite 6 close to median axis of thorax; covered by soft membrane, sternal vulvar cover absent.

**Type species.** *Cancer (Eucrate) crenatus* De Haan, 1835 (by monotypy, gender feminine) [Opinion 85, Direction 37].

**Remarks.** De Man (1887: 88) stated that the genus *Eucrate* "is a very natural one, distinguished not only by its entire physiognomy, but also by the structure of the external antennae". *Heteroplax* was nevertheless considered a junior synonym of *Eucrate* by some authors, although most preferred to keep both as independent genera (see Remarks for *Heteroplax* below). *Eucrate*, presumed to be in the Goneplacinae, was included in the Euryplacinae by Guinot (1969b: 508). Campbell (1969) revised the genus but essentially restricted his work to Australian species. His work left several unanswered questions, particularly the status of the poorly understood *E. sulcatifrons* Stimpson, 1858.

The G1 and G2 respectively, are remarkably similar among the species of *Eucrate*. The long and slender G1 is invariably sinuous (Fig. 11E; straight in *E. tripunctata*; Fig. 15J), with small denticles along the distal portion and an acuminate apex (e.g. Fig. 14A, B, D, E). Sakai (1976: 537) nevertheless points out differences in the extension of the spinular portion of the G1 of three species. These differences, as well as the relative size and distribution of the spinules, are not clear cut and appear to be related to the size of the individuals. The short G2 is also very similar among the *Eucrate* species (e.g. Fig. 14C, F), and in most details, among all euryplacids.

Table 1 summarizes differences between *Eucrate* and the other genera of the Euryplacidae.

| Character                    | Eucrate   | Euryplax   | Frevillea  | Henicoplax n. gen.  | Heteroplax  |
|------------------------------|---|--|--|---|---|
| Carapace                     | Trapezoidal, slightly<br>wider than long;<br>smooth, sometimes<br>with discontinuous,<br>setose grooves;<br>arched anterolateral<br>borders, each with 2<br>or 3 low teeth, only<br>second may be<br>acute, dorsally<br>salient (Figs. 2; 3A;<br>4) | Transversely<br>rectangular, wider<br>than long; smooth;<br>straight<br>anterolateral<br>borders, each with<br>2, often nearly<br>equal, teeth (Figs.<br>16A; 17A, B; 39A,<br>B) | Quadrate,<br>slightly wider<br>than long;<br>smooth; straight<br>anterolateral<br>borders, each<br>with acute<br>anterolateral<br>tooth (Figs. 18E,<br>F; 19A) | Hexagonal,<br>transversally<br>rectangular, wider than<br>long, convex, smooth,<br>postorbital ridge from<br>anterolateral tooth<br>(absent in <i>H.</i><br><i>trachydactylus</i> <b>n. sp.</b> );<br>short, nearly straight<br>anterolateral borders,<br>each with 1 triangular,<br>short anterolateral tooth<br>(Figs. 21A; 22A; 25A) | Transversally<br>rectangular, much<br>wider than long;<br>smooth, with<br>elevation below<br>orbital margin;<br>arched anterolateral<br>borders, each with 3<br>teeth: first, third<br>short, acute; second<br>largest, triangular,<br>acute tip (Fig. 28A) |
| Front                        | Straight, median<br>sulcus typically<br>present (Fig. 3B–D)   | Straight, or weakly<br>lobed, with small<br>median notch (Fig.<br>17A, B)  | Weakly bilobed<br>with small<br>median<br>prominence or<br>straight (Fig.<br>19A)  | Straight, median notch<br>absent or barely visible<br>(Figs. 21A; 22A)  | Nearly straight,<br>median notch<br>visible in most<br>individuals (Fig.<br>28A)  |
| Orbits                       | Short, shorter than front (Fig. 3B)   | Long, only longer<br>than half front<br>length (Fig. 16C)  | Long, longer<br>than front (Fig.<br>19B)   | Long, longer or almost<br>as long as front (Figs.<br>21A; 22A)  | Long, longer than front (Fig. 28B)  |
| Eye<br>peduncles             | Short, much shorter<br>than front, as long as<br>or slightly longer<br>than cornea (Fig.<br>3B)   | Long, shorter than<br>wide front, slightly<br>longer than cornea<br>(Fig. 16C)   | Long, nearly as<br>long as front,<br>longer than<br>cornea (Fig.<br>19B)   | Long, more than half of<br>front width, much<br>longer than cornea<br>(Figs. 22A; 23C)  | Long, almost as<br>long as front, much<br>longer than cornea<br>(Fig. 28B)  |
| Corneas                      | Spherical (Fig. 3B)   | Spherical (Fig.<br>16C)  | Reniform (Fig.<br>19B)   | Slightly elongated (Figs. 22A; 23C)   | Spherical (Fig. 28B)  |
| Supraorbital<br>borders      | Thick, 2 notches;<br>conspicuous outer<br>orbital tooth (Fig.<br>3A, B)   | Thin, 1 notch;<br>triangular outer<br>orbital tooth (Fig.<br>17A, B)   | Thin, small<br>notch; slender,<br>acute, outwardly<br>oriented outer<br>orbital tooth<br>(Fig. 19A)  | Thin, sinuous, entire<br>(notches absent);<br>triangular, anteriorly-<br>oriented outer orbital<br>tooth ( Figs. 21A; 22A)  | Thin, small notch;<br>triangular outer<br>orbital tooth;<br>triangular,<br>anteriorly oriented<br>outer orbital tooth<br>(Fig. 28A)   |
| Suborbital<br>borders        | Thick; conspicuous,<br>high inner orbital<br>tooth; short, wide<br>median lobe (Fig.<br>3B, D)  | Thin; inner<br>suborbital tooth<br>absent, short<br>median lobe (Figs.<br>16C; 17C, E)   | Thin; triangular<br>inner suborbital<br>tooth, long,<br>sinuous median<br>lobe (Fig. 19B,<br>C)  | Thin; sinuous, with<br>broad median lobe,<br>inner suborbital tooth<br>absent (Figs. 22C;<br>23C)   | Thin; inner<br>suborbital tooth<br>absent, short<br>median lobe (Fig.<br>28C)   |
| Basal<br>antennal<br>article | Immobile,<br>distolateral process<br>closing orbital hiatus<br>(Fig. 3B, C;<br>Campbell 1969: fig.<br>1C)   | Mobile, distolateral<br>process absent but<br>closing orbital<br>hiatus (Fig. 16C;<br>Guinot 1969b: fig.<br>41)  | Immobile by<br>small process at<br>inner edge of<br>suborbital<br>border, does not<br>close orbital<br>hiatus (Fig. 19B;<br>Guinot 1969b:<br>fig. 40)          | Slightly mobile,<br>distolateral process<br>absent but orbital hiatus<br>is closed (Figs. 22C;<br>23C)  | Mobile, distolateral<br>process absent but<br>closing orbital<br>hiatus (Fig. 28B)  |

TABLE 1. Contrasting morphological characters and geographical distributions of the genera of Euryplacidae.

| Character  | Eucrate  | Euryplax   | Frevillea  | Henicoplax n. gen.  | Heteroplax   |
|--|--|--|--|---|--|
| Third<br>maxillipeds<br>meri                                       | Anteroexternal<br>margin usually<br>angular (Fig. 3D),<br>auriculiform in some<br>species (Fig. 9B)  | Anteroexternal<br>margin<br>auriculiform (Fig.<br>17C)   | Anteroexternal<br>margin<br>auriculiform<br>(Fig. 19C)   | Anteroexternal margin<br>auriculiform (Fig. 22B)<br>or angular (Fig. 25F)   | Anteroexternal<br>margin angular<br>(Fig. 28C)   |
| Thoracic suture 2/3  | Convex, close to<br>anterior margin of<br>sternum (Fig. 3C)  | Straight, close to<br>anterior margin of<br>sternum (Fig. 17D)   | Slightly convex<br>(Fig. 19D, H)   | Convex (Figs. 21B;<br>23B)  | Convex, close to<br>anterior margin of<br>sternum (Fig. 28C)   |
| Thoracic<br>sutures<br>posterior to<br>2/3                         | 4/5, 6/7, 7/8<br>interrupted, 5/6<br>complete (Fig. 3G)  | 4/5, 6/7, 7/8<br>interrupted, 5/6<br>complete<br>(Fig. 17D, G)   | 4/5, 6/7, 7/8<br>interrupted, 5/6<br>complete<br>(Fig.19F, H)                                    | 4/5, 6/7, 7/8<br>interrupted, 5/6<br>complete<br>(Figs. 21D; 26F)   | 4/5, 6/7, 7/8<br>interrupted, 5/6<br>complete  |
| Setation of chelipeds  | Tomentum along<br>distal margin of<br>carpus in most<br>species (Fig. 3E)  | Tomentum may be<br>present along distal<br>margins of merus,<br>carpus (Figs. 18C;<br>39A, B)  | Tomentum on<br>proximal margin<br>of propodus and<br>distal margin of<br>carpus<br>(Fig. 18E, F) | Varying from setae<br>along margins of<br>carpus, merus to dense<br>tomentum on dactylus,<br>propodus, carpus,<br>merus ( <i>H. eriochir</i> ;<br>Fig. 21A, B)                  | Long setae along<br>distal margin of<br>carpus (tomentum<br>absent) (Fig. 28F)                           |
| Ρ5   | Propodus slender<br>(proportionally<br>wide, subcylindical<br>in some species);<br>dactylus long,<br>slender, with<br>shallow longitudinal<br>depression, fringed<br>with scattered, long<br>setae (Fig. 3A) | Propodus<br>proportionally<br>stout,<br>subcylindrical;<br>dactylus<br>proportionally<br>slender, fringed<br>with long, simple<br>setae, short teeth<br>(Fig. 16A) | Propodus, long,<br>subcylindrical;<br>dactylus slender,<br>fringed with long<br>setae (Fig. 19A) | Propodus, long,<br>subcylindrical; dactylus<br>slender, fringed with<br>setae, sometimes short<br>spines (Fig. 27A, B;<br>Serène & Soh 1976:<br>fig. 22D, as <i>H. nitida</i> ) | Propodus, dactylus<br>proportionally long,<br>slender, dactylus<br>fringed with<br>scattered, long setae |
| Male<br>abdomen  | Narrow, slender, T-<br>shaped<br>(Figs. 1D; 3C)  | Proportionally<br>wide, triangular,<br>not T-shaped<br>(Fig. 16D)  | Proportionally<br>wide, triangular,<br>not T-shaped<br>(Fig. 19D)                                | Narrow, slender, T-<br>shaped<br>(Figs. 21C; 22D)   | Narrow, slender, T-<br>shaped<br>(Fig. 28D, E)   |
| Exposure of<br>thoracic<br>sternite 8 by<br>closed male<br>abdomen | Covered<br>(Figs. 3F; 6F)  | Small portion<br>exposed (Figs.<br>16F; 17F; 18D)  | Covered<br>(Fig. 19G;<br>Guinot 1969b:<br>fig. 33)   | Covered or small<br>portion exposed (Figs.<br>22D; 25D); large<br>portion exposed in <i>H.</i><br><i>eriochir</i> <b>n. sp.</b><br>(Fig. 21C)                                   | Small portion<br>exposed (Fig. 28E)  |
| G1   | Acuminate apex,<br>many small denticles<br>(Fig. 14A, B)   | Acuminate apex,<br>small denticles<br>(Fig. 20A, B)  | Acuminate apex,<br>many small<br>denticles<br>(Fig. 20D, E)                                      | Acuminate apex, many<br>small denticles (Fig.<br>24A, B, D, E)  | Acuminate apex,<br>many small<br>denticles<br>(Fig. 27G, H)  |
| G2   | Apex with 2<br>processes unequal in<br>size (Fig. 14C)   | Apex with 2<br>processes unequal<br>in size (Fig. 20C)   | Apex with 2<br>processes<br>unequal in size<br>(Fig. 20F)  | Apex with 2 processes<br>unequal in size<br>(Fig. 24C, F)   | Apex with 2<br>processes unequal<br>in size (Fig. 27I)   |
| Covering of<br>vulva   | Soft membrane,<br>sternal vulvar cover<br>absent (Fig. 11F)  | Soft membrane,<br>sternal vulvar cover<br>absent (Fig. 18B)  | Soft membrane,<br>sternal vulvar<br>cover absent<br>(Fig. 19H)                                   | Soft membrane, sternal<br>vulvar cover absent<br>(Figs. 21F; 23D)   | Soft membrane,<br>sternal vulvar cover<br>absent   |
| Geographical distribution  | Indo-West Pacific  | Western Atlantic<br>and Tropical<br>Eastern Pacific  | Western Atlantic   | Indo-West Pacific   | Indo-West Pacific<br>(western Pacific)   |

# TABLE 1 (continued).

| Character    | Machaerus               | Nancyplax           | Platyozius              | Psopheticoides                        | Systroplax n. gen.                |
|--------------|-------------------------|---------------------|-------------------------|---------------------------------------|-----------------------------------|
| Carapace     | Hexagonal, slightly     | Quadrate, slightly  | Trapezoidal, almost as  | Trapezoidal, almost                   | Suboctagonal,                     |
| •            | wider than long;        | wider than long,    | wide as long; curved    | as wide as long;                      | nearly round,                     |
|              | dorsal surface          | dorsal surface      | elevation between       | arched anterolateral                  | short, spherical                  |
|              | relatively smooth,      | smooth; arched      | second teeth (low in    | borders, each with 2                  | granules on dorsal,               |
|              | with shallow sulcus     | anterolateral       | small individuals);     | teeth, first short,                   | ventral surface;                  |
|              | extending from          | borders; arched     | arched anterolateral    | elongated, following                  | arched                            |
|              | each third              | borders each with   | short teeth: long       | rounded outline of                    | borders, each with                |
|              | arched                  | conspicuous.        | slightly convex         | second short, acute,                  | 2 short, obtuse                   |
|              | anterolateral           | acute anterolateral | posterolateral          | dorsally salient: large               | teeth:                            |
|              | borders, each with      | tooth               | margins; irregular,     | orange-red circle on                  | posterolateral                    |
|              | 3 obtuse or             | (Fig. 31A)          | brightly coloured lines | cardiac                               | borders long,                     |
|              | acute teeth             |                     | (Figs. 33; 34)          | (Figs. 36A; 39C)                      | arched                            |
|              | (Figs. 29A; 30A)        |                     |                         |                                       | (Figs. 37A; 38I, J)               |
| Front        | Straight, with small    | Straight, with      | Straight, with small    | Straight, with small                  | Nearly straight                   |
|              | median notch            | small median        | median notch            | median notch (absent                  | (outer edges                      |
|              | (Figs. 29A; 30A)        | notch               | (Fig. 35A, C)           | in large individuals) $(Fig. 26P, C)$ | slightly curved in                |
|              |                         | (Fig. 51D, C)       |                         | (Fig. 50D, C)                         | small median notch                |
|              |                         |                     |                         |                                       | (Fig. 37B, C)                     |
| Orbits       | Moderately long.        | Short, shorter than | Moderately short.       | Long, almost as long                  | Moderately short.                 |
|              | almost as long as or    | front (Fig. 31B)    | shorter than front;     | as front; wide,                       | much shorter than                 |
|              | slightly longer         |                     | oblique (Fig. 35A)      | spherical                             | front; wide,                      |
|              | than front              |                     |                         | (Fig. 36B, C)                         | spherical                         |
|              | (Figs. 29A; 30B)        |                     |                         |                                       | (Fig. 37B)                        |
| Eye          | Moderately long,        | Moderately short,   | Short, much shorter     | Short, much shorter                   | Short, much shorter               |
| peduncles    | shorter than front,     | much shorter than   | than front, as long as  | than front, shorter                   | than front, as long               |
|              | slightly longer than    | front, about as     | or slightly longer      | than cornea (Fig.                     | (Fig. 37B)                        |
|              | 30B)                    | (Fig. 31B, C)       | (Fig. 35A, C)           | 50 <b>D</b> , C)                      | (11g. 57b)                        |
| Corneas      | Spherical (Figs.        | Spherical (Fig.     | Spherical.              | Reniform (Fig. 36B)                   | Spherical                         |
|              | 29A; 30B)               | 31B, C)             | proportionally large    |                                       | (Fig. 37B)                        |
|              |                         |                     | (Fig. 35A, C)           |                                       |                                   |
| Supraorbital | Thick or thin,          | Thin, 2 notches;    | Thin; entire (small     | Thick; 2 small                        | Thick, arched; 2                  |
| borders      | triangular or           | simple, unarmed     | notch in small          | notches, raised lobe                  | notches; very                     |
|              | rounded; anteriorly     | outer orbital angle | individuals); short,    | immediately before                    | short, triangular                 |
|              | oriented, outer         | (Fig. 31A, B)       | obtuse outer orbital    | inner notch; deep,                    | outer orbital tooth $(E; a, 27P)$ |
|              | (Figs $294 \cdot 30B$ ) |                     | aligle (Fig. 55A)       | triangular outer                      | (Fig. 57B)                        |
|              | (11g3. 2)11, 30D)       |                     |                         | orbital tooth                         |                                   |
|              |                         |                     |                         | (Fig. 36A, B)                         |                                   |
| Suborbital   | Thick or thin;          | Thin; inner         | Thin; inner suborbital  | Thick; broad, straight                | Thick; arched, 2                  |
| borders      | salient inner           | suborbital tooth    | lobe (tooth absent),    | when seen ventrally;                  | very small notches                |
|              | suborbital tooth;       | absent, sinuous     | nearly straight margin  | small, low inner                      | in larger                         |
|              | straight margin         | margin              | without notches         | suborbital tooth                      | individuals; large,               |
|              | (Figs. 29B, D;          | (Fig. 31B, C)       | (Fig. 35A, C)           | (Fig. 36B, C)                         | granular, salient                 |
|              | 50C)                    |                     |                         |                                       | tooth (Fig. 37B, C)               |
| Racal        | Immobile                | Immobile            | Mobile or slightly      | Slightly mobile                       | Immobile                          |
| antennal     | distolateral process    | distolateral        | mobile, distolateral    | distolateral process                  | distolateral process              |
| article      | absent but closing      | process absent but  | process closing orbital | absent but closing                    | closing orbital                   |
|              | orbital hiatus          | closing orbital     | hiatus (Fig. 35A, C)    | orbital hiatus                        | hiatus                            |
|              | (Fig. 30B, C;           | hiatus (Fig. 31B,   |                         | (Fig. 36B, C)                         | (Fig. 37B, C)                     |
|              | Monod 1956:             | C; Lemaitre et al.  |                         |                                       |                                   |
|              | figs. 445, 451)         | 2001: fig. 2a)      |                         |                                       |                                   |

| Character  | Machaerus  | Nancyplax   | Platyozius   | Psopheticoides   | Systroplax n. gen.   |
|--|--|---|--|--|--|
| Third  | Anteroexternal   | Anteroexternal  | Anteroexternal   | Anteroexternal   | Anteroexternal   |
| maxillipeds  | margin angular   | margin angular  | margin auriculiform  | margin auriculiform  | margin   |
| meri   | (Figs. 29D; 30C)   | (Fig. 31C)  | (Fig. 35C)   | (Fig. 36C)   | auriculiform<br>(Fig. 37C)   |
| Thoracic suture 2/3  | Convex (Fig. 29D)  | Straight<br>(Fig. 31D)  | Convex (Fig. 35C, D)   | Straight (Fig. 36E)  | Straight (Fig. 37E)  |
| Thoracic   | 4/5, 6/7, 7/8  | 4/5, 5/6, 6/7, 7/8  | 4/5, 6/7, 7/8  | 4/5, 6/7, 7/8  | 4/5, 5/6, 6/7, 7/8   |
| sutures  | interrupted; 5/6   | interrupted (Fig.   | interrupted, 5/6   | interrupted, 5/6   | interrupted (Fig.  |
| posterior to 2/3   | complete (Fig. 29D)  | 31F, G)   | complete<br>(Fig. 35F, G)  | complete (Fig. 36G)  | 37G)   |
| Setation of<br>chelipeds   | Tomentum on<br>proximal margin of<br>propodus and distal<br>margin of carpus<br>(Figs. 29C; 30A,<br>D) | Sparse setae along<br>distal margin of<br>propodus, carpus<br>(tomentum absent)<br>(Fig. 31E);<br>stridulating ridge<br>on merus<br>(Lemaitre <i>et al.</i><br>2001: fig. 3f) | Sparse setae along<br>distal margin of<br>propodus, carpus<br>(tomentum absent)<br>(Fig. 35B)  | Row of short setae<br>along distal margin of<br>carpus (tomentum<br>absent) (Fig. 36D)                         | Row of short setae<br>along distal margin<br>of carpus<br>(tomentum absent)<br>(Fig. 37D)                |
| Ρ5   | Propodus<br>subcylindrical;<br>dactylus long,<br>slender, fringed<br>with long setae<br>(Fig. 30A)     | Propodus,<br>dactylus<br>proportionally<br>long, slender,<br>dactylus fringed<br>with scattered,<br>long setae (Fig.<br>31A; Lemaitre <i>et</i><br><i>al.</i> 2001: fig. 4d)  | Propodus, dactylus<br>proportionally short,<br>flattened, fringed with<br>scattered, long setae,<br>spines on dactylus<br>(Figs. 33; 34) | Propodus, dactylus<br>proportionally short,<br>flattened, fringed<br>with many short setae<br>(Figs. 36A; 39C) | Propodus, dactylus<br>proportionally<br>long, slender,<br>fringed with many<br>short setae (Fig.<br>37A) |
| Male<br>abdomen  | Proportionally<br>wide, triangular,<br>not T-shaped (Figs.<br>1B; 30E)                                 | Proportionally<br>wide, triangular,<br>not T-shaped (Fig.<br>32G)   | Narrow, slender, T-<br>shaped (Fig. 35D)   | Narrow, slender, T-<br>shaped (Fig. 36E)   | Narrow, slender, T-<br>shaped<br>(Figs. 1C; 37E, F)  |
| Exposure of<br>thoracic<br>sternite 8 by<br>closed male<br>abdomen | Small portion<br>exposed (Figs.<br>30G; 32A, C)  | Small portion<br>exposed<br>(Lemaitre <i>et al.</i><br>2001: fig. 2b)   | Covered (Fig. 35E)   | Covered (Fig. 36F)   | Covered (Fig. 37F)   |
| G1   | Acuminate apex,<br>many small<br>denticles (Figs.<br>30F; 32B, D, E)                                   | Acuminate apex,<br>many small<br>denticles (Fig.<br>32H, I)   | Acuminate apex,<br>many small denticles<br>(Figs. 35F; 38A, B)   | Arrowhead-shaped<br>apex, relatively large<br>denticles, slightly<br>sinuous (Fig. 38D, E)                     | Acuminate apex,<br>many small<br>denticles (Fig.<br>38G)   |
| G2   | Apex with 2<br>processes unequal<br>in size (Fig. 32F)   | Apex with 2<br>processes unequal<br>in size<br>(Fig. 32J, K)  | Apex with 2 processes<br>unequal in size (Fig.<br>38C)   | Apex with 2<br>processes unequal in<br>size (Fig. 38F)   | Apex with 2<br>processes, one<br>much reduced,<br>lobate (Fig. 38H)                                      |
| Covering of vulva  | Soft membrane,<br>sternal vulvar<br>cover absent (Fig.<br>29D)   | Soft membrane,<br>sternal vulvar<br>cover absent (Fig.<br>31G)  | Soft membrane,<br>sternal vulvar cover<br>absent (Fig. 35G)  | Sternal vulvar cover<br>present (Fig. 36G)   | Soft membrane,<br>sternal vulvar<br>cover absent (Fig.<br>37G)   |
| Geographical distribution  | Eastern Atlantic   | Western Atlantic  | Indo-West Pacific  | Indo-West Pacific<br>(western Pacific)   | Indo-West Pacific<br>(western Pacific)   |

# **TABLE 1** (continued).

| Character                    | Trissoplax n. gen.   | Trizocarcinus   | Villoplax n. gen.  | Xenocrate  |
|------------------------------|--|---|--|--|
| Carapace                     | Hexagonal, transversally<br>elongated, wider than<br>long; short sulcus from<br>third anterolateral tooth,<br>low, elongated boss on<br>each branchial of larger<br>individuals; nearly<br>straight anterolateral<br>borders (slightly arched<br>in small individuals),<br>each with 3 teeth: first<br>triangular, obtuse; second<br>acute, dorsally salient;<br>third small, obtuse<br>(Figs. 39D–F; 40; 42A) | Quadrate, slightly wider than<br>long; anterolateral borders<br>slightly arched, each with 2<br>triangular, acute teeth<br>(Figs. 44A; 45A) | Quadrate, slightly<br>wider than long;<br>anterolateral borders<br>nearly straight, each<br>with one triangular,<br>acute tooth<br>(Figs. 47A, B; 48A) | Subhexagonal, almost as<br>wide as long; anterolateral<br>borders arched, each with 2<br>teeth (second acute, dorsally<br>salient; small third tooth in<br>small individuals);<br>granular surface<br>(Fig. 49A) |
| Front                        | Straight, with median<br>notch<br>(Figs. 40; 41B; 42A)   | Straight to weakly bilobed,<br>with small median notch<br>(Figs. 44A, B; 45A)   | Straight or weakly<br>bilobed, with small<br>median notch<br>(Figs. 47B; 48A)  | Nearly straight with<br>median notch<br>(Fig. 49B, C)  |
| Orbits                       | Long, almost as long as<br>front length<br>(Figs. 41A,B; 42A)  | Long to moderately long,<br>shorter than front or almost as<br>long as front; wide<br>(Figs. 44B; 46A, G)                                   | Moderately long,<br>nearly as long as<br>front; wide<br>(Figs. 47B, C; 48B)  | Short, shorter than front;<br>wide, spherical (Fig. 49C)   |
| Eye<br>peduncles             | Moderately long, nearly<br>half of front width, much<br>longer than cornea<br>(Figs. 41A,B; 42E)   | Moderately long, shorter than<br>front, approximately as long<br>as cornea<br>(Figs. 44B; 45A; 46A, G)                                      | Moderately long,<br>shorter than front,<br>approximately as<br>long as cornea<br>(Figs. 47B, C; 48B)   | Short, much shorter than<br>front, about as long as<br>cornea<br>(Fig. 49C)  |
| Corneas                      | Spherical to slightly<br>elongated<br>(Figs. 41A,B; 42E)   | Spherical<br>(Figs. 44B; 45A; 46G)  | Spherical<br>(Figs. 47B, C; 48B)   | Spherical<br>(Fig. 49C)  |
| Supraorbital<br>borders      | Thin (thick in largest<br>individuals of <i>T</i> .<br><i>dentata</i> ); 1 or 2 notches<br>(notch on outer portion<br>more noticeable in larger<br>individuals of <i>T</i> .<br><i>dentata</i> ); triangular outer<br>orbital tooth<br>(Figs. 40A–E; 41B; 42A)   | Thin, granular or smooth, 2<br>notches; triangular, anteriorly<br>oriented outer orbital tooth<br>(Figs. 44A; 45A)                          | Thin, 2 notches;<br>narrowly triangular,<br>acute, anteriorly<br>oriented outer orbital<br>tooth<br>(Figs. 47B, C; 48A)                                | Thick, 2 notches; short,<br>rounded outer orbital tooth<br>(Fig. 49A, C)   |
| Suborbital<br>borders        | Thin (thick in largest<br>individuals of <i>T</i> .<br><i>dentata</i> ); triangular inner<br>suborbital tooth, short<br>median lobe, outer notch,<br>tooth and lobe (Fig. 41A,<br>B) (absent in <i>T. tuberosa</i><br><b>n. sp.</b> ; Fig. 42E)  | Thin, granular or smooth;<br>inner suborbital tooth absent,<br>sinuous median lobe,<br>outer notch<br>(Figs. 44B, C; 46A, G)                | Thin, granular; short<br>inner suborbital<br>tooth, sinuous<br>median lobe, outer<br>notch<br>(Figs. 47C; 48B)   | Thick; large, high, inner<br>suborbital tooth; shorter<br>median tooth, outer notch<br>(Fig. 49B, C)   |
| Basal<br>antennal<br>article | Immobile, small<br>distolateral process<br>closing orbital hiatus<br>(Fig. 41A, B)   | Immobile, with distolateral<br>process absent but closing<br>orbital hiatus<br>(Figs. 44B, C; 46A, G)                                       | Immobile, with<br>distolateral process<br>absent but closing<br>orbital hiatus<br>(Fig. 47C)   | Immobile, distolateral<br>process absent but closing<br>orbital hiatus<br>(Fig. 49B, C)  |

| Character   | Trissoplax n. gen.   | Trizocarcinus  | Villoplax n. gen.   | Xenocrate  |
|---|--|--|---|--|
| Third<br>maxillipeds<br>meri  | Anteroexternal margin<br>auriculiform<br>(Fig. 41A)  | Anteroexternal margin<br>auriculiform<br>(Figs.44C; 46A, G)  | Anteroexternal<br>margin auriculiform<br>(Figs. 47C; 48B)   | Anteroexternal margin<br>auriculiform<br>(Fig. 49B)  |
| Thoracic suture 2/3   | Convex, close to anterior<br>margin of sternum<br>(Figs. 41C; 42C)   | Convex<br>(Figs. 45B; 46A)   | Convex, close to<br>anterior margin<br>(Figs. 47D; 48B)   | Straight<br>(Fig. 49G)   |
| Thoracic<br>sutures<br>posterior to<br>2/3                            | 4/5, 6/7, 7/8 interrupted,<br>5/6 complete<br>(Fig. 45B)   | 4/5, 6/7, 7/8 interrupted,<br>5/6 complete<br>(Figs. 45B)  | 4/5, 6/7, 7/8<br>interrupted, 5/6<br>complete   | 4/5, 5/6, 6/7, 7/8 interrupted<br>(Fig. 49G, H)  |
| Setation<br>of chelipeds  | Tomentum along distal<br>margin of carpus in <i>T.</i><br><i>dentata</i> (Figs. 39D–F;<br>40A–E; 41E), clump of<br>short setae in <i>T. tuberosa</i><br><b>n. sp.</b> (Fig. 42E) | Tomentum along merus,<br>carpus, sometimes propodus<br>(Figs. 44A, D; 45A)                               | Tomentum along<br>merus, carpus,<br>propodus<br>(Figs. 47A; 48A, C)   | Short setae along distal<br>margin of merus<br>(tomentum absent)<br>(Fig. 49D)                           |
| P5  | Propodus proportionally<br>long, slender, fringed<br>with scattered, long<br>setae; dactylus<br>subcylindrical, with<br>many short setae<br>(Figs. 39D–F; 40A, C, E;<br>42A, B)  | Propodus, dactylus<br>proportionally long, slender,<br>fringed with many short setae<br>(Figs. 44A; 45A) | Propodus, dactylus<br>proportionally long,<br>slender, fringed with<br>many short setae<br>(Figs. 47A; 48A) | Propodus, dactylus<br>proportionally short,<br>flattened, fringed with many<br>short setae<br>(Fig. 49A) |
| Male<br>abdomen   | Narrow, slender, T-<br>shaped (Figs. 41D; 42C)   | Proportionally wide,<br>triangular, not T-shaped<br>(Figs. 1A; 44E; 46C, I)                              | Proportionally wide,<br>triangular, not T-<br>shaped<br>(Figs. 47D; 48D)                                    | Narrow, slender, T-shaped<br>(Fig. 49E)  |
| Exposure of<br>thoracic<br>sternite 8<br>by closed<br>male<br>abdomen | Covered (Fig. 41D) or small portion exposed  | Small portion exposed<br>(Figs. 44G; 46D, J)   | Covered   | Covered<br>(Fig. 49F)  |
| G1  | Acuminate apex, many<br>small denticles<br>(Fig. 43A, B, D, E)   | Acuminate apex, many small<br>denticles<br>(Fig. 46E, K)   | Acuminate apex,<br>many small denticles<br>(Fig. 48E, F)  | Acuminate apex, many<br>small denticles, some<br>relatively large<br>(Fig. 50A–C)                        |
| G2  | Apex with 2 processes<br>unequal in size<br>(Fig. 43C, F)  | Apex with 2 processes<br>unequal in size<br>(Fig. 46F, M)  | Apex with 2<br>processes unequal<br>in size<br>(Fig. 48G)   | Apex with one process<br>(Fig. 50D)  |
| Covering of vulva   | Sternal vulvar cover<br>present (Fig. 41G); only<br>soft membrane in <i>T.</i><br><i>tuberosa</i> <b>n. sp.</b>  | Soft membrane, sternal<br>vulvar cover absent<br>(Fig. 45B)  | Soft membrane,<br>sternal vulvar cover<br>absent (in juvenile<br>females)                                   | Soft membrane, sternal<br>vulvar cover absent<br>(Fig. 49H)  |
| Geographical distribution   | Indo-West Pacific  | Western Atlantic and<br>Tropical Eastern Pacific   | Tropical Eastern<br>Pacific   | Indo-West Pacific (western Pacific)  |

# Species included.

Eucrate alcocki Serène, in Serène & Lohavanijaya, 1973
= Eucrate maculata Yang & Sun, 1979
Eucrate crenata (De Haan, 1835)
= Pilumnoplax sulcatifrons Stimpson, 1858
Eucrate dorsalis (White, 1849)
= Eucrate hamiltoni McCulloch, 1908
= Galene ? laevimanus Lucas, in Jacquinot & Lucas, 1853
Eucrate formosensis Sakai, 1974
Eucrate indica n. sp.
Eucrate solaris Yang & Sun, 1979
Eucrate tripunctata Campbell, 1969
The genus is restricted to the Indo-West Pacific region.

Species excluded from *Eucrate* De Haan, 1835:

Eucrate affinis Haswell, 1882 [= Trissoplax dentata (Stimpson, 1858)] Eucrate costata Yang & Sun, 1979 [= Trissoplax dentata (Stimpson, 1858)] Eucrate haswelli Campbell, 1969 [= Trissoplax dentata (Stimpson, 1858)]

# Key to species of *Eucrate*

| 1. | Third (excluding outer orbital tooth) anterolateral tooth absent (only slight elevation may be present), carapace with relatively long posterolateral borders (e.g. Fig. 4)                            |
|----|--|
| _  | Third (excluding outer orbital tooth) anterolateral tooth present, even if short, sometimes barely noticeable in large   |
|    | individuals, carapace without relatively long posterolateral borders (e.g. Fig. 12)  |
| 2. | Conspicuous frontal notch present; large purple-pink spots on anterior two thirds of dorsal surface of carapace  |
|    | (Campbell 1969: fig. 1B) E. sexdentata   |
| -  | Frontal notch absent or barely noticeable; variously shaped red-brown spots, dots or many small dots on anterior half of dorsal surface of carapace  |
| 3. | Anterior half or most of carapace and chelipeds with small red-brown dots (Fig. 2E), larger dots in small individuals (Fig. 2F)  |
| _  | Median portion of carapace with large, irregular dark red-brown spots; small red-brown spots on anterior third of carapace and chelipeds (Fig. 2C, D)  |
| 4. | Median portion of carapace with one large, rounded spot in centre, typically flanked on each side and anteriorly by smaller spots (Fig. 2C); western Pacific in distribution                           |
|    | Median portion of carapace with two large, irregular, red-brown spots in centre, typically flanked by two smaller, vertically placed spots (Fig. 2D); Indian Ocean in distribution                     |
| 5. | P5 propodus noticeably short, wide (Figs. 12, 13C; Campbell 1969: fig. 4G); three anterolateral teeth short, second and third nearly equal (Fig. 13B–D)  |
| _  | P5 propodus slender not wide: three anterolateral teeth of varying size first much smaller than second 6   |
| 6. | First anterolateral tooth very short, nearly disappearing in large individuals (Fig. 6A–C; Campbell 1969: fig. 6B, K);<br>twoically one large spot on central region of carapace (Figs. 5A, B, D; 6A). |
| _  | First anterolateral tooth well developed, not noticeably reduced in size; carapace with reticulated pattern of spots or two spots on anterior half   |
| 7  | Ventral surface of chelined meri with conspicuous high tubercles: intricate reticulated pattern of dots spots across   |
| 7. | carapace chelineds ambulatory legs (Fig. $7C-F$ ) (preserved specimens with two triangular or hexagonal patterns on  |
|    | mesogastric region)  |
| _  | Ventral surface of cheliped meri smooth or with short granules: small dots on anterior third of carapace and on cheli-   |
|    | peds plus two small, oval, red-brown spots may be present on branchial region of carapace at some distance from  |
|    | each other (Fig. 2A)   |

# Eucrate alcocki Serène, in Serène & Lohavanijaya, 1973

(Figs. 2C; 4A–C; 14A–C)

- Eucrate alcocki Serène 1971: 916 (nomen nudum) [Viet Nam]. Serène & Lohavanijaya 1973: 71, pl. 16, figs. B, C [Viet Nam]. Serène & Vadon 1981: 118, 123 [part]. Dai et al. 1986: 372 [in key], 373, fig. 196(2), pl. 54, fig. 4 [China] [part]. Dai & Yang 1991: 401 [in key], 403, fig. 196(2), pl. 54, fig. 4 [China] [part]. Naiyanetr 1998: 78; 2007: 90 [Gulf of Thailand] [part]. Ng et al. 2008: 78 [in list] [part]. Yang et al. 2008: 770 [in list] [China] [part].
- (?) Eucrate crenata var. dentata Alcock 1900: 299 [in key], 301 [Hong Kong].
- not *Eucrate alcocki* Sakai 1976: 535 [in key], 536, pl. 192, fig. 2 [Taiwan]. Ng *et al.* 2001: 34 [discussion], fig. 7g [colour] [Taiwan]. Hsueh & Huang 2001: 130 [in key], 132, figs. 8G, 16 [Taiwan]. (= *Eucrate formosensis* Sakai, 1974)

Eucrate maculata Yang & Sun 1979: 3, 9, fig. 2, plate, figs. 3, 4, 8 [China].

not *Eucrate alcocki* — Ng & Davie 2002: 378 [Andaman Sea coast of Thailand]. — Rajkumar *et al.* 2009: 832, fig. 1 [India] (= *Eucrate indica* **n. sp.**)

**Type material.** Male holotype,  $21.2 \text{ mm} \times 24.6 \text{ mm}$  (MNHN-B10134); 1 female, cl 20.8 mm [remainder of carapace damaged], same data as holotype, designated herein as paratype (MNHN-B10133).

Type locality. Viet Nam, Nhatrang Bay.

**Type material of** *Eucrate maculata* **Yang & Sun, 1979,** male holotype (BMNH J79139; 1 male paratype, 15.9 mm × 18.7 mm (BMNH J79139; Fig. 4C); type locality: China, Fujian Province, Dongshan.

Material examined. *Hong Kong.* Unknown location, 1992: 3 males (SWIMS CRU-92-002); pre-adult female (SWIMS SML-Z-419).

*Viet Nam.* Nhatrang Bay, R. Serène coll., 1958, ION 9688, photograph ION 911: male holotype, 21.2 mm  $\times$  24.6 mm (MNHN-B10134); R. Serène coll., 1958, ION 44.144: 1 female paratype, cl 20.8 mm [rest of carapace damaged] (MNHN-B10133); Institute Océanographique Nhatrang leg., récolte 2558, no. E 48.363, 13.11.1969: 1 male, 26.1 mm  $\times$  30.5 mm; récolte 2552, no. E 48.2231, 09.09.1969: 1 female, 18.2 mm  $\times$  21.4 mm (MNHN-B10135); N. V. Luom coll., 13.11.1969, R. Serène id.: 1 male, 20.2 mm  $\times$  23.0 mm (ZRC 1970.8.24.2); 20–30 m, 22.08.1995: 2 males, 22.5 mm  $\times$  26.7 mm, 25.3 mm  $\times$  29.2 mm, 1 female, 20.8 mm  $\times$  23.5 mm (MNHN-B30543).

*Philippines*. MUSORSTOM 1: stn. 1, 14°28'N, 120°42'E, 36–37 m, 18.03.1976: 1 male, 23.6 mm  $\times$  28.4 mm (MNHN-B10346).

*Thailand.* Gulf of Thailand, Chonburi, Angsila fishing port, P. K. L. Ng coll., 29.09.1998: 1 male, 17.3 mm  $\times$  19.0 mm, 7 males, 18.9 mm  $\times$  22.1 mm, 18.9 mm  $\times$  21.9 mm, 19.0 mm  $\times$  22.5 mm, 19.4 mm  $\times$  22.1 mm, 22.0 mm  $\times$  25.2 mm, 22.00 mm  $\times$  25.3 mm, 19.0 mm  $\times$  22.3 mm, 9 females, 14.3 mm  $\times$  16.3 mm, 14.7 mm  $\times$  17.0 mm, 15.7 mm  $\times$  18.0 mm, 17.3 mm  $\times$  20.1 mm, 17.5 mm  $\times$  20.7 mm, 17.8 mm  $\times$  21.0 mm, 18. 8 mm  $\times$  22.4 mm, 18.0 mm  $\times$  21.6 mm, 19.2 mm  $\times$  23.3 mm (ZRC 1998.1055); 11.1999: 1 male, 17.7 mm  $\times$  21.2 mm, 1 female, 20.6 mm  $\times$  24.2 mm (ZRC 2000.022).

Gulf of Thailand, 150 km SW of Bangkok, A. C. J. Burgers leg., 05–18.11.1986: 1 female, 17.9 mm  $\times$  20.3 mm (RMNH D 36596).

Gulf of Thailand, Songkhla, Sakom fishing port, P. K. L. Ng *et al.* coll., 15–17.10.2003: 1 female, 15.1 mm  $\times$  17.7 mm (ZRC 2003.0605).

Gulf of Thailand, Pattani fishing port, P. K. L. Ng *et al.* coll., 16.10.2003: 1 ovigerous female,  $18.4 \text{ mm} \times 21.2 \text{ mm}$  (ZRC 2003.0621).

Singapore. East coast, fishermen tangle nets, 5–7 m, P. K. L. Ng coll., 01.1986: 1 male, 17.5 mm  $\times$  20.7 mm (ZRC 1999.1189).

Unknown location. Capt. E. Sirencom leg., 12.1993: 2 females, 17.4 mm  $\times$  20.6 mm, 19.7 mm  $\times$  22.9 mm (MNHN-B22358).

**Diagnosis.** Third anterolateral tooth absent or reduced as slight elevation, carapace with relatively long posterolateral borders (Figs. 2C; 4A–C). P5 propodus slender (Fig. 2C). Varying number of large, irregular red-brown spots across carapace, with smaller, anterior spots or dots (Fig. 2C).



**FIGURE 2.** Fresh colours of *Eucrate* species. A, B, *E. crenata* (De Haan, 1835); A, male (22.5 mm × 27.1 mm) (ZRC 2002.0493), China, Qingdao; B, male, Hong Kong, not preserved; C, *E. alcocki* Serène, in Serène & Lohavanijaya, 1973, ovigerous female (18.4 mm × 21.4 mm) (ZRC 2003.0621), Thailand, Pattani, Thailand; D, *E. indica* **n. sp.**, female, Persian Gulf, not preserved; E, F, *E. formosensis* Sakai, 1974; E, female (22.2 mm × 27.1 mm) (ZRC 1993.739), Taiwan, Kaohsiung, Taiwan; F, juvenile, northern Taiwan, not preserved. Photo credits: B by D. Poon; D by R. Naderloo (Forschunginstitut Senckenberg, Frankfurt); E by K. Li.

**Remarks.** *Eucrate alcocki* is morphologically very close to *E. formosensis*, *E. indica* **n. sp.**, and *E. sexdentata*. The three species share a well developed and dorsally elevated second anterolateral tooth that sometimes has an acute tip, a third anterolateral tooth that is absent or nearly absent, even in small individuals, and long, slender ambulatory legs, the distal end of the P5 merus reaching between the second anterolateral tooth and the slight elevation that often indicates the missing third anterolateral tooth (Figs. 2C–F; 4; 8A, B; 9A; 10A, B). Sakai (1976: 537) commented that in *E. alcocki* and *E. formosensis* the P5 dactylus is "slender and markedly recurved", whereas in *E. dorsalis* and *E. sexdentata* the dactylus is "straight and not recurved". The distal third of the dactylus has nevertheless been found to be dorsally recurved in all species of *Eucrate sensu lato*.

*Eucrate formosensis* Sakai, 1974, was placed in synonymy with *E. alcocki* by Sakai (1976) (see also Ng *et al.* 2001) but its unique colour pattern warrants regarding it as a separate species (see Remarks for *E. formosensis* below). *Eucrate maculata* Yang & Sun, 1979, was similarly included as a synonym of *E. alcocki* by Dai & Yang (1991). Photographs of the dry male paratype of *E. maculata* (Fig. 4C; 15.9 mm × 18.7 mm, BMNH

J79139), however, confirm the synonymy. It is also clearly apparent from the photograph of the dorsal surface of the carapace of the holotype (Yang & Sun 1979: plate, fig. 3; Ng *et al.* 2001: 34, fig. 7g). The spots diagnostic of *T. alcocki* can still be faintly seen on both the holotype and paratype (Fig. 4C) of *E. maculata*.

*Eucrate sexdentata* has so far been unquestionably recorded only from Queensland, Australia, whereas *E. alcocki* is known as far south as Singapore. One feature distinguishing the two species is the complete absence of a frontal notch (or inconspicuous, if present) in *E. alcocki*, a character noted by Serène (in Serène & Lohavanijaya 1973: 71) when comparing his new species with *E. crenata* (De Haan, 1835). The notch is well developed in *E. sexdentata*. Serène (in Serène & Lohavanijaya 1973) unfortunately did not compare *E. alcocki* with *E. sexdentata* although he must have seen the figures given by Campbell (1969: fig. 1). The two species also differ in their colour patterns. Whereas *E. alcocki* has mostly small spots across the anterior two thirds of the carapace (Figs. 2C; 4A, B; see "Colour" below), *E. sexdentata* has many relatively large reddish spots on the carapace (Campbell 1969: fig. 1B; barely visible in Fig. 10A). Campbell (1969: 120) described the colour pattern as "pale cream with purple-pink spots... or with two additional posterior spots".

The G1 and G2 of *E. alcocki*, *E. formosensis*, *E. indica*, and *E. sexdentata* are similar. The G1 and G2 of *E. alcocki* are illustrated herein for the first time (Fig. 14A–C).

Differences between *E. alcocki* and *E. indica* **n. sp**. are discussed in the description of the latter (see below).

There are also similarities between *E. alcocki* and *E. dorsalis* in terms of the salient second anterolateral teeth, but the first anterolateral teeth are much shorter than in *E. dorsalis*, where both the first and second teeth become shorter with size and ultimately almost disappear in large specimens (Campbell 1969: fig. 6K).

In addition to the male holotype (MNHN-B10134), a specimen labelled as such and which was clearly shown as "type" in Serène & Lohavanijaya (1973: 71, pl. 16, fig. B), a second specimen from the type locality (MNHN-B10135) also carries a label by Serène designating it the "holotype". Although this second specimen (Serène & Lohavanijaya 1973: 71, pl. 16, fig. C), a female (erroneously referred to as a "juvenile female"), is now badly damaged, it shows the characteristics diagnostic of the species and is here recognised as a paratype.

**Colour pattern.** There is some variation in the pattern of spots on the carapace (Figs. 2C; 4A, B). The dorsal surface of the carapace invariably has a varying number of large, often irregular red-brown spots across in addition to smaller spots or dots anterior to the large spots. The anterior spots vary from medium-size spots that decrease in size anteriorly to many spots of evenly small size.

The male holotype from Viet Nam (Serène & Lohavanijaya 1973: pl. 16, fig. B) shows many small dots plus three large ones. The specimen now designated as paratype, referred to by Serène & Lohavanijaya (1973) as a "juvenile female" (see Remarks above) has many small, anterior spots plus irregular, large spots on the rest of the dorsal surface of the carapace, and small spots on the chelipeds (Serène & Lohavanijaya 1973: pl. 16, fig. C). Serène & Lohavanijaya (1973: 71) describe the species as having "generally very bright colors, the pattern distribution of the color being variable; generally there is a larger median gastric red-brown spot and a pair of smaller but similar epigastric spots".

Three specimens from Viet Nam collected in 1995 (MNHN-B30543) still show a pattern where the size and shape of the spots are different in each of the specimens. A round or triangular central spot on the gastric region is flanked by two smaller, irregular spots in all specimens. The eight spots immediately above are relatively large in the female, much smaller in the two males. The spots are numerous and small along the anterior border of the carapace in all three specimens. Small dots are still visible on the chelipeds of the female.

According to Serène & Lohavanijaya (1973), the records of *Eucrate crenata* var. *dentata* by Alcock (1900: 299, 301) from India and Hong Kong (see also Indian list in Sankarankutty 1966: 350) may be *Eucrate alcocki*. However, as Alcock's notes are so brief, we cannot be certain. Certainly they are unlikely to be *Trissoplax dentata* (Stimpson, 1858) as defined here (see below). If Serène & Lohavanijaya (1973) are correct, then the Hong Kong record is probably *E. alcocki* whereas the Indian one is more likely to be *E. indica* **n. sp.** (see below). Chhapgar's (1957: 39, pl. 11, figs. j, k, l) record of "*Eucrate crenata dentata*", however, is clearly *Trissoplax dentata* (Stimpson, 1858) (see below).

**Distribution.** Southern China (Yang & Sun 1979, as *E. maculata* Yang & Sun, 1979), Hong Kong, Philippines, Viet Nam, Gulf of Thailand, eastern Peninsular Malaysia, Singapore. Depth: subtidal to 37 m.

# Eucrate crenata (De Haan, 1835)

(Figs. 2A, B; 3A–G; 14D–F)

Cancer (Eucrate) crenatus De Haan, 1835: 51, pl. 15, fig. 1 [Japan].

*Pilumnoplax sulcatifrons* Stimpson, 1858: 93 (39); 1907: 90 [Hong Kong]. — Miers 1886: 226 [in list]. — Targioni-Tozzetti 1877: 102, pl. 7, figs. 2, 2a-d [Japan].

- Eucrate sulcatifrons De Man 1887: 92 [in passim]. Tesch 1918: 158 [in key], 158 [Indonesia]. Stebbing 1920b: 268 [South Africa]. —Sakai 1965: 169, pl. 83, fig. 3 [colour]; 1976: 535 [in key], 536, fig. 284b [Japan]. Campbell 1969: 119 [in key], 126. Guinot 1971: 1080 [in list]. Kensley 1981: 46 [in list; South Africa]. Miyake 1991: 220 [in list; Japan]. Naiyanetr 1998: 78; 2007: 90 [Gulf of Thailand]. Minemizu 2000: 291 [Japan]. Rodríguez & Suárez 2001: 284 [in list]. Hsueh & Huang 2002: 130 [in key], 131, fig. 15. Ng et al. 2008: 78 [in list]. Yang et al. 2008: 770 [in list] [China].
- *Eucrate crenata* Ortmann 1894: 688, pl. 23, fig. 4. Alcock 1900: 299 [in key], 300 [India, Hong Kong]. Nobili 1906a: 145 [Persian Gulf]; 1906b: 296 [Red Sea, Gulf of Aden]. Rathbun 1903: 23 [Japan]; 1911: 237 [Seychelles]. Tesch 1918: 158 [in key]. Balss 1922a: 137 [in list]. Calman 1927: 214, 218, 219 [Suez, Red Sea]. Shen 1932: 114, figs. 66, 67, pl. 5, fig. 2; 1937: 170 [in list] [China]. Sakai 1934: 314; 1935: 183, fig. 94; 1939: 562, 722, pl. 102, fig. 1; 1940: 42, 45 [in lists]; 1956: 46 [in list]; 1965: 168, pl. 83, fig. 4; 1976: 535 [in key], 535, pl. 192, fig. 1 [colour] [Japan]. Miyake 1961: 21 [in list; Japan]. Miyake *et al.* 1962: 130 [in list] [Japan]. Campbell 1969: 119 [in key], 136, fig. 7 [Japan]. Guinot 1971: 1080 [in list]. Kim 1970: 16; 1973: 408, 636, fig. 163, pl. 32; 1977: 206 [in list] [Korea]. Kim & Kim 1982: 141, 151 [Korea]. Yamaguchi *et al.* 1987: 22, pl. 9, fig. 11; 2003: 52. Dai & Yang 1991: 401 [in key], 401, fig. 195, pl. 54, fig. 2 [China]. Miyake 1991: 146, 220 [in list], pl. 49, fig. 5 [Japan]. Rikuta 1991: 21, 24 [Japan]. Galil 1992: 117 [Mediterranean]. Yamaguchi & Baba 1993: 433, fig. 153; 2003: 52. Karasawa 1997: 61, pl. 15, fig. 2, pl. 18, fig. 6. Naiyanetr 1998: 78; 2007: 90 [Gulf of Thailand]. d'Udekem d'Acoz 1999: 241 [in list, references for Mediterranean Sea records]. Ito & Honma 2001: 29 [in list] [Japan]. Galil *et al.* 2002: 138, unnumbered colour fig. [in list, references for Mediterranean Sea records]. Karasawa & Kato 2003b: 130 [in list]. Ng *et al.* 2008: 78, 79 [in list]. Yang *et al.* 2008: 770 [in list] [China].
- Eucrate aff. crenata Guinot 1969b: fig. 35, fig. 52 [Suez Canal].
- *Eucrate crenate* [sic] Yamaguchi *et al.* 1976: 38 [in list] [Japan].
- not *Eucrate crenata* var. *dentata* Alcock 1900: 299 [in key], 301 [Hong Kong]. (? = *Eucrate alcocki* Serène, in Serène & Lohavanijaya 1973)
- not *Eucrate crenata* var. *dentata* Alcock 1900: 299 [in key], 301 [India]. Sankarankutty 1966: 350 [in list; India]. (? = *Eucrate indica* **n. sp.**)
- (?) Eucrate crenata Nobili 1903: 35 [Singapore]. (? = Eucrate tripunctata Campbell, 1969)
- not *Eucrate sulcatifrons* Stephensen 1946: 167, fig. 45 A, B. Barnard 1950: 282 [in key], 295, fig. 54 d, e. [= *Trissoplax dentata* (Stimpson, 1858)]
- not Eucrate crenata dentata Chhapgar 1957: 437, pl. 11, figs. j, k, l. [west coast of India]. [= Trissoplax dentata (Stimpson, 1858)]
- not *Eucrate sulcatifrons* Edmondson 1962: 4, figs. 1 b, 2a-c [Hawaiian Is.]. McLaughlin *et al.* 2005: 257 [in list]. [= *Platyozius laevis* (Borradaille, 1902)]
- not *Eucrate crenata* Tirmizi & Ghani 1982: 107, fig. 3; 1996: 77 [in key], 80, fig. 31 [Pakistan]. (? = *Eucrate tripunc-tata* Campbell, 1969)

not Eucrate crenata — Shen & Jeng 2005: 150, 152, colour photographs [Taiwan]. (= Eucrate formosenis Sakai, 1974)

**Type material.** Male lectotype, 2 female paralectotypes (RMNH D 287); 2 dry female paralectotypes (RMNH D 42176); mouthparts of paralectoptype (RMNH D 42177) (see Yamaguchi & Baba 1993: 433; 2003: 52; Fransen *et al.* 1997: 111).

Type locality. Japan, unknown location.

**Type material of** *Pilumnoplax sulcatifrons* **Stimpson, 1858,** lost; type locality: Hong Kong. Neotype of *Pilumnoplax sulcatifrons* Stimpson, 1858 (see Remarks below): male, 34.0 mm × 49.1 mm (QM W27449; Figs. 3, 14D–F); type locality: Hong Kong, New Territories, Mirs Bay, mouth of Tolo Channel, stn. 2, 22°47'N, 114°28'E, P. Davie coll., 12.04.1989.

**Material examined.** *Mediterranean Sea, Israel.* Off Palmahim, 36 m, B. Galil coll., 03.06.2000: 1 male, 21.8 mm × 28.3 mm (RMNH 48621).

*Suez Canal.* A. Gravel coll., 1932: 11 males, 2 females (MNHN-B10145); Great Bitter Lake ? ("Tiursah Lake"), A. Gravel coll., 1933: 9 males, 20.2 mm  $\times$  26.6 mm, 18.3 mm  $\times$  23.5 mm, 17.1 mm  $\times$  21.7 mm, 15.6

 $mm \times 20.0 mm$ , 11.8 mm  $\times 16.2 mm$ , 10.0 mm  $\times 13.2 mm$ , cl 10.0 mm [rest of carapace damaged], 8.6 mm  $\times 11.4 mm$ , 7.6 mm  $\times 9.2 mm$ ; 4 females, 20.2 mm  $\times 25.5 mm$ , 10.7 mm  $\times 12.7 mm$ , 9.3 mm  $\times 11.3 mm$ , 8.0 mm  $\times 9.9 mm$  (MNHN-B10146), 1 male, 20.2 mm  $\times 25.6 mm$  (MNHN-B9316).

*Red Sea.* F. Jousseaume coll., 1897 (G. Nobili det., 1905): 2 males, 12.4 mm  $\times$  16.2 mm, 10.4 mm  $\times$  13.9 mm, 1 male, 19.2 mm  $\times$  25.0 mm (MNHN-B10148); F. Jousseaume coll. ? (G. Nobili det., 1905): 1 male, 13.1 mm  $\times$  16.8 mm (MNHN-B10147).

*Persian Gulf.* Stn.4, 25°55'N, 50°16'E, from *Hircinia*-like sponge, 13 m, C. E. Dawson coll., 06.09.1956: 1 male, 10.1 mm  $\times$  13.8 mm (RMNH D 16333).

(?) Seychelles. REVES 2: stn.26, 08.09.1980: 1 female, 5.3 mm  $\times$  6.5 mm (MNHN-B30533); stn.29, 09.1980: 1 female, 3.9 mm  $\times$  4.7 mm (MNHN-B30541); stn.30, 09.09.1980: 1 male, 5.0 mm  $\times$  6.1 mm (MNHN-B30542); stn. 35, 10.09.1980: 1 ovigerous female, 4.9 mm  $\times$  6.3 mm (MNHN-B30536); stn. 40, 44 m, 13.09.1980: 1 male, 6.2 mm  $\times$  7.9 mm (MNHN-B30532); stn. 44, 62 m, sand, 14.09.1980: 1 female, 4.6 mm  $\times$  4.9 mm (MNHN-B30538).

(?) *Madagascar.* Nosy Be, stn. H50–52, R. Humes coll.: 1 male, 16.6 mm  $\times$  19.7 mm (MNHN-B30531); West of Nosy Tanikely, 37 m, gritty mud, stn. H39, R. Humes & J. Ostheimer coll., 15.09.1960: 1 male, 14.3 mm  $\times$  16.6 mm (MNHN-B30530); Procal Bay, 55 m, A. Crosnier col.: 3 males, 9.6 mm  $\times$  12.4 mm, 14.0 mm  $\times$  17.2 mm, 17.1 mm  $\times$  21.0 mm (MNHN-B30529).

*Japan. Shikoku*, Mimase near Kochi, 17.05, 1979, L. B. Holthuis, K. Sakai & H. Suzuki coll.: 1 male, 17.3  $mm \times 21.7 mm$  (RMNH D 32744).

*Kyushu*, Arike Bay, NW Simabase, near Mitsushu, 08.11.1968, T. Sakai & L. B. Holthuis coll.: dry carapace (RMNH D 25143).

*Amakusa Archipelago*, tidal flat, 08.1983, T. Yamaguchi leg: 2 males, 23.0 mm  $\times$  29.1 mm, 24.9 mm  $\times$  31.6 mm; 1 female, 24.4 mm  $\times$  30.6 mm (RMNH D 41888).

*Japan*. Unknown location, Male lectotype, 2 female paralectotypes (RMNH D 287); 2 dry female paralectotypes (RMNH D 42176); mouthparts of paralectoptype (RMNH D 42177).

*China*. Amoy, G. Schlegel coll.: 1 male, 30.1 mm × 37.0 mm, 2 pre-adults females, 3 females, 2 ovigerous females (RMNH D 286).

Off Qingdao, from fishermen, 23–25.08.2002: 3 males, 4 females (ZRC 2002.0493).

Fou Choi (= present day Fuchow): 1 male, 27.3 mm × 33.6 mm (MNHN-B24488).

Guandong Province, Nanao I., Nanao Qianjing fishing port, Y. Cai & P. K. L. Ng coll., 12.11.1998: 12 males, 1 female (ZRC 1999.0676); 14.11.1998: 4 males (ZRC 1999.0675); 14.11.1998: 1 male, 14.2 mm  $\times$  18.0 mm (ZRC 1999.0673); 2 pre-adult females, 13.6 mm  $\times$  16.8 mm, 14.4 mm  $\times$  17.8 mm (ZRC 1999.0674). Unidentified location. Stn. 2, 25 m, 11.07.1967, id. as *E. costata* by H. Chen, 07.03.1986: 1 male, 21.3 mm  $\times$  27.2 mm (MNHN-B30544). – Stn. N118, 23.06.1970, id. as *E. costata* by H. Chen, 07.03.1986: 1 male, 16.6 mm  $\times$  20.4 mm (MNHN-B30545).

*Hong Kong.* New Territories, Tolo Channel, stn. 2,  $22^{\circ}47$ 'N,  $114^{\circ}28$ 'E, P. Davie coll., 12.04.1989: male neotype of *Pilumnoplax sulcatifrons* Stimpson (here designated), 1858, 34.0 mm × 49.1 mm (QM W27449); stn. 2, 1 male, damaged carapace, 1 female,  $22.3 \text{ mm} \times 27.5 \text{ mm}$  (QM W27392). – New Territories, Mirs Bay, stn. 8,  $22^{\circ}55$ 'N,  $114^{\circ}40$ 'E, P. Davie coll., 13.04.1989: 1 male,  $17.5 \text{ mm} \times 21.5 \text{ mm}$  (QM W27392); stn.4: 1 male, 16.9 mm × 20.4 mm (QM W27391). – Unknown location: 1 female,  $27.6 \text{ mm} \times 34.9 \text{ mm}$  (SWIMS CRU-XX-134).

*Indonesia. Java*, Surabaja, 1927: 1 male, 20.7 mm × 26.6 mm (RMNH D 27699).

*Kai Is.*, Danish Kei Islands Expedition, stn. 103, Sunda Strait, 06°05'S, 105°42'E, 52 m., 04.08.1922: 2 males 8.6 mm  $\times$  10.3 mm, 10.0 mm  $\times$  12.5 mm (ZMUC).

(?) *Aru Is.* Mariel King Memorial Expedition: stn. A I/3, Trangan I.,  $06^{\circ}58$ 'S,  $134^{\circ}05$ 'E, 26-27 m, 20.06.1970: 1 female, 6.7 mm × 8.7 mm (MNHN-B30784). – Stn. A III/5–6, Trangan I.,  $06^{\circ}46$ 'S,  $133^{\circ}58$ 'E, 11–16 m, 21.06.1970: 1 male, 8.7 mm × 11.1 mm, 1 pre-adult female, 9.3 mm × 11.9 mm (MNHN-B30783), 2 males, 6.7 mm × 8.5 mm, 11.1 mm × 13.4 mm (MNHN-B30785).

(?) *Australia*. Northern Territory. Mariel King Memorial Expedition: stn. B I/4–7, Bathurst I., Clarence Straits,  $12^{\circ}01$ 'S,  $130^{\circ}08$ 'E, 30.06.1970: 1 pre-adult female,  $4.0 \text{ mm} \times 4.9 \text{ mm}$  (MNHN-B30786).

**Diagnosis.** Third anterolateral tooth visible (except large individuals), carapace with relatively short posterolateral borders (Figs. 2A, B; 3A). P5 propodus slender (Figs. 2A; 3A). Typically 2 adjacent red-brown spots on upper branchial region of carapace; small red-brown spots on chelipeds, anterior portion of carapace.



**FIGURE 3.** *Eucrate crenata* (De Haan, 1835); A–F, male neotype of *Pilumnoplax sulcatifrons* Stimpson, 1858 (34.0 mm  $\times$  49.1 mm) (QM W27449), Hong Kong, New Territories, Tolo Channel; G, female (22.1 mm  $\times$  27.1 mm) (ZRC 2002.0493), China, Qingdao. A, overall view; B, frontal view showing orbits and antennae; C, anterior portion of male thoracic sternum and abdomen; D, third maxillipeds, antennules, antennae and orbits; E, outer surface of right chela; F, posterior portion of male thoracic sternum and abdomen; G, female thoracic sternum and vulvae. Abbreviations: a1-a6 = male abdominal somites 1–6, respectively; cx5 = coxa of fifth pereopod (P5); s3–s7 = thoracic sternites 3 to 7, respectively; t = telson; v = vulva.

**Remarks.** Diagnostic of *E. crenata* is a depression on the carapace around each orbit and the relatively low and triangular outer orbital teeth and three anterolateral teeth, the second of which is obtuse and slightly dorsally elevated (Fig. 3A, B). A shallow sulcus extends posteriorly for a short distance from the median

notch of the front and bifurcating on the gastric region. It becomes less pronounced with size as the carapace becomes somewhat inflated, especially in females. A shallow sulcus with very short, scattered setae extends for a short distance from each third anterolateral tooth onto the gastric region; the sulcus becomes less pronounced and devoid of setae in larger individuals. These are characters are consistent among numerous specimens collected throughout its wide geographical range, from the Mediterranean Sea (as an introduced species) to Japan, its type locality.

Many of these characters, however, are also diagnostic of *Eucrate solaris*. The ventral surface of the cheliped meri of *E. crenata*, however, is smooth or with shallow granules whereas there are conspicuous, high tubercles in *E. solaris*. The colour pattern is also very distinctive in each of the two species (see Remarks for *E. solaris* below).

The alcohol-preserved type material of *Cancer (Eucrate) crenatus* De Haan, 1835 (RMNH D 287), actually consists of a male and two females, not one female as stated by Yamaguchi & Baba (1993: 433; 2003: 52) and Fransen *et al.* (1997: 111). No particular specimen was actually indicated as being the lectotype, even if this was stated as such by Fransen *et al.* (1997: 112). The male specimen (21.4 mm  $\times$  27.0 mm; RMNH D 287) is herein designated the lectotype and the two alcohol-preserved females (23.8 mm  $\times$  30.1 mm, 12.3 mm  $\times$  16.1 mm; RMNH D 287), two dry females (24.4 mm  $\times$  29.8 mm, 24.6 mm  $\times$  31.0 mm; RMNH D 42176), and the dry mouthparts of a sixth specimen (RMNH 42177) as paralectotypes.

The status of *Pilumnoplax sulcatifrons* Stimpson, 1858, described from a male and a second specimen "which appears to be the female" from Hong Kong, has always been a problem as its description is rather incomplete, there were no illustrations, and the type material is lost (see Campbell 1969: 126; Evans 1967; Deiss & Manning 1981; Manning 1993; Manning & Reed 2006). Tesch (1918: 159) had nevertheless stated that "*E. crenata* and *E. sulcatifrons* are so very much alike, that there may be no sufficient reason to separate them: both have the front transversely sulcate, the same dentition of the carapace and the same characteristic patch of hairs at the distal end of the wrist of the cheliped". There is enough evidence to support Tesch's assertion.

The information given in the description (Stimpson 1907: 90) agrees well with the material of *E. crenata* on hand from Hong Kong, the type locality (three males, 16.9 mm  $\times$  20.4 mm, 17.5 mm  $\times$  21.5 mm, one with damaged carapace, one female, 22.3 mm  $\times$  27.5 mm; QM W27449, W27391, W27392), the type material of *E. crenata* (as *Cancer (Eucrate) crenatus* De Haan, 1835, see above), the abundant material of *E. crenata* examined from other locations, and the carapace-width to carapace-length ratio given by Stimpson (cl 0.325, cw 0.41 inch = 8.25 mm  $\times$  10.41 mm; 1:1.26 for his male specimen) and that of the three males and one female Hong Kong specimens on hand (1:1.2).

*Eucrate sulcatifrons* was nevertheless considered different from *E. crenata* by Sakai (1965: 126 [Japanese part]; 1976: 535, 536). Campbell (1969: 126) summarized these differences from Sakai's Japanese text: *E. sulcatifrons* "smaller than *E. crenata*, has a marked concavity posterior to each of the orbits, a well developed inner orbital spine, four anterolateral teeth that are more acute than those of *E. crenata*, the hand of the cheliped is much enlarged, and the colour is variable but many specimens have paler carapace margins". Sakai (1976: 535, 536) separated the two species in a key using different characters. *Eucrate crenata* was described as being of a medium size, "the carapace evenly convex fore and aft", and with a "purplish red spot on either side of the carapace"; *E. sulcatifrons* as small in size, depressed carapace with "transverse ridges along frontal and orbital margins", a groove running from the third anterolateral teeth, heavy chelipeds (with distal border "furnished with short hair"), and "uniformly purplish-red, rimmed with yellowish white along ... borders". *Eucrate crenata* is indeed shown in Sakai's colour figures (Sakai 1965: pl. 83, fig. 4; 1976: pl. 192, fig. 1) as having the typical red spots on the carapace and chelipeds that have been observed in other specimens (see "Colour" below), whereas *E. sulcatifrons* (Sakai 1965: pl. 192, fig. 1) is shown with most of its carapace dark brown in colour. Most if not all of these characters appear to be ontogenetic differences, although the purplish-red phase shown by Sakai has not been observed here or reported elsewhere.

None of the specimens examined by Campbell were identified as *E. sulcatifrons*, but the species was included in his key and separated from *E. crenata* by having a "carapace width less than 25 mm" (*E. sulcatifrons* with "carapace width less than 25 mm"). *Eucrate sulcatifrons* was separated from other species of

*Eucrate* by having a deep "median longitudinal groove, dividing on the gastric region" (Campbell 1969: 119), a character also found in *E. crenata*.

*Pilumnoplax sulcatifrons* Stimpson, 1858, was designated as the type species of *Pilumnoplax* by Rathbun (1918). All species originally included in *Pilumnoplax* (see Ng *et al.* 2008), however, have by now been assigned to other genera (Table 2).

In view of the confused taxonomic history of this species and in the interest of long-term nomenclatural stability, we hereby designate a male neotype ( $34.0 \text{ mm} \times 49.1 \text{ mm}$ ; QM W27449; Figs. 3; 14D–F) from Hong Kong, the type locality of Stimpson's species, as the neotype of *Pilumnoplax sulcatifrons* Stimpson, 1858.

The small specimens from the Aru Is. and the Northern Territory, Australia collected by the Mariel King Memorial Expedition and identified as *E. haswelli* by R. Serène, are closer to *E. crenata* because of the general shape of their carapace. This identification, however, is questionable, as in the case of the small specimens from the Seychelles. They may well represent pre-adults and small individuals of *E. crenata* but equally may potentially belong to a different species. Also questionable are five male specimens from Madagascar (MNHN-B30529-30531). The identity of these specimens needs to be re-examined and compared with fresh material.

The Pakistan specimens identified as "*E. crenata*" by Tirmizi & Ghani (1996: 82) and described as "beautiful dark purplish red, with chelipeds and legs white, the carapace [with] a band of white ... on the anterior and lateral borders" are certain not to belong to *E. crenata*. This colour pattern is similar to that found in some specimens of *E. tripunctata* (Fig. 12). Their figures (Tirmizi & Ghani 1982: fig. 3; 1996: fig. 31) also show strong similarities with *E. tripunctata*, which is characterised by anterolateral teeth that are short, rounded and similar in appearance to the outer orbital teeth (Figs. 12A–E; 13A–D; Campbell 1969: fig. 4B, K, L). *Eucrate tripunctata* is known to occur only as far west as the Gulf of Thailand and is not yet known from the Indian Ocean (see below).

| Species described under <i>Pilumnoplax</i><br>Stimpson, 1858 | Current designation   | Family                               |
|--|---|--------------------------------------|
| P. acanthomerus Rathbun, 1911                                | Linnaeoxanthus acanthomerus                                     | Xanthidae MacLeay, 1838              |
| P. americana Rathbun, 1898                                   | Neopilumnoplax americana  | Mathildellidae Karasawa & Kato, 2003 |
| P. atlantica Miers, 1881                                     | Machaerus atlanticus  | Euryplacidae                         |
| P. ciliata Stimpson, 1858                                    | Heteropilumnus ciliatus   | Pilumnidae Samouelle, 1819           |
| P. cooki Rathbun, 1906                                       | Thyraplax cooki   | Goneplacidae MacLeay, 1838           |
| P. elatus (Boone, 1927)                                      | (?) <i>Trapezioplax tridentata</i> (A. Milne-<br>Edwards, 1880) | Pseudorhombilidae Alcock, 1900       |
| P. inaequalis Yokoya, 1933                                   | Carcinoplax inaequalis  | Goneplacidae MacLeay, 1838           |
| P. incerta Cano, 1889  | (?)Machaerus oxyacanthus (Monod, 1956)                          | (?) Euryplacidae                     |
| P. longipes Stimpson, 1858                                   | Heteropilumnus longipes   | Pilumnidae Samouelle, 1819           |
| P. nitida Chace, 1940  | Perunorhombila nitida   | Pseudorhombilidae Alcock, 1900       |
| P. oxyacantha Monod, 1956                                    | Machaerus oxyacanthus   | Euryplacidae                         |
| P. sinclairi (Alcock & Henderson, 1899)                      | Neopilumnoplax sinclairi  | Mathildellidae Karasawa & Kato, 2003 |
| P. sulpta Simpson, 1858                                      | Lophoplax sculpta   | Pilumnidae Samouelle, 1819           |
| P. sulcatifrons Stimpson, 1858                               | Eucrate crenata (De Haan, 1835)                                 | Euryplacidae                         |

TABLE 2. Current status of species originally described under Pilumnoplax Stimpson, 1858.

**Colour pattern.** Typical of many specimens of are two adjacent red-brown spots on the upper branchial region of the carapace (Fig. 2A). Two large red-brown spots are still clearly visible in one of the dry paralectotypes (24.6 mm  $\times$  31.0 mm; RMNH 42176) and many other preserved specimens examined. A larger but

lighter coloured patch may be found between the two spots in some specimens. Also typical in most individuals are small red-brown spots on the chelipeds and sometimes along the anterior portion of the carapace (Fig. 2A). Larger specimens may not have any spots at all, the carapace being light orange-brown (Fig. 2A).

As in other species of *Eucrate*, several colour patterns have been reported for *E. crenata*. Galil *et al.* (2002: 138) described Mediterranean specimens as having "carapace cream, finely speckled with purple, with two prominent hepatic marks". This generally agrees with the colour of the Chinese material.

**Distribution.** Mediterranean Sea (introduced), Red Sea; Persian Gulf, Arabian Sea; western Pacific Ocean from Korea and Japan to the Gulf of Thailand, Indonesia, and questionably Western Indian Ocean (Madagascar, Seychelles) and northern Australia. Depth: shallow subtidal to at least 36 m.



**FIGURE 4.** Variation in colour patterns of carapace of *Eucrate* species. A–C, *Eucrate alcocki* Serène, in Serène & Lohavanijaya, 1973; A, female (15.1 mm × 17.7 mm) (ZRC 2003.0605), Gulf of Thailand; B, male (19.2 mm × 23.3 mm) (ZRC 1998.1055), Gulf of Thailand; C; male paratype of *Eucrate maculata* Yang & Sun, 1979 (= *E. alcocki*) (15.9 mm × 18.7 mm) (BMNH J79139), China, Fujian Province, Dongshan; D–F, *Eucrate indica* **n. sp.**; D, male (22.8 mm × 28.3 mm) (ZRC 2001.0867), India, Tamil Nadu, fish landing opposite Vellar estuary; E, male holotype (23.4 mm × 28.3 mm) (ZRC 1998.1058), Thailand, Andaman Sea, Phuket I.; F, female (22.8 mm × 28.3 mm) (ZRC 2001.0867), India, Tamil Nadu, fish landing opposite Vellar estuary.

# *Eucrate dorsalis* (White, 1849)

(Figs. 5A–F; 6 A–F; 7A, B; 14G–I)

Cancer (Galene) dorsalis White, 1849: 144, pl. 6, figs. 2, 2a [Australia].

Galene ? laevimanus Lucas, in Jacquinot & Lucas, 1853: 40, pl. 9, figs. 4, 4" [unknown location].

Galene dorsalis White 1861: pl. 2.

*Eucrate hamiltoni* McCulloch 1908: 58, pl. 12, figs. 1, 1<sup>a</sup> [Queensland, Australia]. — Tesch 1918: 158 [in key]. — Serène *et al.* 1974: 24 [Moluccas, Indonesia].

Eucrate dorsalis — McCulloch 1909: 314 [Queensland, Australia]. — Campbell 1969: 118 [in key], 133, figs. 2, 6 [Queensland, Australia]. — Guinot 1971: 1080 [in list]. — Davie 1998: 252 [colour photograph]; 2002: 199 [in list]. — Thoma 2007: 300 [Western Australia.] — Hutchins & Gomez 2007: 331 [in list] [Western Australia]. — Ng et al. 2008: 78 [in list].

**Type material.** Male dry lectotype, 20.2 mm  $\times$  24.8 mm (NHM 1852.71; Fig. 5D); 1 male paralectotype, 36.6 mm  $\times$  46.5 mm (NHM 1850.112; Fig. 5B, C); 1 male paralectotype, 22.0 mm  $\times$  29.6 mm (NHM 1856.135).

Type locality. Australia, Queensland, Moreton Bay.

**Holotype of** *Galene ? laevimanus* Lucas, in Jacquinot & Lucas, 1853: 1 dry male, 28.7 mm × 36.5 mm, *Astrolabe* and *Zélée* Expedition, unknown location (MNHN-B2960).

**Material examined.** *Australia.* Queensland, Moreton Bay, purchased by Warwick: male dry lectotype,  $20.2 \text{ mm} \times 24.8 \text{ mm}$  (NHM 1852.71).

Queensland, east end of Mud I., 15–22.10.1979, S. Cook coll.: 1 pre-adult female, 1 female (LACM); 26.10.1979: 1 male (LACM).

Queensland, Townsville Closure, C. Jones coll., 11.02.1986: 1 female, 31.7 mm  $\times$  40.7 mm (QM W12788).

Queensland, Bundaberg, 1–1.5 miles south of Burnett River, 40 miles offshore, 9 m, sand and mud, G. Limpus coll., 18.12.1969, B.M. Campbell id.: 1 male, 39.0 mm × 46.7 mm (QM W3191).

Australia, unknown location, coll. Mr. Statchbury, purchased by Cuming: 1 male dry paralectotype, 22.0 mm  $\times$  29.6 mm (NHM 1856.135).

Australia, unknown location, coll. Mr. MacGillivray, presented by Mr. Doubleday, voyage of HMS *Rattlesnake*: 1 male dry paralectotype, 36.6 mm × 46.5 mm (NHM 1850.112).

*Unknown location. Astrolabe* and *Zélée* Expedition, M. Languillou coll.: 1 male holotype of *Galene ? lae-vimanus* Lucas, in Jacquinot & Lucas, 1853, dry, 28.7 mm × 36.5 mm (MNHN-B2960).

**Diagnosis.** Third anterolateral tooth visible (except large individuals), carapace with relatively short posterolateral borders (Figs. 5A, B, D–F; 6A, B; 7B). P5 propodus slender (Figs. 5A, E; 6B). Large reddish median spot, scattered small dots on carapace (Figs. 5A, B, D; 6A).

**Remarks.** White (1849:144) provided an excellent drawing that shows a large nearly hexagonal spot on the dorsal surface of the carapace and small dots on the anterior and anterolateral portions of the carapace and chelipeds. It was described as having "beautiful dotted surface, the large liver-coloured mark on the middle of its carapace". This colour pattern is diagnostic of the species although the small dots are always present but the large spot may be absent. The small dots are grouped in clusters, sometimes forming circles.

White's syntypes, three dry males, are still extant at NHM. One of these specimens (NHM 1850.112) has a hexagonal spot on the carapace that almost exactly matches that of the specimen figured by White (1849). The most complete of the two specimens still showing the characteristic carapace spot (20.2 mm  $\times$  24.8 mm [NHM 1852.71, Fig. 5D]) is hereby selected as the lectotype, the other two specimens as paralectotypes (36.6 mm  $\times$  46.5 mm [NHM 1850.112, Fig. 5B, C]; 22.0 mm  $\times$  29.6 mm, [NHM 1856.135]).

Also diagnostic of the species is the reduction of the anterolateral teeth in large individuals, although in smaller ones the second tooth is conspicuous and dorsally salient (Campbell 1969: fig. 6K), somewhat similar to that in *E. alcocki*, *E. formosensis*, and *E. sexdentata* (see Remarks for *E. alcocki*).

*Galene ? laevimanus* Lucas, in Jacquinot & Lucas, 1853, is probably a junior synonym of *E. dorsalis*. The dry male holotype (28.7 mm  $\times$  36.5 mm; MNHN-B2960; 3060 in catalog; Fig. 5E, F) and the description by Lucas (Jacquinot, H. & Lucas, H. 1853: 40, pl. 9, figs. 4, 4") agree well with White's description and illustration of *E. dorsalis* and with the rest of the material examined. The colour of Lucas' specimen, however, was

described as *gris cendré clair* (light ash-gray) without any indication of the characteristic red spot on the carapace. No spot was shown in the gray-brown carapace shown in the colour figure (Fig. 7A; Jacquinot & Lucas 1853: pl. 9, figs. 4, 4" in *Atlas* [by Hombron, J.B. & Jacquinot, H. 1852] and original print in RMNH), and the dry male holotype does not show any remains of colour. The holotype was obtained from an unknown location (*Cette espèce a pour patrie ?*) by the *Astrolabe* and *Zélée* expedition, which traversed the western and southern Pacific Ocean.



**FIGURE 5.** *Eucrate dorsalis* (White, 1849); A, male paralectotye (NHM 1850.112) as originally illustrated in White (1849: pl. 6, fig. 2), Australia, Queensland; B, C, dry male paralectotype of *Cancer (Galene) dorsalis* White, 1849 (36.6 mm × 46.5 mm; NHM 1850.112), Australia, Queensland; D, dry male lectotype of *Cancer (Galene) dorsalis* White, 1849 (20.2 mm × 24.8 mm; NHM 1852.71), Australia, Queensland; *Galene ? laevimanus* Lucas, in Jacquinot & Lucas 1853; E, F, dry male lectotype (28.7 mm × 36.5 mm) (MNHN-B2960); A, D, E, overall views; B, F, dorsal views of carapaces; C, ventral view of carapace. Photo credits: B–D by P. Crabb (NHM); E, F by J.-F. Dejouannet (IRD, Paris).

**Colouration.** Large reddish spot on the median portion of the carapace and small dots along most of the dorsal surface of the carapace (Figs. 5A, B, D; 6A; 7B; Davie 1998: 252 [colour photograph]). Campbell (1969: 134) describes specimens where the central spot is replaced by a complete or incomplete ring of "speckles with or without more sparsely distributed specks inside this ring".

Distribution. Western Australia and Queensland, Australia. Depth: shallow subtidal to at least 9 m.



**FIGURE 6.** *Eucrate dorsalis* (White, 1849); A, female (31.7 mm × 40.7 mm) (QM W12788), Australia, Queensland, Townsville Closure; B–F, male (39.0 mm × 46.7 mm) (QM W3191), Australia, Queensland, Bundaberg. A–B, overall views; C, frontal view showing orbits and antennae; D, outer surface of right chela; E, anterior portion of male thoracic sternum and abdomen; F, posterior portion of male thoracic sternum and abdomen.



**FIGURE 7.** Fresh colours of *Eucrate* species. A, *Galene ? laevimanus* Lucas, in Jacquinot & Lucas, 1853 [= *E. dorsalis* (White, 1849]), male lectotype (28.7 mm × 36.5 mm) (MNHN-B2960) (after Lucas, in Jacquinot & Lucas 1853: pl. 6 fig. 2); B, *E. dorsalis* (White, 1849), Queensland, Australia; C–F, *E. solaris* Yang & Sun, 1979; C, male (23.3 mm × 28.1 mm) (ZRC 2008.1333), Philippines, Bohol, Panglao; D, female (26.2 mm × 31.5 mm) (ZRC 2008.1335), Vanuatu, Santo; E, male (19.5 mm × 23.5 mm) (ZRC 2001.0537), Philippines, Bohol, Panglao; F, male (23.6 mm × 28.1 mm) (ASIZ-74626), Penghu Bay, Taiwan. Photo credit: B by Queensland Museum.

# Eucrate formosensis Sakai, 1974

(Figs. 2E, F; 8A–F; 14J–L)

Eucrate formosensis Sakai, 1974: 94 [Taiwan]. — Ng et al. 2008: 78 [in list].

Eucrate alcocki — Sakai 1976: 535 [in key], 536, pl. 192, fig. 2 [Taiwan]. — Ng et al. 2001: 34 [discussion], fig. 7g [colour] [Taiwan]. — Hsueh & Huang 2001: 130 [in key], 132, figs. 8G, 16 [Taiwan]. (not Eucrate alcocki Serène, in Serène & Lohavanijaya, 1973)

Eucrate crenata — Shen & Jeng 2005: 150, 152, colour photographs [Taiwan]. [not Eucrate crenata (De Haan, 1835)]

**Type material.** Unknown. No specimens of *E. formosensis* Sakai, 1974, are listed as part of T. Sakai's material deposited at the Kanagawa Perfectural Museum (Muraoka 1998) or at the Forschunginstitut Senckenberg, Frankfurt, so it is probable that the type material is no longer extant.

Type locality. Taiwan, Kaoshiung County.

**Material examined.** *Taiwan.* Kaoshiung County, Tung-Kang fishing port, P. K. L. Ng coll., 05.08.1996: 2 females,  $13.6 \text{ mm} \times 15.9 \text{ mm}$ ,  $22.2 \text{ mm} \times 27.1 \text{ mm}$  (ZRC 1993.739).

Taichung County, Wuchi fishing port, gill net, 15 m, 06.12.1991: 1 male, 22.9 mm  $\times$  28.3 mm (ZRC 2008.1355).

Penghu Bay, Y. L. Shen coll., 6.10.2007: 1 male, 19.8 mm × 24.1 mm (ASIZ-74623).

**Diagnosis.** Third anterolateral tooth absent or reduced as slight elevation, carapace with relatively long posterolateral borders (Figs. 2E; 8A, B). P5 propodus slender (Figs. 2E, F; 8A, B). Small red-brown dots through most of carapace (Fig. 2E), larger spots in juveniles (Fig. 2F).

**Remarks.** *Eucrate formosensis* was described as a new species mostly on account of its unique colour pattern (Sakai 1974: 94). Although it was distinguished by Sakai from *E. sexdentata*, with which it shares the general shape of the carapace, and *E. dorsalis*, the colour pattern of the new species was the only reliable way to identify it.



**FIGURE 8.** *Eucrate formosensis* Sakai, 1974; A, C–F, male (19.8 mm  $\times$  24.1 mm) (ASIZ-74623), Taiwan, Penghu; B, female (22.2 mm  $\times$  27.1 mm) (ZRC 1993.739), Taiwan, Kaohsiung. A, B, overall views; C, anterior portion of male thoracic sternum and abdomen; D, posterior portion of male thoracic sternum and abdomen; E, frontal view showing orbits and antennae; F, outer surface of right chela.

No differences were found in the morphology of the G1 of the three species. The G1 of *E. formosensis* (Fig. 14J, K) and *E. dorsalis* (Fig. 14G, H) were described by Sakai (1976: 537) as being slender and thin along the anterior half of their lengths, in contrast to that of *E. sexdentata* (Fig. 15D, E), where it was described as slender and thin only along the anterior third. Examination of the G1 of several specimens of the three species did not show any reliable differences.

Sakai (1976) could not find any morphological differences between *E. formosensis* and *E. alcocki* and placed his species in synonymy with the later (see Ng *et al.* 2001: 34). Both species are indeed morphologically very similar but the colour pattern of *E. formosensis*, small red-brown spots throughout most of the carapace and chelipeds (Fig. 2E, F), is different from that of *E. alcocki* (Fig. 2C). We opt to retain *E. formosensis* as a distinct species as originally described by Sakai until additional material is collected and/or DNA analysis is carried out.

The whereabouts of the holotype of *E. formosensis* is unknown (see above). The only type specimen was collected by T. Watabe of the Manazuru Marine Laboratory (Sakai 1974: 94) and it is possible that the specimen was returned to the collector. Although we believe the type is probably no longer extant, we also do not see an urgent need to select a neotype as the species is not known outside Taiwanese waters, and fresh specimens cannot be mistaken for any other species owing to their distinct coloration.

**Colour pattern.** Small red-brown dots throughout at least the anterior half of the carapace (Fig. 2E; Sakai 1976: pl. 192, fig. 2 [colour]; Ng *et al.* 2001: fig. 7g; Shen & Jeng 2005: 150, 152, [colour photographs], as *E. crenata*). The dots remain visible for a relatively long time in specimens preserved in alcohol.

Li Kuan-Xin from the Peikuan Crab Museum in northern Taiwan gave the second author a photograph (Fig. 2F) of an unidentified *Eucrate* species collected off Tahsi, Ilan Province, which we believe is *E. formo-sensis*. Unfortunately, the specimen was not preserved after it died in an aquarium. The dense pattern of similarly sized spots on the specimen, which was about 1.5 cm in carapace width, is characteristic of *E. formosensis*. We are of the opinion that the spots get proportionately smaller as the specimen grows in size, eventually developing into the finely spotted pattern seen in adults (Fig. 2E). The absence of larger spots on the carapace of the small Taiwanese specimen argues against it being *E. alcocki*.

Distribution. Only known from Taiwan thus far. Depth: shallow subtidal to at least 15 m.

# *Eucrate indica* n. sp.

(Figs. 2D; 4D–F; 9A–F; 15A–C)

*Eucrate alcocki* — Ng & Davie 2002: 378 [Andaman Sea coast of Thailand]. — Rajkumar *et al.* 2009: 832, fig. 1 [India]. (not *Eucrate alcocki* Serène, in Serène & Lohavanijaya, 1973)

(?) Eucrate crenata var. dentata — Alcock 1900: 299 [in key], 301 [India]. — Sankarankutty 1966: 350 [in list; India].

**Type material.** Male holotype, 23.8 mm  $\times$  28.4 mm (ZRC 2001.1058; Figs. 4E, 9, 15A–C); 1 female paratype, 17.6 mm  $\times$  20.8 mm (ZRC 1999.0135), 1 male paratype, 20.1 mm  $\times$  24.2 mm, 1 female paratype, 20.0 mm  $\times$  24.2 mm (ZRC 1998.1119), 1 male paratype, 18.1 mm  $\times$  21.8 mm, 1 female paratype, 13.5 mm  $\times$  17.1 mm (ZRC 2001.1058).

Type locality. Thailand, Andaman Sea coast, Phuket I. fishing port

**Material examined.** *India.* Tamil Nadu, fish landing opposite Vellar estuary, A. S. Fernando & P. K. L. Ng coll., 24.03.2001: 1 male, 22.3 mm × 27.3 mm, 1 female, 22.8 mm × 28.3 mm (ZRC 2001.0867). – Chennai [Madras], Kasimedu fishing port, shrimp trawlers, Z. Jaafar coll., 23.11.2004: 1 male, 21.5 mm × 26.7 mm, 1 ovigerous female, 18.5 mm × 23.1 mm (ZRC 2004.0764). – Bay of Bengal, D. Rajkumar leg., 06.2006: 1 male, 23.8 mm × 29.1 mm (MNHN-B30155).

*Thailand*. Andaman Sea, Phuket I., Pichai fishing port, P. K. L. Ng coll., 04.1997: 1 female paratype, 17.6 mm  $\times$  20.8 mm (ZRC 1999.0135). – N. K. Ng *et al.* coll., 17–20.01.2000: carapace, 18.6 mm  $\times$  23.2 mm (ZRC 2000.0764). – Phuket I. fishing port, S. Chaitiamwong *et al.*, 1 male paratype, 20.1 mm  $\times$  24.2 mm, 1 female paratype, 20.0 mm  $\times$  24.2 mm (ZRC 1998.1119). – Phuket I. fishing port, P. K. L. Ng *et al.* coll., 17.02.2001: male holotype, 23.8 mm  $\times$  28.4 mm, 1 male paratype, 18.1 mm  $\times$  21.8 mm, 1 female paratype, 13.5 mm  $\times$  17.1 mm (ZRC 2001.1058).

*Peninsular Malaysia*. Andaman Sea Coast, between Penang and Langkawi, trawling, C. P. How & C. O. Lau coll., 12.11.1991: 1 female, 15.3 mm × 19.0 mm (ZRC 1992.10458).

**Diagnosis.** Third anterolateral tooth absent or reduced as slight elevation, carapace with relatively long posterolateral borders (Figs. 2D; 4D–F; 9A). P5 propodus slender (Figs. 2D; 9A). Irregular, large, red-brown spots on median portion of carapace (Figs. 2D; 4D–F; 9A).

**Description.** Carapace (Figs. 2D; 4D–F; 9A) transversely hexagonal, wider than long (1.19 wider than long in male holotype), anterolateral borders arched, dorsal surface without clear indication of regions; front wide, with median notch, deep transverse sulcus along margin. Three anterolateral teeth posterior to short, triangular outer orbital tooth (first short, triangular, obtuse tip; second largest, slender, acute; third short, barely noticeable). Orbits short (Fig. 9C), shorter than front (0.6 frontal width in holotype), conspicuous notch between front, orbit; conspicuous notch on median portion, shallower notch on outer portion of curved, thick supraorbital border; suborbital border (Fig. 9B) sinuous, with short, obtuse inner suborbital tooth, short median lobe; eye peduncles short (0.2 frontal width in holotype), as long as corneas; large, spherical corneas. Basal antennal article slightly immobile, with disto-lateral process so that orbital hiatus is closed excluding antennal flagellum from orbit.

Posterior margin of epistome lobular; lateral lobes large, with sinuous margins, separated from median portion by deep fissure; median portion with 2 lobes separated by deep fissure (Fig. 9C). Anterior margin of endostome well demarcated from buccal cavern, endostomial ridges low. Pterygostomian region with low granules. Third maxillipeds (Fig. 9B) completely closing buccal cavern; ischium rectangular with deep sub-median line; merus relatively square in shape but anteroexternal part angular, rounded; exopod long, reaching to just before anterior edge of merus with long flagellum.

Cheliped fingers (Fig. 9D) moderately stout, slightly longer than swollen propodus, distal portion light in colour. Inner (dorsal) margin of carpus with large tooth; short tomentum on anterior margin of carpus; outer (dorsal) margin of merus with large, obtuse tooth, row of short tubercles. Dorsal, ventral margins of ambulatory legs (P2–P5) with short tubercles, dorsal margins of carpus with long, simple setae; dactyli long, slender; P5 merus (Fig. 9A) long, moderately slender (16.2 mm long in holotype), ventral margin slightly curved, distal end reaches past third anterolateral tooth but not second anterolateral tooth when folded against carapace; P5 propodus (9.8 mm long, 3.0 mm wide in holotype), proportionally stout, subcylindrical; inner, outer margins fringed with row of numerous short, simple setae; P5 dactylus (9.5 mm long, 2.0 mm maximum width in holotype) proportionally slender, subcylindrical, fringed with short, simple setae.

Thoracic sternum (Fig. 9E) wide, thoracic suture 2/3 complete, convex; 3/4 deep, short, interrupted; 4/5, 6/7, 7/8 interrupted, 5/6 complete; median groove on thoracic sternites 7, 8. Sterno-abdominal cavity of male deep, nearly reaching anterior margin of sternite 4. Press-button of male abdominal-locking mechanism as tubercle near thoracic suture 4/5.

Male abdomen (Fig. 9E) narrow, slender (T-shaped), lateral margins of somites 4–6 abruptly narrowing from somite 3 to transversely narrow, pointed telson; somite 3 reaching inner margins of P5 coxae (Fig. 9F); no portions of thoracic 8 exposed by closed abdomen, somite 2 slightly transversely shorter than somite 3. G1 long, slender, sinuous, acuminate apex, with small denticles (Figs. 15A, B); G2 (Fig. 15C) less than one-third of G1, straight, with 2 processes: one long, tip obtuse; second much shorter, tip acute. Male genital opening (gonopore) coxal; coxo-sternal disposition of long penis, protected by concave posterior portion of thoracic sternite 7.

Vulva ovoid, extending across anterior portion of sternite 6 close to median axis of thorax; covered by soft membrane, sternal vulvar cover absent.

**Colour pattern.** Two large, irregular, red-brown spots on the median portion of the dorsal surface of the carapace, each flanked by two smaller, vertically placed spots (Figs. 2D; 4D–F; 9A; see Remarks below). The central or lateral spots may coalesce into a single lateral spot (Fig. 4E). All spots may also coalesce, forming irregular patterns bearing a striking resemblance to letters or numbers (Fig. 2D). Small red-brown spots are located along the anterior border of the carapace and dorsal surface of chelipeds.

**Etymology.** *Indica* from India and Indian Ocean, to denote the distributional range of this species in contrast to two similar species, *Eucrate alcocki* in China and southwestern Asia, and *E. formosensis* in Taiwan.

**Remarks.** The populations that had been identified as "*E. alcocki*" from the Indian and western Pacific oceans are clearly different in their carapace colour patterns. In true *E. alcocki* from China, Vietnam, Gulf of Thailand and Singapore, there are consistently one to six large spots or blotches on the median portion of the carapace, and the anterior portion has numerous smaller spots (Figs. 2C; 4A, B). In specimens from the Indian Ocean and as far west as the Andaman Sea coast of Thailand and the northern Straits of Malacca (Phuket I., Langkawi, and Penang islands), there are usually six large spots arranged transversely across the median portion of the carapace and numerous smaller spots on the anterior portion of the carapace. This colour pattern is consistent for the large series of specimens examined.



**FIGURE 9.** *Eucrate indica* **n. sp.**; male holotype (23.8 mm  $\times$  28.4 mm) (ZRC 1998.1058), Thailand, Andaman Sea, Phuket I. A, overall view; B, third maxillipeds, antennules, antennae, and orbits; C, frontal view; D, outer surface of right chela; E, anterior portion of male thoracic sternum and abdomen; F, posterior portion of male thoracic sternum and abdomen. Abbreviations: a1-a3 = male abdominal somites 1 to 3, respectively; cx5 = coxa of fifth pereopod (P5); t = telson.

There are also several morphological differences. Specimens from the Indian Ocean have proportionately wider carapaces (width to length ratio 1.18-1.26, n = 13, mean = 1.21; 1.09-1.29, n = 32, mean = 1.16 in *E. alcocki*) (Figs. 2D, 4D–F for *E. indica*; Figs. 2C, 4A, B for *E. alcocki*), the frontal margin is generally more prominent, well produced, and with a distinct median notch (Figs. 4D–F; 9C) (less prominent, with the median notch shallow or barely visible in *E. alcocki*, Figs. 4A–C), the cleft between the frontal margin and

inner suborbital tooth is deep and pronounced (Fig. 9C) (shallow in *E. alcocki*), and the supraorbital border has a deep and prominent notch (Figs. 4D–F; 9C) (shallow and less distinct in *E. alcocki*, Figs. 4A–C). As such, we are of the opinion that the Indian Ocean material should be referred to as a separate species.

As has been discussed earlier under *E. alcocki*, the record of *Eucrate crenata* var. *dentata* by Alcock (1900: 299, 301) from India (see also list of Indian taxa in Sankarankutty 1966: 350) may be *Eucrate indica* **n. sp.** as well. Serène & Lohavanijaya (1973) had suggested it may be *E. alcocki*.

The geographic distributions of *E. indica* **n. sp.** and *E. alcocki* are noteworthy as, *E. indica* **n. sp.** is found in the Persian Gulf, Indian Ocean, and the Andaman Sea, whereas *E. alcocki* is found on the Gulf of Thailand and the western Pacific Ocean. A similar pattern has also been observed for several other species of brachyurans, with one species occurring in the Indian Ocean (e.g. the xanthid *Liagore erythematica* Guinot, 1971, the calappid *Calappa bilineata* Ng, Lai & Aungtonya, 2002, the portunid *Portunus reticulatus* (Herbst, 1799)) and a close species present in the Pacific (*Liagore rubromaculata* (De Haan, 1835), *Calappa philargius* (Linnaeus, 1758), *Portunus pelagicus* (Linnaeus, 1758), respectively) (see Ng *et al.* 2002; Ng & Chen, 2004; Ng *et al.* 2008; Lai *et al.* 2010).

**Distribution.** Persian Gulf, India, Andaman Sea coasts of Thailand and Peninsular Malaysia. Depth: shallow subtidal.

# Eucrate sexdentata Haswell, 1882

(Figs. 10A-F; 15D-F)

Eucrate sexdentatus Haswell, 1882a: 548; 1882b: 86 [Queensland, Australia].

- Eucrate sexdentata Campbell 1969: 118 [in key], 120, fig. 1 [Queensland, Australia]. Griffin & Campbell 1969: 150 [Queensland, Australia]. Guinot 1971: 1080 [in list]. Davie 2002: 199 [in list]. Ng et al. 2008: 78 [in list].
- (?) Eucrate sexdentata Alcock 1900: 299 [in key], 301 [Myanmar = Burma].
- not *Pseudorhombila vestita* var. *sexdentata (Pseudorhombila haswelli* Miers, 1884) Miers 1884: 240, pl. 24, fig. B [Arafura Sea]. [= *Homoioplax haswelli* (Miers, 1884)]

**Type material.** Dry male lectotype,  $8.3 \text{ mm} \times 10.5 \text{ mm}$  (AM P719; Fig. 10E); 1 female paralectotype, 9.5 mm  $\times 10.6 \text{ mm}$  (AM P719; Fig. 10F).

Type locality. Australia, Port Denison, off Holborn I., 36 m.

**Material examined.** *Australia*, Queensland, stn. 9–79, 20.09.79: 5 males, 22.8 mm × 26.6 mm, 2 females (LACM).

Queensland, Moreton Bay, muddy bottom, 25 m, N. Coleman coll., 06.1986: 1 male, 19.6 mm  $\times$  23.1 mm, 2 pre-adult females, 13.7 mm  $\times$  15.7 mm, 15.0 mm  $\times$  16.9 mm (QM W16032); east of Mud I., trawling, S. Cook coll., 22.10.1979: 1 male, 20.1 mm  $\times$  23.2 mm (QM W12057).

**Diagnosis.** Third anterolateral tooth absent or reduced as slight elevation, carapace with relatively long posterolateral borders (Fig. 10A, B, E, F). P5 propodus slender (Fig. 10A, B). Large purple-pink spots on anterior two-thirds of dorsal surface of carapace (Fig. 10A, B; Campbell 1969: fig. 1B).

**Remarks.** Characteristic of *E. sexdentata* is the presence of only two anterolateral teeth posterior of each outer orbital tooth (Fig. 10A, B, E, F), the third tooth is absent, leaving only a slightly elevated margin, even in the two pre-adult females that were examined. The second anterolateral tooth is acute and dorsally projecting. Also diagnostic are the relatively long posterolateral margins (Fig. 10A, B, E, F) and the long and slender P2–P5 (Fig. 10A, B), the distal end of the P5 merus reaching the proximal portion of the second anterolateral tooth, the tip in pre-adults. These characters, however, are shared with *E. alcocki* and *E. formosensis*. Differences among the three species are discussed in the Remarks for *E. alcocki*.

The type material of *Eucrate sexdentatus* Haswell, 1882, consists of two dry syntypes (male, 8.3 mm  $\times$  10.5 mm; female, 9.5 mm  $\times$  10.6 mm [AM P719]). Neither could be examined on loan because of their very fragile condition. Colour photographs of the specimens, however, clearly show that they agree well with Haswell's description as well as with the Australian specimens on hand. The dry male specimen (Fig. 10E) is

hereby designated as the lectotype and the dry female (Fig. 10F) as paralectotype. The mesobranchial regions of the male paralectotype are visibly inflated, making the posterolateral borders of the carapace prominently more convex than in the female. A handwritten label glued underneath the slide where the specimens are kept reads "1 specimen distorted by parasites" (H. Stoddart, personal communication). The swellings on both sides of the carapace are symmetrical to each other but this does not preclude that both sides were parasitised by bopyriids. In the more recently collected specimens examined, however, the posterolateral borders of the carapace are slightly more convex in males (Fig. 10A) than in females (Fig. 10B), so this may be normal sexual dimorphism.



**FIGURE 10.** *Eucrate sexdentata* Haswell, 1882; A, C, D, male (19.6 mm  $\times$  23.1 mm) (QM W16032), Australia, Queensland, Moreton Bay; B, female (15.0 mm  $\times$  16.9 mm) (QM W16032), Australia, Queensland, Moreton Bay; E, dry male lectotype of *E. sexdentatus* Haswell, 1882 (8.3 mm  $\times$  10.5 mm) (AM P719), Australia, Port Denison, Holborn I.; F, dry female paralectotype of *E. sexdentatus* Haswell, 1882 (9.5 mm  $\times$  10.6 mm), same data as paralectotype. A, B, overall views; C, frontal view showing orbits and antennae; D, anterior portion of male thoracic sternum and abdomen; E, F, dorsal views of carapaces. Photo credits: E, F by R.T. Springthorpe © (AM).
The identification by Alcock (1900: 301) of a male specimen from the Gulf of Martaban (Andaman Sea coast of Myanmar [= Burma]) as *E. sexdentata* is questionable. The species has only been reported from Queensland, Australia, and it is possible that Alcock was mistaken since he based his identification solely from Haswell's description. Neither the short description (Haswell 1882a: 548) nor a longer discussion of the species (Haswell 1882b: 86) included illustrations. A character given in Alcock's (1900: 299) key, "dactylus of last pair of legs almost styliform", also applies to *E. alcocki*, which has been recorded from several locations in the Andaman Sea (see Material examined for *E. alcocki*) and which had not been described until well after Alcock's lifetime. Nevertheless, Alcock clearly stated in his key that the Myanmar (Burma) specimen had only two anterolateral teeth ["three teeth (including the orbital angle)"], a character diagnostic of *E. sexdentata*. Specimens of *E. alcocki* of the same size as Alcock's male (11.5 mm × 13.5 mm) do show three anterolateral teeth unlike specimens of *E. sexdentata*.

**Colour pattern.** "Pale cream with purple-pink spots" on the anterior two-thirds of the dorsal surface of the carapace, decreasing in size anteriorly (barely visible in Fig. 10A, B; Campbell 1969: 120, fig. 1B).

**Distribution.** Queensland, Australia and, questionably, Myanmar [= Burma] (Alcock 1900). Depth: shallow subtidal to 180 m (Campbell 1969).

#### Eucrate solaris Yang & Sun, 1979

(Figs. 7C–F; 11A–F; 15G–I)

Eucrate solaris Yang & Sun, 1979: 1, 8, fig. 1, plate, figs. 1, 2, 7 [China]. — Dai *et al.* 1986: 372 [in key], 373, fig. 196(1), pl. 54, fig. 3 [China] — Chen 1998: 277, 310 [in list], fig. 8. — Dai & Yang 1991: 401 [in key], 402, fig. 196(1), pl. 54, fig. 3 [China]. — Naiyanetr 1998: 78; 2007: 90 [Gulf of Thailand]. — Ng *et al.* 2001: 34, fig. 7h [Taiwan]. — Hsueh & Huang, 2002: 130 [in key], 133, figs. 8H, 17. — Ng *et al.* 2008: 78 [in list]. — Yang *et al.* 2008: 770 [in list] [China].

Eucrate crenata — Shen & Jeng 2005: 153, colour photograph [Taiwan]. [not Eucrate crenata (De Haan, 1835)]

**Type material.** Male holotype (BMNH J79136); female allotype, 21.3 mm  $\times$  27.0 mm (BMNH J79137; Fig. 11A), 1 male, 3 female paratypes (BMNH).

Type locality. China, Guanxi Province, Beihai.

**Material examined.** (?) *Japan. Ryukyu Islands.* Kamejima I., Ahra, coral reef, intertidal, 13.06.1995, K. Nomura coll.: 1 female (CBMZC 3191).

Taiwan. Kaohsiung County, Tung-Kang fishing port, P. K. L. Ng coll., 05.05.1996: 1 female (ZRC 1997.752).

I-Lan County, Tahsi, K. X. Lee coll., 2000: 1 female, 21.4 mm × 26.2 mm (ZRC 2001.0023).

Penghu Bay, 50 m, 3.31.1998: 1 female (ASIZ-71966); Y. L. Shen coll., 5.10.2006: 1 male, 23.6 mm × 28.1 mm (ASIZ-74626).

*Philippines. Bohol.* Balicasag I., off Panglao I., tangle nets, purchased from fishermen, 200–300 m, 12.2000: 4 males, 20.0 mm × 25.0 mm, 21.6 mm × 26.4 mm, 23.4 mm × 28.5 mm, 23.5 mm × 28.4 mm (ZRC 2001.0394); 50–500 m, 28.11.2001: 1 male, 19.5 mm × 23.5 mm (ZRC 2001.0537), 1 female (ZRC 2001.0538), 1 male, 2 females (ZRC 2001.0655); 200–300 m, 06.2002: 1 male, 1 female (ZRC 2002.0650); 25–30.07.03: 6 males, 11 females (ZRC 2004.0751); 50–500 m, 02.03.2004: 1 male, 3 females (ZRC 2004.0733); 25–30.07.2003: 5 males, 7 females (ZRC); 04.2004, 1 male (ZRC 2004.0762), 04.2004: 1 male, 15.5 mm × 18.6 mm, 2 females, 20.3 mm × 24.2 mm, 22.7 mm × 27.6 mm (MNHN-B29727); 29.05.2004: 2 males, 4 females (ZRC 2009.0976); 05.2004: 1 female (ZRC 2009.0977).

PANGLAO 2004: stn. P1, 09°36.00'N, 123°45.00'E, 150–200 m, 27.06.2004: 1 female (ZRC 2009.0978), 1 male (ZRC 2009.0979). – Stn. P4, 11.06.2004: 1 male (ZRC 2009.0980). – Stn. L40, Panglao I., Tangnan, 9°37.3'N, 123°46.5'E, 100–120 m, 24.06.2004: 1 male, photograph, 23.3 mm × 28.1 mm (ZRC 2008.1333).

*Vanuatu.* SANTO 2006: stn. EP04, northeast Aoré I., Aimbué Bay,  $15^{\circ}33.0/33.4$ 'S,  $167^{\circ}11.7/12.8$ 'E, tangle net, 89–109 m, 12.09.2006: 2 males, 26.2 mm × 31.6 mm, 25.6 mm × 31.1 mm, 1 female, 22.0 mm × 27.3 mm (ZRC 2008.1237). – Stn. EN31, east Aoré I., Aimbué Bay,  $15^{\circ}32.9$ 'S,  $167^{\circ}12.9$ 'E, traps, 107 m,

 $12.09.2006: 10 \text{ males}, 17.3 \text{ mm} \times 20.3 \text{ mm} - 29.4 \text{ mm} \times 35.0 \text{ mm}, 4 \text{ females}, 19.5 \text{ mm} \times 23.8 \text{ mm} - 25.0 \text{ mm}$ × 31.5 mm (ZRC 2008.1238). – Stn. EP10, east Aoré I., 15°34.5/38.0'S, 167°05.1/13.6'E, tangle net, 45–101 m, 15.09.2006: 1 male, 17.6 mm × 22.3 mm (MNHN-B31628). - Stn. EP12, Scorff Passage, 15°31.9'S, 167°15.1'E, tangle net, 97 m, 16.09.2006: 1 female, photograph, 22.2 mm × 27.7 mm (MNHN-B31629). -Stn. EP18, Aoré I., Aimbué Bay, 15°33.1/33.3'S, 167°11.8/12.2'E, tangle net, 71–102 m, 18.09.2006: 4 males, 18.9 mm × 22.6 mm - 26.2 mm × 32.1 mm, 2 females, 18.4 mm × 22.5 mm, 24.5 mm × 30.2 mm (MNHN-B31630). – Stn.EP15, northeast Urélapa I., 15°36.6/36.7'S, 167°01.7/02.1'E, tangle net, 103–108 m, 16.09.2006: 1 female, 20.8 mm × 25.9 mm (MNHN-B31631), 3 males, 1 female (MNHN-B31988). - Stn. EP21, northwest coast of Mao I.,  $15^{\circ}37.7$ 'S,  $167^{\circ}5.2$ 'E, tangle nets, 99 m: 1 male, 21.0 mm  $\times$  25.4 mm, 1 female, 20.8 mm × 25.0 mm (MNHN-B31989). – Stn. EP23, 15°32.8/33.0'S, 167°12.1/12.3'E, north Aoré I., Aimbué Bay, tangle net, 74–88 m, 22.09.2006: 1 male, 25.6 mm × 30.7 mm, 1 female, 24.4 mm × 29.6 mm (MNHN-B31632). – Stn. EP24, west Urélapa I., 15°36.5'S, 167°00.9/01.7'E, tangle net, 108–121 m, 25.09.2006: 1 pre-adult female, 15.2 mm × 18.5 mm (ZRC 2008.1334). - Stn. AT41, 15°36.7/37.0'S, 167°02.7/02.8'E, east Urélapa I., 88–118 m, 28.09.2006: 1 female, 24.7 mm × 30.8 mm (ZRC 2009.0075). – Stn. FP48, Aoré I., Aimbué Bay, 15°32.4'S, 167°12.7'E, tangle net, 45–50 m, 03.10.2006: 1 male, 21.5 mm × 26.5 mm, 1 female 22.0 mm × 27.2 mm, 1 ovigerous female, 24.8 mm × 31.1 mm (MNHN-B31633). -Stn.FP49, Aoré I., Aimbué Bay, 15°32.4'S, 167°12.7'E, tangle net, 45–50 m, 03.10.2006: 3 males, 19.8 mm × 25.1 mm – 25.7 mm  $\times$  31.1 mm, 1 pre-adult female, 8.3 mm  $\times$  10.4 mm, 1 female, 22.8 mm  $\times$  27.7 mm (MNHN-B31634). – Stn. EP27, Tutuba I., 15°33'S, 167°16.0'E, tangle net, 155 m, 07.10.2006: 1 female, 24.5 mm × 30.1 mm (ZRC 2008.1239). – Stn. EN33, east Aoré I., Aimbué Bay, 15°32.6'S, 167°12.5'E, traps, 80 m, 14.10.2006: 4 females, 22.6 mm × 27.9 mm - 25.0 mm × 31.7 mm (ZRC 2008.1240). - Stn. EP35, east Aoré I., off Aimbué Bay, 15°34.9/35.1'S, 167°13.9/14.1'E, tangle net, 10-51 m, 15.10.2006: 2 males, 21.1 mm × 26.2 mm, 25.3 mm × 30.5 mm, 1 female, 22.2 mm × 27.1 mm (MNHN-B31635). – Stn. EP40, west Tutuba I., 15°33.1/33.6'S, 167°16.4/16.5'E, tangle net, 125–156 m, 18.10.2006: 1 female, photograph, 26.2 mm × 31.5 mm (ZRC 2008.1335), 1 female, photograph, 21.9 mm × 26.7 mm (ZRC 2008.1336).

**Diagnosis.** Third anterolateral tooth visible (except large individuals), carapace with relatively short posterolateral borders (Figs. 7C–F; 11A, B). P5 propodus slender (Figs. 7C–F; 11A, B). Variegated pattern of irregular red-brown, red-pink dots, spots variously arranged on carapace (Fig. 7C–F).

**Remarks.** Diagnostic of *E. solaris* is a carapace that is sculptured by ridges and deep, sometimes setous grooves, most especially in the largest specimens. A groove extends from the median notch of the front, cutting through a transverse ridge that extends across the frontal region posterior to the front before bifurcating on the mesogastric region. A depression, sometimes setous, extends posterior to each orbit and continuing to the anterolateral border between the first and second anterolateral teeth. Anther groove, typically setous, extends from each of the third anterolateral teeth into the mesogastric region. These grooves are particularly conspicuous in large specimens collected from deep-water tangle nets in the Philippines (e.g. ZRC 2001.0394, 2001.0655, 2004.0751). The supraorbital borders and the hepatic regions in some of these specimens are sculptured by relatively deep, round or irregular depressions.

The first anterolateral tooth is triangular in outline; the second, the largest, is also triangular but slightly dorsally elevated; the third is the smallest but conspicuous in relation to other species of *Eucrate*.

*Eucrate solaris* can be differentiated from all other known species of *Eucrate* by its distinctive variegated colour pattern. Preserved specimens, which do not show the distinctive colour pattern, do show two diagnostic triangular or hexagonal patterns on the mesogastric region. Also diagnostic is the short tomentum, never conspicuous as in other species of *Eucrate*, along the anterior margin of the cheliped carpus.

*Eucrate solaris* is closest to *E. crenata* in the general shape of its carapace, particularly in the anterolateral teeth: first tooth being well developed, triangular, and with an obtuse tip; second tooth the largest, triangular, dorsally salient, and with an obtuse tip; third tooth short, with an obtuse tip, and always present. *Eucrate solaris* can be morphologically differentiated by: (1) a row of a varying number of obtuse granules and conspicuous tubercles on the outer (dorsal) margin of the cheliped merus (only short granules in *E. crenata*), (2) the absence of a conspicuous tomentum, only fewer and shorter setae, along the anterior margin of the cheliped merus (long and conspicuous tomentum in *E. crenata*), and (3) a relatively shallow frontal notch (Fig.

12A–C) (well defined in *E. crenata*; Fig. 3B–D). The colour pattern of preserved specimens of both *E. solaris* and *E. crenata* invariably consists of two red-brown dots on the branchial region and many small dots on the anterior third of the carapace. In *E. solaris*, however, two roughly triangular or a single hexagonal pattern remains on the mesogastric region, a pattern that is never present in *E. crenata*.

In addition to its unique colour pattern, *E. solaris* can be distinguished from *E. alcocki*, *E. formosensis*, and *E. sexdentata* by having well developed third anterolateral teeth, which, although small, is always visible (Fig. 11A, B) whereas in the other three species the teeth are absent or only evident by a slight elevation on each of the relatively long posterolateral borders of the carapace. As in *E. alcocki* and *E. formosensis*, however, the frontal notch is very small or absent. The P5 propodus of *E. solaris* is slender (Fig. 11A, B) whereas it is noticeably short and wide in *E. tripunctata* (Figs. 12; 13C; Campbell 1969: fig. 4G); the first anterolateral teeth become even shorter (Campbell 1969: figs. B, K) in contrast to the more conspicuous teeth of *E. solaris*.



**FIGURE 11.** *Eucrate solaris* Yang & Sun, 1979; A, female allotype (21.3 mm  $\times$  27.0 mm) (BMNJ-J79137), China, Guangxi Province, Beibu Bay; B, C, F, female (21.4 mm  $\times$  26.2 mm) (ZRC 2001.0023), Taiwan, I-Lan County, Tahsi; D, E, male (23.3 mm  $\times$  28.1 mm) (ZRC 2008.1333), Philippines, Bohol, Panglao. A, B, overall views; C, frontal view showing orbits and antennae; D, anterior portion of male thoracic sternum and abdomen; E, male sterno-abdominal cavity and G1; F, female thoracic sternum and vulvae. Abbreviations: a2, a3 = male abdominal somites 2, 3, respectively; cx5 = coxa of fifth pereopod (P5); G1 = first male pleopod; mg = median groove; p = penis; pb = press-button of the male abdominal-locking mechanism; s4–s8 = thoracic sternites 4 to 8, respectively; sc = sterno-abdominal cavity; t = telson; v = vulva.

**Colour pattern.** Variegated pattern of irregular red-brown and red-pink dots and spots symmetrically but variously arranged on the carapace (Fig. 7C–F). Two small, irregular spots are located on the branchial region at the inner end of the v-shaped groove that runs from each third anterolateral tooth; two triangular or hexagonal patterns on the mesogastric region (two dark spots in a Philippines specimen; Fig. 7C). There is a white band along the proximal portion of the meri of the ambulatory legs, the remaining portion being red-pink. Freshly preserved specimens from the Philippines also showed a red-brown sternum continuing as a vertical band along the margins of the abdomen and extending into the posterior portion of the carapace, which can be seen in the colour photograph (Fig. 7D). The fingers can be dark or light brown.

A colour photograph of presumably fresh material from Taiwan (Shen & Jeng 2005: 153, as *E. crenata*) shows a yellow carapace with a red-brown, elongated spot across the mesogastric region of the carapace bordered by two large, red-brown spots. The chelipeds are yellow and the ambulatory legs light yellow, with distal portions with wide, red-brown bands. There are many variations in the number and shape of the carapace spots, however, being round, elongated or crescent-shaped, and two, three or four in number (Fig. 7C–F; Yang & Sun 1979: plate, fig. 1).

**Distribution.** Taiwan, South China Sea (Yang & Sun 1979), Philippines, Gulf of Thailand, Vanuatu, and questionably the Ryukyu Is., Japan. Depth: subtidal to at least 200 m, but also collected from tangle nets reaching 500 m (see Ng *et al.* 2009).

#### Eucrate tripunctata Campbell, 1969

(Figs. 12A-F; 13A-F; 15J-L)

*Eucrate tripunctata* Campbell, 1969: 119 [in key], 127, figs. 2, 4 [Queensland, Australia]. — Guinot 1971: 1080 [in list] — Davie 2002: 199 [in list]. — Ng *et al.* 2008: 78 [in list].

(?) *Eucrate crenata* — Nobili 1903: 35 [Singapore]. — Tirmizi & Ghani 1982: 107, fig. 3; 1996: 77 [in key], 80, fig. 31 [Pakistan]. [not *Eucrate crenata* (De Haan, 1835)]

**Type material.** Male holotype (QM W3034), 2 male paratypes, 26.7 mm  $\times$  33.8 mm, cl 27.0 mm [rest of carapace damaged], 1 pre-adult female paratype, 16.8 mm  $\times$  20.7 mm, 1 female paratype, 29.6 mm  $\times$  37.6 mm (QM W1070, Fig. 15J–L; AM: see Davie 2002: 199).

Type locality. Australia, Queensland, Moreton Bay.

**Material examined.** *Thailand.* Gulf of Thailand, Songkhla, Sakom fishing port, 3 males, 24.3 mm  $\times$  29.4 mm, 37.0 mm  $\times$  47.0 mm, 37.5 mm  $\times$  47.2 mm, 2 ovigerous females, 34.9 mm  $\times$  45.5 mm, 35.6 mm  $\times$  44.8 mm (ZRC 2003.0606). – 1 male, 38.0 mm  $\times$  48.9 mm (ZRC 2003.0191).

*Singapore.* No data: 1 male, 41.4 mm × 52.6 mm (ZRC 1985.1378); K. L. Yeo coll., 8–15.06.1990: 1 male, 32.6 mm × 41.0 mm (ZRC 1991. 0341).

Tuas, trawling, W. M. Lee coll., 8–18.09.1982: 1 male, 38.1 mm  $\times$  47.8 mm, 3 females, 38.0 mm  $\times$  48.8 mm, 38.3 mm  $\times$  49.0 mm, 33.8 mm  $\times$  41.7 mm (ZRC 1984.7844–7847); C. M. Yang coll., 12.08.1982: 1 male, 32.5 mm  $\times$  40.0 mm (ZRC 1984.5796); 09.05.1984: 1 ovigerous female, 32.3 mm  $\times$  40.0 mm, 1 female, 35.4 mm  $\times$  45.2 mm (ZRC 1984: 6315–6316).

(?) Changi Beach Club, 3 m, D. C. Yeo coll., 01.01.2002: 1 female, 13.6 mm  $\times$  16.0 mm (ZRC 2002.0248). – Cyrene Reefs, Southern Islands, Singapore, P. F. Clark coll., 10.3.2005: 1 male, 7.0 mm  $\times$  8.3 mm (ZRC 2008.066).

*Australia*, Queensland, Moreton Bay, Mud I., dredging, V. F. Collin coll., 7.06.1940: 2 males paratypes, 26.7 mm  $\times$  33.8 mm, cl 27.0 mm [rest of carapace damaged], 1 pre-adult female paratype, 16.8 mm  $\times$  20.7 mm, 1 female paratype, 29.6 mm  $\times$  37.6 mm (QM W1070).

**Diagnosis.** Third anterolateral tooth visible (except large individuals), carapace with relatively short posterolateral borders (Figs. 12; 13A–C). P5 propodus noticeably short, wide (Figs. 12, 13C). Proportionally short ambulatory legs (Figs. 12; 13C). G1 is straight along median portion (Fig. 15J). Colour pattern varying from light gray-brown anterior third of carapace (Fig. 12A–C) to various patterns of bright colours (Fig. 12D–F).



**FIGURE 12**. Fresh colours of *Eucrate tripunctata* Campbell, 1969. A, female (34.9 mm × 45.5 mm) (ZRC 2003.0606), Thailand, Gulf of Thailand (specimen slightly tilted when photographed); B, male (24.3 mm × 29.4 mm) (ZRC 2003.0606), Thailand, Gulf of Thailand; C, male (37.5 mm × 47.2 mm) (ZRC 2003.0606), Thailand, Gulf of Thailand; C, male (37.5 mm × 47.2 mm) (ZRC 2003.0606), Thailand, Gulf of Thailand; C, male (37.5 mm × 47.2 mm) (ZRC 2003.0606), Thailand, Gulf of Thailand; C, male (37.5 mm × 47.2 mm) (ZRC 2003.0606), Thailand, Gulf of Thailand; C, male (37.5 mm × 47.2 mm) (ZRC 2003.0606), Thailand, Gulf of Thailand; C, male (37.5 mm × 47.2 mm) (ZRC 2003.0606), Thailand, Gulf of Thailand; C, male (37.5 mm × 47.2 mm) (ZRC 2003.0606), Thailand, Gulf of Thailand; D. female (13.6 mm × 16.0 mm) (ZRC 2002.0248), Singapore; E, F, male (7.0 mm × 8.3 mm) (ZRC 2008.066), Singapore.

**Remarks.** Diagnostic of *E. tripunctata* are arched anterolateral borders with the two anterolateral teeth that are short, rounded and very similar in appearance to the outer orbital tooth (Figs. 12A–E; 13A–D; Campbell 1969: fig. 4B, K, L). The second anterolateral tooth is triangular in small individuals; the third short but always visible even in the largest individuals. The ambulatory legs are also proportionally short (Figs. 12; 13C), the P5 not reaching the third anterolateral tooth when folded. The P2–P5 meri are short, wide and the P5 propodus conspicuously short and broad (Fig. 13C; Campbell 1969: fig. 4G). The male telson is very long and slender, longer than abdominal somite 6 (Campbell 1969: fig. 4J), the G1 is straight along the median portion (Fig. 15J; Campbell 1969: fig. 4H, I), in contrast to being sinuous as in other species of *Eucrate*.

Campbell (1969: 128) referred to *E. tripunctata* the four Mergui Archipelago (Myanmar [= Burma]) specimens identified "with some hesitation" as *E. affinis* Haswell, 1882, by De Man (1887: 89, pl. 5, figs. 5–7), as well as the single specimen of the same collection identified by Alcock (1900: 300) as *E. crenata* var. *affinis*. *Eucrate affinis* is a junior synonym of *Trissoplax dentata* (Stimpson, 1858) (see below). Campbell's decision was made on account of the restriction of the cheliped tomentum to "the upper border of the wrist of the cheliped", the proportions of the P5 propodus, and the similarity between the outer orbital teeth and the first two anterolateral teeth. Based solely on De Man's description and his figures, however, it is clear that the specimens do not belong to *E. tripunctata*. The anterolateral teeth, described by De Man (1887: 90, pl. 5, fig. 5) as "rather acute", do not resemble the conspicuously short teeth of *E. tripunctata*, a feature that is observed even in pre-adults (Campbell 1969: fig. 4K, L). Furthermore, the male telson (De Man 1887: pl. 5, fig. 6) is shorter than that in *E. tripunctata*. Alcock's specimen was described as being "more sculptured" than that of *E. crenata*, which is in sharp contrast to the smoother carapace of *E. tripunctata*.



**FIGURE 13.** *Eucrate tripunctata* Campbell, 1969; A, female (29.6 mm  $\times$  37.6 mm) (QM W1070), Australia, Queensland, Moreton Bay; B, male (26.7 mm  $\times$  33.8 mm) (QM W1070), Australia, Queensland, Moreton Bay; C–F, male (38.0 mm  $\times$  48.9 mm) (ZRC 2003.0191), Thailand, Gulf of Thailand. A–C, overall views; D, frontal view showing orbits and antennae; E, anterior portion of male thoracic sternum and abdomen; F, outer surface of right chela.

**FIGURE 14.** Gonopods of *Eucrate* species. A–C, *E. alcocki* Serène, in Serène & Lohavanijaya, 1973, male (17.50 mm × 20.67 mm) (ZRC 1999.1189), Singapore; D–F, *E. crenata* (De Haan, 1835), male neotype of *Pilumnoplax sulcatifrons* Stimpson, 1858 (34.0 mm × 49.1 mm) (QM W27449), Hong Kong, New Territories, Tolo Channel; G–I, *E. dorsalis* (White, 1849), male (39.0 mm × 46.7 mm) (QM W3191), Australia, Queensland, Bundaberg; J–L, *E. formosensis* Sakai, 1974, male (19.8 mm × 24.1 mm) (ASIZ-74623), Taiwan, Penghu Bay. A, B, D, E, G, H, J, K, right G1, dorsal view; C, F, I, L, right G2, dorsal view. Scale bars: A, D, G, J, 2.0 mm; B, C, E, F, H, I, K, 1.0 mm; L, 0.5 mm.





**FIGURE 15.** Gonopods of *Eucrate* species (continued). A–C, *Eucrate indica* **n.** sp., male holotype (23.83 mm × 28.43 mm) (ZRC 2001.1058), Thailand, Andaman Sea, Phuket I.; D–F, *E. sexdentata* Haswell, 1882, male (20.1 mm × 23.2 mm) (QM W12057), Australia, Queensland, Moreton Bay; G–I, *E. solaris* Yang & Sun, 1979, male (23.6 mm × 28.1 mm) (ASIZ-74626), Taiwan, Penghu Bay; J–L, *E. tripunctata* Campbell, 1969, male paratype (26.7 mm × 33.8 mm) (QM W1070), Australia, Queensland, Moreton Bay. A, B, D, E, G, H, J, K, right G1, dorsal view; C, F, I, L, right G2, dorsal view. Scale bars: A, D, G, J, 2.0 mm; B, C, E, F, I, K, L, 1.0 mm; H, 0.5 mm.

A relatively small female from Singapore (Fig. 12D; 13.6 mm  $\times$  16.0 mm, ZRC 2002.0248) had more prominent anterolateral and outer orbital teeth than those of the much larger specimens available or of a smaller male (cw 8 mm) shown by Campbell (1969: fig. 4L). The teeth were similarly prominent, however, in a small male from Singapore (Fig. 12E, F; 7.0 mm  $\times$  8.3 mm, ZRC 2008.066).

Nobili (1901: 35) identified a Singapore specimen as *E. crenata* and described it as having a large spot on the gastric region and two adjacent, irregular spots. The specimen may have belonged instead to *E. tripunc-tata. Eucrate crenata* has never been recorded from or near Singapore.

Also possibly identical to *E. tripunctata* are specimens reported from Pakistan by Tirmizi & Ghani (1996: 82). Their colour pattern ("dark purplish red, with chelipeds and legs white, the carapace [with] a band of white ... on the anterior and lateral borders" is indeed similar to that of *E. tripunctata*. Their figures also show similarities with *E. tripunctata*, because of the short and rounded anterolateral teeth that are similar in appearance to the outer orbital teeth.

**Colour pattern.** Campbell (1969: 128, fig. 4K) described alcohol-preserved specimens as "pale cream with three large reddish spots on carapace ... median spot of variable extent sometimes coalescing with the two smaller lateral spots". In some of the Singapore and Thailand specimens the anterior third of the carapace is light gray-brown without a clear trace of spots (Fig. 12A–C), except some of the males, where there are hints of large coloured spots (Fig. 12B, C). The chelipeds, and sometimes the anterior margin of the carapace, of large specimens have red-brown dots (Fig. 12A–C). The carapaces of smaller specimens show various patterns of bright colours (Fig. 12D–F).

Distribution. Gulf of Thailand, Singapore, Australia (Queensland). Depth: shallow subtidal.

## Genus Euryplax Stimpson, 1859

*Euryplax* Stimpson, 1859: 60. — Rathbun 1918: 16 [in key], 34 [diagnosis], 34 [key to species]. — Tesch 1918: 41 [in list]. — Guinot 1969b: 512 [discussion]; 1971: 1080 [in list, list of species]; 1984: 95. — Karasawa & Kato 2003a: 151 [in list]; 2003b: 130 [in list], 139 [in list]. — Ng & Castro 2007: 44 [in list]. — Ng *et al.* 2008: 78, 79 [in list]. — De Grave *et al.* 2009: 33 [in list].

**Diagnosis.** Carapace (Figs. 16A; 17A, B; 18C) transversely rectangular, wider than long, dorsal surface smooth without clear indication of regions; anterolateral borders straight, nearly parallel to each other; front wide, straight or slightly lobed, with small median notch, transverse sulcus along margin. Two obtuse or acute, often nearly equal, anterolateral teeth posterior to rounded, obtuse, outwardly or anteriorly oriented outer orbital tooth. Small notch on inner portion of thin supraorbital border (Figs. 16A; 17A, B; 18C); short, triangular median lobe on thin suborbital border (Figs. 16C; 17C, E; 18A), inner suborbital tooth absent. Orbits long (shorter than front but longer than half front length); eye peduncles long, slightly longer than large, spherical corneas (Figs. 16C; 17A–C; 18A). Basal antennal article immobile, disto-lateral process absent, orbital hiatus closed excluding antennal flagellum from orbit (Fig. 16C; Guinot 1969b: fig. 41). Anteroexternal margin of third maxilliped merus auriculiform (Figs. 17C; 18A). Cheliped fingers moderately slender, shorter than propodus, light in colour (Figs. 16B; 18C); carpus with tooth on inner margin; short tomentum may be present along anterodistal margins of merus, carpus (Fig. 18C). Dorsal margins of ambulatory legs (P2–P5) meri, carpi, propodi unarmed, dactyli slender, smooth, setose. P5 propodus proportionally stout, subcylindrical, margins fringed with long, simple setae; P5 dactylus proportionally slender (Fig. 16A),

margins fringed with long, simple setae, short teeth. Thoracic sternum wide; thoracic suture 2/3 complete, straight (Fig. 17D); 4/5, 6/7, 7/8 interrupted, 5/6 complete; thoracic sternites 7, 8 overlapping over penis (Figs. 16E; 17G); median groove on thoracic sternites 7, 8 (Figs. 16E; 17G). Sterno-abdominal cavity of male deep, nearly reaching anterior margin of sternite 4 (Figs. 17D, G). Male abdomen proportionally wide, triangular (not T-shaped), proportionally narrow telson (Figs. 16D; 17E); somite 3 transversely longer than somites 4–6, not reaching inner margins of P5 coxae; small portion on each side of thoracic sternite 8 left exposed by closed abdomen even if somite 2 transversely longer than somite 3 (Figs. 16F; 17F; 18D). Press-button of male abdominal-locking mechanism as large tubercle near thoracic suture 4/5 (Fig. 17D) (small tubercle present in pre-adult females). G1 long, slender, slightly sinuous, acuminate apex, with many denticles (Figs. 18D; 20A, B); G2 less than one-third of G1, straight, apex with 2 unequal processes (Fig. 20C). Male genital opening (gonopore) coxal, protected by enlarged, widened episternite 7; coxo-sternal disposition of long penis, protected by overlapping episternite 7, thoracic sternite 8 (Figs. 16E; 17G). Female abdomen relatively narrow, not covering outer portions of thoracic sternum (Fig. 18A). Vulva small, ovoid, extending from margin of thoracic sternite 6 far from median axis of thorax; covered by soft membrane, sternal vulvar cover absent (Fig. 18B).

**Type species.** *Euryplax nitida* Stimpson, 1859 (by monotypy, gender feminine) [Opinion 85, Direction 37].

**Remarks.** *Euryplax* is noteworthy for the protection of the proximal portion of the penis by the partial closure of thoracic sternites 7 and 8 (Figs. 16E; 17G; also see Guinot 1969b: fig. 39; Castro *et al.* 2010: 8C, D). Stimpson (1859: 60) had noted this in his description of *E. nitida*: "Verges [penis] of the male arising from the coxae of the posterior feet, and passing to the abdominal appendages through canals in the sternum". The penis of *Euryplax* is protected by episternite 7 extending close to but never fusing with thoracic sternite 8, thus never forming a closed channel as in the case of *Sotoplax robertsi* Guinot, 1984, a goneplacoid now placed in its own family (see Castro *et al.* 2010). Penial protection in *Euryplax* may be considered an extreme case among euryplacids, where the penis is protected only by a concavity along the posterior portion of thoracic sternite 7, an expansion of episternite 7, and the transversely wide abdominal somite 3 of the closed abdomen. Another peculiarity of *Euryplax* that departs from most other euryplacids is that somite 3 of the male abdomen, although transversely longer than somites 4–6, does not reach the inner margins of the P5 coxae (Figs. 16F; 17F; 18D). Furthermore, a small portion on each side of thoracic sternite 8 is left exposed by the closed abdomen even if somite 2 transversely longer than somite 3 (Figs. 16F; 17F; 18D); Rathbun 1918: fig. 11a; Guinot 1969b: figs. 39, 47).

The significance of the shape of the abdomen and sternal protection of the penis in *Euryplax* and the Euryplacidae in general is discussed below ("Evolution of Penial Protection in the Euryplacidae").

*Euryplax bevisi* Stebbing, 1921 (Stebbing 1921: p. 14, pl. II), described from Natal, South Africa, does not belong in *Euryplax* (see Barnard 1950: 283; Guinot 1969b: 512; Ng et al. 2008: 78, 79) or in the Euryplacidae. It is a portunid, as previously suggested by Barnard ("reminds one very much of a *Thalamita*"). However, the unusual carapace depicted by Stebbing (1921: pl. II) is a problem as no known *Thalamita* species has such elongated proportions. *Euryplax bevisi* was subsequently designated as the type species of *Lipkeplax* Števčić, 2005, which was included in a list of "new genera incertae sedis" (Števčić 2005: 134) without any indications as to their inclusion in any particular supra-generic taxa. The generic name is unavailable since it was not accompanied by a description or definition to differentiate it from other genera (International Code of Zoological Nomenclature, Article 13.1).

The holotype of *E. bevisi* Stebbing, 1921, was recently found in the NHM and examined by the second author. The specimen, measuring 22.8 mm  $\times$  13.8 mm, collected by A. L. Bevis, was dismembered and there is a label indicating it was once dried. However, all the key characters are intact, including the gonopods. Ng & Clark (in press) showed that the species is clearly a portunid of the genus *Thalamita* (see Barnard 1950: 283; Guinot 1969b: 512; Ng *et al.* 2008: 78, 79), and is a senior synonym of *Thalamita dakini* Montgomery, 1931, which is known from many parts of the Indo-West Pacific (Apel & Spiridonov 1998; Retamal 2004). There is thus no basis for Števčić (2005) establishing a new genus for the species.

## Species included.

Euryplax nitida Stimpson, 1859 Euryplax polita Smith, 1870 The genus is restricted to the Western Atlantic and Tropical Eastern Pacific regions.

# Euryplax nitida Stimpson, 1859

(Figs. 16A-F; 17A-G; 18A, B; 20A-C; 39A, B)

Euryplax nitidus Stimpson, 1859: 60 [Florida Keys]. — Smith 1870: 162 [Florida, Gulf of Mexico].

Euryplax nitida Stimpson 1871: 150 [Florida Keys]. — Rathbun 1918: 34 [in key], 34, fig. 11, pl. 7 [Florida, Puerto Rico]; 1933: 78, fig. 69 [Puerto Rico]. — Boone 1927: 14 [Cuba]. — Williams 1965: 202, fig. 185; 1984: 431 [in key], 432, fig. 343 [Atlantic coast of the U.S.]. — Guinot 1969b: 512 [discussion], figs. 39, 41, 47, 56, 57; 1971: 1080 [in list]; 1984: pl. 1, figs. F, G. — Felder 1973: 70 [in key], pl. 10, fig. 1 [in list] [Gulf of Mexico]. — Powers 1977: 113 [in list] [Gulf of Mexico]. - Camp 1998: 148 [in list]. - Karasawa & Kato 2003b: 130 [in list]. McLaughlin et al. 2005: 257 [in list]. — Hernández-Ávila et al. 2007: 35, 40 [in list] [Venezuela]. — Ng et al. 2008: 78 [in list]. — Coelho et al. 2008: 12 [in list] [Brazil].

Type material. Lost; type locality: Florida, Florida Keys.

Neotype of *Euryplax nitidus* Stimpson, 1859: male, 7.1 mm  $\times$  11.3 mm (UF 15166; Figs. 16, 39A); type locality: Florida, Gulf of Mexico, west of St. Petersburg, 27.4815°N, 82.8872°W, 0–12 m.

Material examined. Florida. Gulf of Mexico, west of St. Petersburg, 27.4815°N, 82.8872°W, Capetown dredge, 0-12 m, G. Paulay coll., 12.11.2007: male neotype (here designated), 7.1 mm  $\times$  11.3 mm (UF 15166); male,  $4.4 \text{ mm} \times 7.0 \text{ mm}$  (UF 15168).

Gulf of Mexico, Marco Beach, L. B. Holthuis coll., 12.09.1960: 2 males, 7.2 mm × 10.4 mm, 4.2 mm × 5.6 mm, 1 pre-adult female, 3.9 mm  $\times$  5.8 mm, 1 female, 4.2 mm  $\times$  6.6 mm (RMNH D 15769).

Off southern Florida, 25°17.32'N, 81°39.49'W, 13 m, Suncoaster, 10.12.1983: 1 female (USNM 276579). Colombia. Off Bahía Honda, stn. A15–39, 5–6 m, 8.04.1939: 3 males, 6.2 mm × 9.6 mm, 6.3 mm × 9.5

mm, 7.5 mm  $\times$  11.3 mm, 2 ovigerous females, 6.0 mm  $\times$  8.8 mm, 6.4 mm  $\times$  9.8 mm (LACM); 16–18 m,

8.04.1939: 12 males, 1 pre-adult female, 7 females, 7 ovigerous females (LACM).

SW of Cape de la Vela, stn. A1339, CN 106, 5–7 m, 8.04.1939: 1 male, 6.4 mm × 10.2 mm (LACM); 18– 24 m, 2 males, 2 pre-adult females, 3 ovigerous females (LACM).

Venezuela. North of Coche I., stn. A32-39, 35-60 m, 8.04.1939: 1 female (LACM).

North of Margarita I., stn. A42-39, 21.04.1939: 1 female, 1 ovigerous female (LACM).

Cubagua I., stn. A28-39, 4 m, 15.04.1939: 1 pre-adult female (LACM).

Trinidad. Gulf of Paria near San Fernando, 4.5 m, Shell Expedition, 02.05.1952: 1 male (RMNH D 9764). *Curaçao.* Prof. Boeke coll., 26.05.1905: 1 ovigerous female, 10.3 mm × 16.2 mm (RMNH D 2263).

*Brazil.* Dertero (?), M. Muller leg.: 1 male, 13.9 mm × 23.2 mm, 1 male, 9.8 mm × 16.4 mm (MNHN-B8732).

Santos, 20.04.1961, L. R. Tommasi leg.: 1 female (RMNH D 18755).

Unknown location, identified as "Frevillea rosaea": 1 male, 28.3 mm × 16.9 mm (NHM 1850.32).

Diagnosis. Outer orbital angle typically reduced, acuminate (Figs. 16A; 17A, B, E). Dorsal surface of cheliped merus with depression near anterior margin.

**Remarks.** Euryplax nitida, which is Western Atlantic in distribution, is very close to E. polita, a species that is restricted to the Tropical Eastern Pacific region. Both species may be distinguished from each other by the shape of the outer orbital angle: typically reduced and acuminate in *E. nitida* (Figs. 16A; 17A, B, E; Guinot 1969b: fig. 41) but more expanded anteriorly and broader in E. polita (Fig. 18C; Guinot 1969b: fig. 1). The shape of the anterolateral teeth varies in both species, varying from obtuse to slender. The dorsal surface of the cheliped merus of E. nitida has a depression near its anterior margin, which is absent in E. polita. In the male neotype (7.1 mm  $\times$  11.3 mm; UF 15166) a triangular, setose tooth is located at the proximal margin of the depression. The depression is referred to as a "deep pit" by Rathbun (1918: 34) and "fosette" by Guinot (1969b: 512). The eye peduncles are noticeably shorter in *E. nitida* (Fig. 16A, C) than in *E. polita* (Fig. 18C), and the suborbital border is nearly straight, with two small lobes in *E. nitida* (Figs. 16C; 17E; 18A), but with two lobes folded ventrally in the largest individuals of *E. polita*.



**FIGURE 16.** *Euryplax nitida* (Stimpson, 1859); A–F, male neotype of *Heteroplax nitidus* Stimpson, 1859 (7.1 mm × 11.3 mm) (UF 15166), Florida, Gulf of Mexico, west of St. Petersburg. A, overall view; B, outer surface of chelae; C, frontal view showing orbits and antennae; D, anterior portion of male thoracic sternum and abdomen; E, sternal protection of penis; F, posterior portion of male thoracic sternum and abdomen. Abbreviations:  $a_1-a_3$ ,  $a_6$  = male abdominal somites 1, 2, 3, 6, respectively; cx5 = coxa of fifth pereopod (P5); es7 = episternite 7; G1 = first male pleopod; mg = median groove; p = penis; s4-s8 = thoracic sternites 4 to 8, respectively; t = telson.

Some of the characters given by Rathbun (1918: 34, 36) to differentiate between the two species (i.e. carapace anterolateral borders converging anteriorly and fingers with white tips in *E. nitida*; anterolateral borders parallel and fingers with brown tips) do not agree with all the material examined. In fact, the anterolateral borders of the carapace are parallel in the specimens of *E. nitida* examined (Figs. 16A; 17A, B) as well as in the photograph given by Rathbun (1918: pl. 7) but they converge in at least some specimens of *E. polita* (Fig. 18C). The photograph of the holotype of *E. polita* given by Guinot (1969b: fig. 1) nevertheless shows straight anterolateral borders.

The type material of Stimpson's species, as with most of his material (see Evans 1967; Deiss & Manning 1981; Manning 1993; Manning & Reed 2006) is almost certainly lost. In the interest of long-term nomenclatural stability, we hereby designate a male neotype for *Euryplax nitidus* Stimpson, 1859 (7.1 mm  $\times$  11.3 mm;

UF 15166; Figs. 16; 39A). It was collected in the Gulf of Mexico off St. Petersburg, Florida, approximately 358 km north of the Florida Keys, the type locality of Stimpson's species.

**Colour pattern.** Irregular dark gray spots across tan to light yellow dorsal surface of carapace; irregular spots on chelipeds, dark purple blotch at the base of each finger, and banded ambulatory legs (male neotype, UF 15166) (Fig. 39A). Spots were relatively smaller in a smaller male (UF 15168) (Fig. 39B).

**Distribution.** Western Atlantic from North Carolina, Bermuda and Gulf of Mexico to southern Brazil (Coelho *et al.* 2008). Depth: shallow subtidal to 90 m (Powers 1977).



**FIGURE 17.** *Euryplax nitida* Stimpson, 1859; A, C, G, male (7.2 mm  $\times$  10.4 mm) (RMNH D 15769), Florida, Marco Beach; B, D, female (USNM 276579), Gulf of Mexico, off Florida; E, F, male (13.9 mm  $\times$  23.2 mm) (MNHN-B8732), Brazil, Dertero (?). A, B, dorsal views of carapaces; C, third maxillipeds; D, anterior portion of male sterno-abdominal cavity and G1; E, anterior portion of male thoracic sternum and abdomen; F, posterior portion of male thoracic sternum and abdomen; G, posterior portion of male sterno-abdominal cavity and G2. Abbreviations: a1-a3 = male abdominal somites 1, 2, 3, respectively; cx5 = coxa of fifth pereopod (P5); es7 = episternite 7; G1 = first male pleopod; G2 = second male pleopod; mg = median groove; p = penis; pb = press-button of male abdominal-locking mechanism; s4–s8 = thoracic sternites 4 to 8, respectively.

# Euryplax polita Smith, 1870

Euryplax politus Smith, 1870: 163 [Pacific coast of Panamá].

*Euryplax polita* — Rathbun 1918: 34 [in key], 36. — Glassel 1934: 301 [in list; Gulf of California]. — Guinot 1969b: 512 [discussion], pl. 2, fig. 1 [holotype]; 1971: 1080 [in list]; 1984: pl. 1, fig. E [holotype]. — del Solar 1970: 44 [Perú]. — del Solar *et al.* 1970: 27 [Perú]. — Garth 1960: 118 [in list]; 1961: 135, 136 [in list], 154 [Pacific coast of Mexico]; 1992: 3, 6 [in list] [Pacific coast of Mexico]. — Hendrickx 1992: 8 [in list]; 1993a: 314 [in list]; 1993b: 10 [in list]; 1994: 110 [in list]; 1995: 139 [in list]; 1996: 616, 617 [in list] [Pacific coast of Mexico]. — Ng *et al.* 2008: 78 [in list].

Type material. Male holotype (YPM 660; Guinot 1969b: fig. 1).

Type locality. Pacific coast of Panamá, unknown location.

**Material examined.** *Mexico* (?) SIPCO IIB<sub>1</sub>, V.V.P., 29.08.1981: 1 male, 9.8 mm  $\times$  16.4 mm, 1 female, 9.7 mm  $\times$  15.4 mm (MNHN-B24040).

*Mexico*. Isabel I., Sinaloa, *Velero*, stn. 747–37, 18–33 m, 2.04.1937: 1 male, 4.7 mm × 7.0 mm (LACM); stn. 870–38, 18–27 m, 8.03.1938: 2 males, 1 pre-adult female (LACM); stn. 974–39, 27–46 m, 9.05.1939: 1 male, cl 8.6 mm [remainder of carapace damaged] (LACM).

Revillagigedo Is., Socorro I., Braithwaite Bay, Velero, stn. 131-34, 3.01.1934: 1 pre-adult female (LACM).

Petlatán Bay, *Velero*, stn. 264–34, 14 m, 3.03.1934: 2 pre-adult females, 5.4 mm  $\times$  7.9 mm, 5.5 mm  $\times$  8.2 mm (LACM).

Chacahua Bay, *Velero*, stn. 765–38, 9–18 m, 9.01.1938: 1 male (LACM); stn. 767–38, 73–91 m, 9.01.1938: 1 male,  $4.9 \text{ mm} \times 7.4 \text{ mm}$  (LACM).

Tangola-Tangola Bay, *Velero*, stn. 259–34, 8–11 m, 28.02.1934: 1 male, 5.7 mm × 9.1 mm (LACM).

Tangola-Tangola Bay, Eastern Pacific Zaca Expedition, stn. 196, D-6, D-8, no. 37,592, 16-13 m,

9.12.1937: 1 male, 5.4 mm × 8.2 mm, 1 female, 5.7 mm × 8.9 mm (LACM); stn. 196, D–13, no. 37,620, 18 m,

12.12.1937: 1 male, 8.7 mm  $\times$  14.7 mm (LACM); stn. 196, D–17, 42 m, 13.12.1937: 1 pre-adult female, 4.3 mm  $\times$  6.0 mm (LACM).

*Guatemala*. Off San José Light, *Velero*, stn. 931–39, 42 m, 23.03.1939: 3 pre-adult females (LACM). *Panamá*. Taboga I., *Velero*, stn. 960–39, 1–3 m, 2.05.1939: 1 male, 7.1 mm × 11.2 mm (LACM).

Piña Bay, Velero, stn. 438-35, 46 m, 29.01.1935: 1 pre-adult female (LACM).

*Ecuador*. La Libertad, *Velero*, stn. 209–34, 4–6 m, 9.02.1934: 1 female, 5.8 mm  $\times$  8.8 mm, 1 ovigerous female, 5.6 mm  $\times$  8.3 mm (LACM).

*Perú*. Caleta La Cruz, Tumbes, no. B–117, E. M. del Solar coll., 15 m, sand, 18.03.1970: 1 male, 18.9 mm  $\times$  33.8 mm (LACM).

Sechura Bay, Velero, stn.845–38, 17 m, 15.02.1938: 1 female, 6.6 mm × 10.5 mm (LACM).

**Diagnosis.** Outer orbital angle typically (but not always) expanded anteriorly, broad (Fig. 18C). Dorsal surface of cheliped merus without depression near anterior margin.

**Remarks.** Differences between *E. polita* and its close congener, *E. nitida*, are given in the Remarks section of the latter.

**Distribution.** Tropical Eastern Pacific region, from the Gulf of California to Perú. Depth: shallow subtidal to 91 m.

## Genus Frevillea A. Milne-Edwards, 1880

Frevillea A. Milne-Edwards, 1880b: 15. — A. Milne-Edwards & Bouvier 1923: 335 [diagnosis]. — Guinot 1969b: 513 [discussion], 520; 1971: 1080 [list of species]. — Abele & Kim 1986: 591 [in key]. — Ng & Castro 2007: 44 [in list]. — Ng et al. 2008: 78 [in list]. — De Grave et al. 2009: 33 [in list].

Freyvillea [sic] — Alcock 1900: 292 [in list].

Goneplax — Rathbun 1918: 16 [in key], 25 (part); Manning & Holthuis 1981: 164 (part).

Fravillea [sic] — Karasawa & Kato 2003a: 151 [in list]; 2003b: 139 [in list].

Diagnosis. Carapace (Figs. 18E, F; 19A) quadrate, slightly wider than long, dorsal surface smooth without clear indication of regions; anterolateral borders straight, nearly parallel to each other; front wide, slightly bilobed with small median prominence or straight. One acute anterolateral tooth posterior to slender, acute, outwardly oriented outer orbital tooth; long, sinuous median lobe on thin suborbital border, triangular inner suborbital tooth (Fig. 19B, C). Orbits long, longer than front; eye peduncles long, nearly as long as front, longer than corneas; corneas reniform, dorsoventrally flattened (Figs. 18E, F; 19A, B). Basal antennal article does not fill orbital hiatus (Fig. 19B; Guinot 1969b: fig. 40), made immobile by small process at inner edge of suborbital border. Anteroexternal margin of third maxilliped merus auriculiform (Fig. 19C). Cheliped fingers (Fig. 19E) moderately slender, shorter than propodus, light in colour; carpus with tooth on inner margin; dense tomentum on posterior margin of propodus and anterior margin of carpus (Figs. 18E, F; 19A). Dorsal margins of ambulatory legs (P2-P5) meri, carpi, propodi unarmed, dactyli slender, smooth, setose. P5 (Figs. 18E, F; 19A) propodus subcylindrical, fringed with long setae; dactylus long, slender. Thoracic sternum (Fig. 19F, H) wide; thoracic suture 2/3 complete, slightly convex (Fig. 19H); 3/4 deep, short, interrupted; 4/5, 6/7, 7/8 interrupted, 5/6 complete (Fig. 19F, H); median groove on thoracic sternites 7, 8 (Fig. 19F). Sterno-abdominal cavity of male deep, reaching anterior margin of sternite 4 (Fig. 19F). Press-button of male abdominal-locking mechanism as large tubercle near thoracic suture 4/5 (presence in pre-adult females unknown). Male abdomen (Fig. 19D) moderately wide, triangular (not T-shaped), proportionally narrow telson; somite 3 transversely longer than somites 4–6, reaching inner margins of P5 coxae, fitting under episternite 7; no portion of thoracic 8 exposed by closed abdomen, somite 2 transversely as long as somite 3 (Fig. 19G; Guinot 1969b: fig. 33). G1 long, slender, slightly sinuous, acuminate apex, with relatively large denticles (Figs. 19F; 20D, E); G2 less than one-third of G1, straight, apex with 2 unequal processes (Fig. 20F). Male genital opening (gonopore) coxal; coxo-sternal disposition of long penis with broad proximal portion, protected by concave posterior portion of thoracic sternite 7 (Fig. 19F). Vulva rounded, extending across most of median portion of sternite 6 close to median axis of thorax (Fig. 19H); thick, slightly elevated posterior margin, covered by soft membrane, sternal vulvar cover absent.

**Type species.** *Frevillea barbata* A. Milne-Edwards, 1880 (by designation, Rathbun 1918: 25; gender feminine).

**Remarks.** *Frevillea* was sometimes confused with *Goneplax* Leach, 1814 (i.e. Rathbun 1918: 25), a genus that is clearly included in the Goneplacidae, even if both taxa share the general morphology of the dorsal surface of the carapace (see Guinot 1969b: 515; Castro 2007: 619).

The inclusion of *Frevillea* in the Euryplacidae is clear, even if the genus has some unusual features. Unique among euryplacid genera is a basal antennal article that does not fill the orbital hiatus (Guinot 1969b: 515, fig. 40). The male abdomen of *Frevillea*, a Western Atlantic genus, is intermediate between the slender, T-shaped abdomen of Indo-West Pacific genera and the wide, triangular abdomen of three Western Atlantic and Tropical Eastern Pacific genera (Fig. 1). Such a moderately wide but clearly not triangular male abdomen (Fig. 19D) is shared with *Euryplax* and *Machaerus* (Fig. 1B). Unusual among euryplacids are the reniform eyes with the corneas dorsoventrally flattened (Figs. 18E, F; 19A, B), a trait shared with the euryplacid *Psopheticoides* (Fig. 36B).

The separation between the three described species of *Frevillea*, all of which are sympatric in at least part of their geographical distribution in the Western Atlantic, is ambiguous and as a result not always clear. Rathbun (1918: 25), in a key to the American species of *Goneplax* that included the three species of *Frevillea*, separated *F. barbata* from *F. hirsuta* and *F. rosaea* by having the sides of the carapace "strongly convergent posteriorly" in contrast to being "almost parallel" in the other two species. Such differences are not apparent in the material examined (Figs. 18E, F; 19A) or in published illustrations and photographs (Rathbun 1918: fig. 7*a*; Guinot 1969b: fig. 3; Williams 1984: fig. 344 for *F. hirsuta*, and A. Milne-Edwards & Bouvier 1923: pl. 6, fig. 1; Rathbun 1918: pl. 4, fig. 1 Guinot 1969b: fig. 2 for *F. barbata*). A. Milne-Edwards & Bouvier (1923: 337), in the detailed descriptions of *F. barbata* and *F. rosaea*, which were briefly described but not illustrated by A. Milne-Edwards (1880b), refer to the differences between the two species as very slight (*differences très légères*). Only one character separates them, the presence in *F. rosaea* of a "tuberculiform swelling" (*un petit renflement tuberculiforme*) between the outer orbital tooth and the anterolateral tooth on each side of the cara-

pace. Such a feature, which was the only character used in Rathbun's key to separate between the two species, is apparent as a short tooth in the figure in A. Milne-Edwards & Bouvier (1923: pl. 6, fig. 1) but it was not found in the male holotype (MNHN-B8733).



**FIGURE 18.** A, B, *Euryplax nitida* Stimpson, 1859; A, female (USNM 276579), Gulf of Mexico, off Florida, ventral view of carapace; B, female (10.1 mm  $\times$  7.1 mm) (LACM), Colombia, Atlantic coast, ventral view of carapace; C, D, *Euryplax polita* Smith, 1870; male (18.9 mm  $\times$  33.8 mm) (LACM), Perú, Tumbes; E, F, *Frevillea hirsuta* (Borradaile, 1916); E, male lectotype of *Goneplax hirsutus* Borradaile, 1916 (10.5 mm  $\times$  15.2 mm) (NHM 1917.1.29.148–9); F, female paralectotype of *Goneplax hirsutus* Borradaile, 1916 (12.0 mm  $\times$  17.8 mm) (NHM 1917.1.29.148–9). A, ventral view; B, D, female sterno-abdominal cavity; C-F, overall view; D; male sterno-abdominal cavity. Abbreviations: a3 = male abdominal somite 3; G1 = first male pleopod; G2 = second male pleopod; pb = press-button of male abdominal-locking mechanism; s4–s8 = thoracic sternites 4 to 8, respectively; v = vulva. Photo credits: B, C, D by J. Martin (LACM); E, F by P. Crabb (NHM).

Characteristic of *F. hirsuta* is the variously long and dense tomentum on the anterior portion of the cheliped propodus and the anterior margin of cheliped carpus (Rathbun 1918: fig. 7; Guinot, 1969b: pl. 2, fig. 3; Williams 1984: fig. 344), a character present in the type material (Fig. 18E, F). Long tufts of tomentum are also present on the inner margin of the carpus. A tomentum is also present, although presumably shorter, in *F. barbata* (A. Milne-Edwards & Bouvier 1923: pl. 6, fig. 2; Rathbun 1918: pl. 4, fig. 1, 3). The length of the tomentum, and even its presence, is a variable character among many species of euryplacids so the use of this to separate species is questionable. The collection of additional material, particularly of *F. rosaea*, should clarify the status of all three putative species of *Frevillea*. As such, no diagnoses are given below for each of the three species of *Frevillea* given the ambiguous character of their supposed diagnostic characters.

A fourth species, described as *F. tridentata* A. Milne-Edwards, 1880, is now included, as *Trapezioplax tridentata*, in the Pseudorhombilidae Alcock, 1900 (see Guinot 1969b: 514; Ng *et al.* 2008: 192). The dorsal surface of this species is almost identical to that of *Frevillea* (as well as of *Goneplax* and other genera of Goneplacidae) but its abdomen and gonopods clearly indicate that it is a pseudorhombilid and not a euryplacid.

## Species included.

Frevillea barbata A. Milne-Edwards, 1880Frevillea hirsuta (Borradaile, 1916)Frevillea rosaea A. Milne-Edwards, 1880The genus is restricted to the Western Atlantic region.

## Frevillea barbata A. Milne-Edwards, 1880

Frevillea barbata A. Milne-Edwards, 1880b: 15 [Gulf of Mexico]. — Rathbun 1898a: 287 [Cuba]. — A. Milne-Edwards & Bouvier 1923: 336, fig. 2, pl. 2, figs. 10, 11, pl. 7, figs. 1, 2 [diagnosis; Gulf of Mexico]. — Guinot 1969b: 513, pl. 2, fig. 2 [syntype]; 1971: 1080 [in list]; 1984: pl. 1, fig. H [cotype]. — Powers 1997: 114 [in list] [Gulf of Mexico]. — Soto 1985: 484, 487, 488; 1986: 3, 4, 36; 1991: 627 [Florida]. — Abele & Kim 1986: 54, 593 [key], fig. a [p. 595] [Florida]. — McLaughlin *et al.* 2005: 257 [in list]. — Ng *et al.* 2008: 78 [in list]. — Thoma *et al.* 2009: 553, 563, figs. 1, 2 [Gulf of Mexico].

not *Frevillea barbata* — Poupin 1994: 48, pl. 5e [French West Indies]. (= *Frevillea hirsuta* (Borradaile, 1916)). *Goneplax barbata* — Rathbun 1918: 25 [in key], 26, pl. 4, figs. 1, 3, pl. 5 [Gulf of Mexico, Cuba, Grenada].

**Type material.** Damaged male lectotype, cw 5.9 mm (MNHN-B8733; Guinot 1969b: fig. 2); 1 male, 1 female, and 1 juvenile paralectotypes (MCZ 9155).

Type locality. Gulf of Mexico, north of Yucatán Channel, 23°13'N, 89°16'W, 151 m.

**Material examined**. *Gulf of Mexico*. North of Yucatán Channel, 23°13'N, 89°16'W, 151 m: damaged male lectotype, cw 5.9 mm (MNHN-B8733).

Diagnosis. See Remarks for Frevillea.

**Remarks.** In the original description, A. Milne-Edwards (1880b) did not designate a holotype specimen so all his material are technically syntypes. A male designated as "cotype" (MNHN-B8733) is damaged, with the chelipeds missing, only the right outer orbital angle remaining, and the ambulatory legs (except left P5, right P4) detached. A. Milne-Edwards & Bouvier (1923: 336), in a more complete treatment than the short description by A. Milne-Edwards (1880b: 15), referred to a male "type", plus two adult females, one pre-adult male, and two pre-adult females; a male was illustrated and referred to as "type" (A. Milne-Edwards & Bouvier (1923: fig. 2, pl. 7, figs. 1, 2). The MNHN "cotype", clearly an adult male , was referred to as the "holotype" by Rathbun (1918: 26), who listed it in her list of material examined. Although damaged, it does show the diagnostic characters of the species according to the description and the more complete treatment afterwards. As all of A. Milne-Edwards' specimens are syntypes, the selection of a "type" by A. Milne-Edwards, 1880. A female specimen referred to as a "co-type" and whose photograph was given by Guinot (1969b: fig. 2) could not be located in the MNHN. It must be part of the type material currently deposited in MCZ: one male, one female and one juvenile, plus many broken appendages (A. Baldinger, personal communication). These three specimens (MCZ 9155) therefore are paralectotypes.

**Distribution.** Western Atlantic from the Gulf of Mexico and Florida to Grenada, West Indies. Depth: subtidal to 300 m

## Frevillea hirsuta (Borradaile, 1916)

(Figs. 18E, F; 19A-H; 20D-F)

Goneplax hirsutus Borradaile, 1916: 77 [in list], 99, fig. 11 [Brazil].

- Goneplax hirsuta Rathbun 1918: 25 [in key], 28, fig. 7. Chace 1956: 20 [Gulf of Mexico]. Williams 1965: 201, fig. 184 [Atlantic coast of the U.S.]. Spivak 1997: 76, 79, 80 [southwestern Atlantic].
- Frevillea hirsuta Guinot 1969b: 513, figs. 33, 40, 58, 59, pl. 2, fig. 3 [Brazil]; 1971: 1080 [in list]. Coelho & Ramos 1972: 194 [Brazil]. Takeda 1983: 31 [in list], 162, colour photograph [Suriname, French Guiana] Williams 1984: 431 [in key], 432, fig. 344 [Atlantic coast of the U.S.]. Soto 1980: 99 [Gulf of Mexico]; 1985: 485; 1986: 3, 4, 36; 1991: 627 [Florida]. Powers 1977: 114 [in list] [Gulf of Mexico]. Abele & Kim 1986: 54, 593 [key], fig. b [p. 595] [Florida]. Coelho & Coelho Filho 1994: 560. [Brazil]. Coelho *et al.* 2008: 12 [in list] [Brazil]. McLaughlin *et al.* 2005: 257 [in list]. Ng *et al.* 2008: 78 [in list].

Frevillea barbata Poupin 1994: 48, pl. 5e [French West Indies].

**Type material.** Male lectotype,  $10.5 \text{ mm} \times 15.2 \text{ mm}$  (NHM 1917.1.29.148–9; Fig. 18E); 1 female paralecto-type,  $12.0 \text{ mm} \times 17.8 \text{ mm}$  (NHM 1917.1.29.148–9; Fig. 18F).

**Type locality.** Off Brazil, 22°56'S, 41°34'W, 73 m.

**Material examined.** *Florida*. Gulf of Mexico, off Tarpon Springs, near Middle Grounds,  $28.1522^{\circ}$ N,  $84.9055^{\circ}$ W, 479 m, B. Olaiver coll., 29.03.2003: 1 male,  $19.0 \text{ mm} \times 27.0 \text{ mm}$  (UF 3747).

Gulf of Mexico, off St. Petersburg, 27.71°N, 84.5755°W, 129.4 m, J. Stamer coll., 21.11.2004: 1 male, 13.5 mm  $\times$  19.3 mm (UF 6577).

Florida Straits, SW of Dry Tortugas, 24.4025°N, 83.1858°W, F. F. Snelson coll., 10.05.2006: 2 males, 13.3 mm  $\times$  20.0 mm, 14.6 mm  $\times$  21.0 mm, 3 females, 13.9 mm  $\times$  19.6 mm, 15.0 mm  $\times$  21.0 mm, 15.5 mm  $\times$  22.0 mm (UF 11537).

*Guadeloupe. Polka*: stn. D5, dredging, 95 m, 23.07.1991: 1 female 13.6 mm  $\times$  21.5 mm (MNHN-B30600). – Off Basse Terre, trap and net, 200–300 m, D. Lamy coll.: 2 males 16.6 mm  $\times$  24.9 mm, 15.5 mm  $\times$  23.3 mm, 1 female 13.3 mm  $\times$  19.9 mm (MNHN-B30601).

*Brazil.* Espíritu Santo, 20°44'S, 40°25'W, 33 m, S. Rodrigues coll., 20.05.1967: 1 male (MZUSP 6132). Rio de Janeiro, Ilha Grande, stn. 301, 75 m, 16.02.1968: 1 ovigerous female (MZUSP 2925).

*Terra Nova*, stn. 42, 22°56'S, 41°34'W, 73 m: male lectotype, 1 female paralectotype (NHM 1917.1.29.148–9).

São Paulo, Santos, Instituto de Pesca, 20.02.1984: 1 female (MZUSP 6649).

São Paulo, Ubatuba, W. Besnard coll., 07.1988: 1 male (MZUSP 11876).

Rio Grande do Sul, GEDIP, stn. 286, 27.04.1968: 1 male (MZUSP 6122), stn. 413: 1 male (MZUSP 3817), stn. 473: 1 male (MZUSP 3441), stn. 588: 1 ovigerous female (MZUSP 3545), stn. 1883: 1 male (MZUSP 9200).

Projeto Integrado, stn. 5201: 1 male (MZUSP 11872).

Projeto Sol, stn.1283, 07.12.1970: 1 ovigerous female (MZUSP 9411).

REVISEE Sul, stn. 6678: 1 male (MZUSP 13771).

No location: 1 male, 1 female (MZUSP 12150).

**Diagnosis.** See Remarks for *Frevillea*.

**Remarks.** Of the two syntypes specimens deposited at NHM (NHM 1917.1.29.148–9), the male (10.5 mm  $\times$  15.2 mm; Fig. 18E) is hereby selected as the lectotype, the female as paralectotype (12.0 mm  $\times$  17.8 mm; Fig. 18F).

Distribution. Western Atlantic from North Carolina to southern Brazil. Depth: 73–476 m.



**FIGURE 19.** *Frevillea hirsuta* (Borradaile, 1916); A, H, female (13.3 mm  $\times$  19.9 mm) (MNHN-B30601), West Indies, Guadeloupe, off Basse Terre; B–G, male (16.6 mm  $\times$  24.9 mm) (MNHN-B30601), West Indies, Guadeloupe, off Basse Terre. A, overall view; B, frontal view showing orbits and antennae; C, third maxillipeds; D, anterior portion of male thoracic sternum and abdomen; E, outer view of right chela; F, male sterno-abdominal cavity, G1, and penis; G, posterior portion of male abdomen; H, female thoracic sternum and vulvae. Abbreviations: a1-a3 = male abdominal somites 1, 2, 3, respectively; cx5 = coxa of fifth pereopod (P5); es7 = episternite 7; G1 = first male pleopod; mg = median groove; p = penis; pb = press-button of male abdominal-locking mechanism; s4-s7 = thoracic sternites 4 to 7, respectively; sc = sterno-abdominal cavity.



FIGURE 20. Gonopods of *Euryplax* and *Frevillea* species. A–C, *Euryplax nitida* Stimpson, 1859; A, B, G1; C, G2 (after Guinot 1969b: figs. 56, 57); D–F, *Frevillea hirsuta* (Borradaile, 1916): D, E, G1; F, G2 (after Guinot 1969b: figs. 58, 59).

## Frevillea rosaea A. Milne-Edwards, 1880

Frevillea rosaea A. Milne-Edwards 1880b: 15 [St. Vincent]. — A. Milne-Edwards & Bouvier 1923: 337, pl. 6, fig. 1 [diagnosis; St. Vincent]. — Chace 1940: 47 [Cuba]. — Guinot 1969b: 513; 1971: 1080 [in list]. — Soto 1985: 483; 1986: 3, 4, 33; 1991: 627 [Florida]. — McLaughlin *et al.* 2005: 257 [in list]. — Ng *et al.* 2008: 78 [in list].
Goneplax rosaea — Rathbun 1918: 25 [in key], 27.

**Type material.** Female lectotype, 15.7 mm  $\times$  22.7 mm, 1 male paralectotype, 10.1 mm  $\times$  16.3 mm, 1 preadult female paralectotype, 5.0 mm  $\times$  7.9 mm (MNHN-B10152).

Type locality. West Indies, off St. Vincent, 13°06.75'N, 61°06.9'W, 158 m.

**Material examined.** West Indies. U.S.C.S.S. Blake, stn. 232: female lectotype, 15.7 mm  $\times$  22.7 mm, 1 male paralectotype, 10.1 mm  $\times$  16.3 mm, 1 pre-adult female paralectotype, 5.0 mm  $\times$  7.9 mm (MNHN-B10152).

Diagnosis. See Remarks for Frevillea.

**Remarks.** The known type material of *F. rosaea* consists of three specimens, one male, one female, and one pre-adult female (MNHN-B10152). Labels indicate "type" and "juv. cotypes" without any indication as to which specimen is the actual holotype. No additional information is given in the description (A. Milne-Edwards 1880b: 15), and as such, all the specimens must be regarded as syntypes. A subsequent publication with a more detailed account of the species (A. Milne-Edwards & Bouvier 1923: 337) refers to a female as the "type" (*le type chargé d'oeufs*) and the specimen illustrated is similarly referred to as *type femelle* (A. Milne-Edwards & Bouvier 1923: 337). Rathbun (1918: 27) referred to the "female holotype in Paris Mus. (After A. Milne Edwards.)". The action by A. Milne-Edwards & Bouvier (1923) is equivalent to the selection of a lectotype for the species. A. Milne-Edwards & Bouvier also referred to the three other specimens. These specimens are all paralectotypes. The whereabouts of the presumed fourth specimen is unknown. It is not found in the collections of the Museum of Comparative Zoology (MCZ), Harvard University, where part of the type material of *F. barbata* is deposited (see above) as both species were described from the same *Blake* material collected by L. Agassiz.

The female specimen (15.7 mm  $\times$  22.7 mm) is here regarded as the lectotype and a damaged male without gonopods (10.1 mm  $\times$  16.3 mm) and the pre-adult female (5.0 mm  $\times$  7.9 mm) as paralectotypes. All three specimens are part of the same lot catalogued as MNHN-B10152.

Distribution. Western Atlantic from Florida and the West Indies. Depth: 159–476 m (Soto 1986).

## Genus *Henicoplax* n. gen.

Heteroplax — Miers 1879: 39 [discussion] (part). — Balss 1922a: 136 (part). — Sakai 1939: 555 [in key], 560 (part); 1976: 531 (part). — Guinot 1969b: 511 (part); 1971: 1080 [in list] (part). — Serène & Lohavanijaya 1973: 71 [discussion] (part). — Karasawa & Kato 2003b: 130 [in list] (part). — Ng et al. 2008: 78 [discussion] (part). — De Grave et al. 2009: 33 [in list] (part).

Otmaroplax Števčić 2005: 134 [nomen nudum] (part).

Diagnosis. Carapace (Figs. 21A; 22A; 23A; 25A; 26A, C) hexagonal, transversely rectangular, wider than long, convex; anterolateral borders short, nearly straight; dorsal surface smooth without clear indication of regions, transverse depression (postorbital ridge; Fig. 25A) below each orbit extending from anterolateral tooth, becoming progressively shallower before disappearing at level of eye (absent in *H. trachydactylus* **n. sp.**); front wide, straight, median notch absent or barely visible, truncate margin. One triangular, short anterolateral tooth posterior to much larger, triangular, anteriorly-oriented outer orbital tooth. Orbits long, longer or almost as long as front (e.g. Figs. 22A, C; 23A, C), sinuous, thin, entire (notches absent) supraorbital border; thin, weakly granular, entire (notches absent), sinuous suborbital border with broad median lobe; inner suborbital tooth absent (e.g. Figs. 21E; 22C; 23C; 26E). Eye peduncles long, more than half of frontal width, much longer than large, slightly elongated corneas (e.g. Figs. 21A, 22C, 23C). Basal antennal article slightly mobile without disto-lateral process, orbital hiatus is closed excluding antennal flagellum from orbit (Figs. 22C, 23C). Anteroexternal margin of third maxilliped merus auriculiform or angular. Cheliped fingers moderately stout, very short granules on dorsal margin of dactylus, slightly longer than slender propodus, light coloured; setation varying from short, simple, setae on anterior margin of carpus, propodus to dense tomentum on dactylus, propodus, carpus, merus (H. eriochir n. sp.; Fig. 21B). Dorsal margins of ambulatory legs (P2–P5) meri, carpi, propodi unarmed, dactyli slender, smooth, setose; P5 propodus long, subcylindrical, fringed with setae; dactylus, long, slender, fringed with setae (Fig. 27A, B). Thoracic sternum (Figs. 21D, F; 22E; 23D; 25G; 26F) wide; thoracic suture 2/3 complete, convex (Figs. 21B; 23B; 26F); 3/4 deep, short, interrupted; 4/5, 6/7, 7/8 interrupted, 5/6 complete (Figs. 21D, F; 23D; 25G; 26F); median groove on thoracic sternites 7, 8. Sternoabdominal cavity of male deep, only reaching median portion of sternite 4, anterior extremity rounded (Figs. 21D; 22B; 25B; 26B). Press-button of male abdominal-locking mechanism as small tubercle near thoracic suture 4/5 (Fig. 21D). Male abdomen narrow, slender, transversely narrow telson, lateral margins of somites 4-6 abruptly narrowing from somite 3 to narrow telson (Figs. 21C; 22D; 25B); somite 3 reaching inner margins of P5 coxae (Figs. 21C; 22D; 25C, D), sometimes locking under thoracic sternite 7 (Fig. 25D), no portion or small portion (Figs. 22D; 25D) on each side of thoracic sternite 8 left exposed by closed abdomen, somite 2 transversely almost as long as somite 3 (except H. eriochir n. sp., where somite 2 transversely shorter than somite 3 leaving large portion on each side of thoracic sternite 8 left exposed by closed abdomen; Fig. 21C). G1 long, slender, slightly sinuous (Fig. 22E), acuminate apex (transversely cut in *H. nitida* and *H. pilimeles* n. sp. [Fig. 24G–J], slightly transverse in *H. maldivensis* [Fig. 24D, E]), with relatively few, small denticles (Figs. 24A, B, D, E, G–J; 27C, D); G2 less than one-third of G1, straight, apex with 2 unequal processes: one long, tip obtuse or acute; second much shorter, tip obtuse or acute (Figs. 24C, F, K; 27E). Male genital opening (gonopore) coxal; coxo-sternal disposition of long penis, protected by concave posterior portion of thoracic sternite 7 (Figs. 21D; 22E; 25E). Vulva small, ovoid, slightly elongated, extending transversely across anterior portion of sternite 6 close to median axis of thorax, sternal vulvar cover absent (Figs. 21F; 23D; 25G; 26F).

Type species. Heteroplax nitida Miers, 1879 (by present designation, gender feminine).

**Etymology.** From *henikos*, Greek for "single", in reference to the single anterolateral tooth diagnostic of the genus, and *plax*, Greek for "plate" or "tablet", which is derived from the generic name *Heteroplax* to denote that the type species of the new genus was formerly included in *Heteroplax sensu lato*.

**Remarks.** The revision of the genus *Heteroplax* Stimpson, 1858, with *H. transversa* as its type species, necessitates the assignment of several species that were long confused with *H. transversa* to other genera that do not share the same type of carapace and other characters of *Heteroplax*. One of these genera is *Henicoplax* **n. gen.**, established here to receive *Goneplax maldivensis* Rathbun, 1902, and *H. nitida* Miers, 1879, plus three new species, all Indo-West Pacific in distribution. Diagnostic of the new genus is the presence on each side of the carapace of only one small and triangular anterolateral tooth (but not large and acute as in *Frevillea* or *Nancyplax*), which are similar in shape to the outer orbital teeth. Also unique is the conspicuous transverse depression, or postorbital ridge, found in four of its five species (*H. eriochir* **n. sp.**, *H. maldivensis*, *H. nitida*, and *H. pilimeles* **n. sp.**; see Table 3) and that extends just below the orbits from each anterolateral tooth. In contrast to the ridge of *Platyozius* Borradaile, 1902 (Fig. 34E), it does not extend along the entire width of the carapace (Fig. 25A). Table 1 contrasts the new genus with other euryplacid genera.

| Characters                           | H. eriochir n. sp.                                  | H. maldivensis                                  | H. nitida   | H. pilimeles n. sp.  | H. trachydactylus n. sp. |
|--------------------------------------|---|---|---|--|--------------------------|
| Postorbital<br>ridges on<br>carapace | Present   | Present (Fig.<br>22A; Rathbun,<br>1902: fig. 3) | Present   | Present (Fig. 25A)   | Absent                   |
| Cheliped setation                    | Dense, conspicuous<br>tomentum (Fig.<br>21A, B)     | Absent  | Short setae along<br>anterior margin<br>of carpus | Simple setae on<br>inner margin of<br>carpus                 | Absent                   |
| Chelipeds<br>dactyli                 | Glabrous (Fig. 21A)                                 | Glabrous  | Glabrous (Fig.<br>23A)                            | Glabrous (Serène &<br>Lohavanijaya 1973:<br>pl. 18, figs. D) | Granular (Fig. 27F)      |
| Somite 2 of male abdomen             | Transversely<br>shorter than somite<br>3 (Fig. 21C) | Almost as long<br>as somite 3 (Fig.<br>22D)     | Almost as long<br>as somite 3                     | Almost as long as somite 3 (Fig. 25C)                        | Unknown                  |
| G1 apex                              | Acuminate (Fig. 24A, B)                             | Slightly<br>transversely cut<br>(Fig. 24D, E)   | Transversely cut<br>(Fig. 24G, H)                 | Transversely cut<br>(Fig. 24I, J)                            | Acuminate (Fig. 27C, D)  |
| Geographical distribution            | Persian Gulf  | Maldives  | Japan and Hong<br>Kong                            | Andaman Sea  | Madagascar               |

**TABLE 3.** Differences between the species of *Henicoplax* n. gen.

All five species of *Henicoplax* **n. gen.** are small in size and apparently restricted to soft sediments in relatively shallow water. A small ovigerous female from the Andaman Sea coast of Thailand that was examined (3.3 mm  $\times$  4.9 mm; Thai-Danish Expedition, stn. 1020–9, 09°28'N, 97°57'E, 42 m, 12.01.1966, ZMUC CRU-10072) and identified as *Heteroplax nitidas* [sic] by Serène & Soh (1976: 23) may represent an undescribed sixth species of *Henicoplax* **n. gen.** A postorbital ridge was present but the anterolateral tooth was acute and the orbits and eye peduncles were proportionally shorter than in *H. nitida* or its congeners. Although we have not examined the specimen, the importance of the morphology of the G1 for identifying members of this genus means that it is best to wait until males become available.

## Species included.

Henicoplax eriochir **n. sp.** Henicoplax maldivensis (Rathbun, 1902) Henicoplax nitida (Miers, 1879) Henicoplax pilimeles **n. sp.**  *Henicoplax trachydactylus* **n. sp.** The genus is restricted to the Indo-West Pacific region.

*Henicoplax eriochir* n. sp. (Figs. 21A–F; 24A–C)

Goneplax maldivensis - Stephensen 1946: 171 [Persian Gulf].

**Type material.** Male holotype, 5.2 mm  $\times$  8.8 mm (MNHN-B12511; Figs. 21A–D, 24 A–C), 1 ovigerous female paratype, 5.4 mm  $\times$  8.9 mm (MNHN-B12511; Fig. 21E, F), 1 female paratype, 4.2 mm  $\times$  7.1 mm (MNHN-B12511).

Type locality. Persian Gulf, unknown location.

**Material examined.** *Persian Gulf.* No data: male holotype, 5.2 mm  $\times$  8.8 mm, 1 ovigerous female paratype, 5.4 mm  $\times$  8.9 mm, 1 female paratype, 4.2 mm  $\times$  7.1 mm (MNHN-B12511).

**Diagnosis.** Chelipeds with conspicuous tomentum (Fig. 21A, B). Somite 2 of male abdomen shorter than somite 3, with relatively large portion of thoracic sternite left exposed by closed abdomen (Fig. 21C). G1 with acuminate apex (Fig. 24A, B) (see also Table 3).

**Description.** Carapace (Fig. 21A) hexagonal, transversely elongated, wider than long (1.7 wider than long in male holotype), anterolateral borders nearly straight, dorsal surface without clear indication of regions; front wide, lacking median notch. Transverse depression (postorbital ridge) below each orbit extending from anterolateral tooth, becoming progressively shallower before disappearing at the level of distal portion of eye peduncle. One short, triangular, obtuse anterolateral tooth posterior to triangular, anteriorly oriented outer orbital tooth; plumose setae along posterolateral borders. Orbits long (Fig. 21A, B, E), longer than front (1.2 frontal width); slightly sinuous, thin supraorbital border lacking notches (Fig. 21A); suborbital border sinuous, with broad median lobe, inner suborbital tooth absent (Fig. 21B, E); eye peduncles long (0.6 frontal width), much longer than corneas (1.8 times cornea length in paratype); large, spherical corneas.

Basal antennal article slightly mobile, orbital hiatus closed excluding antennal flagellum from orbit.

Posterior margin of epistome lobular; lateral lobes large, with straight margins, separated from median portion by deep fissure; median portion with 2 broadly rectangular lobes separated by shallow cleft. Anterior margin of endostome well demarcated from buccal cavern, endostomial ridges low. Pterygostomian region smooth. Third maxillipeds (Fig. 21B, E) completely closing buccal cavern; ischium rectangular with deep submedian line; merus relatively square in shape, anteroexternal margin of merus auriculiform; exopod long, reaching to just before anterior edge of merus with long flagellum.

Cheliped fingers moderately slender, slightly curved in male holotype (Fig. 21 A, B), slightly longer than swollen propodus, dorsal margin of dactylus with microscopic tubercles, distal portion light in colour. Dense tomentum of long, plumose setae along proximal third to half of lower (ventral) margin of dactylus (Fig. 21A, B); smaller clump of tomentum on distal end of propodus immediately below dactylus; dense tomentum on inner margin of carpus, distal, inner margin of merus. Inner (dorsal) margin of carpus with small triangular tooth. Dorsal, ventral margins of ambulatory legs (P2–P5) smooth, with long, sparse simple setae; dactyli long, slender; P5 merus proportionally short, ventral margin slightly curved, distal end does not reach anterolateral tooth when folded against carapace; P5 propodus (1.8 mm long, 0.9 mm wide in largest female paratype), proportionally stout, subcylindrical, inner margin fringed with long, plumose setae; outer margin with scattered long, simple setae; P5 dactylus proportionally slender (1.8 mm long, 0.3 mm maximum in largest female paratype), inner margin fringed with scattered long, simple plus plumose setae.

Thoracic sternum (Fig. 21D, F) wide, thoracic suture 2/3 complete, convex; 3/4 deep, short, interrupted; 4/5, 6/7, 7/8 interrupted, 5/6 complete; median groove on thoracic sternites 7, 8. Sterno-abdominal cavity of male deep, nearly reaching anterior margin of sternite 4, anterior extremity rounded (Fig. 21B, D). Press-button of male abdominal-locking mechanism as very small tubercle near thoracic suture 4/5 (Fig. 21D).

Male abdomen narrow, slender, transversely narrow (T-shaped), lateral margins of somites 4–6 abruptly narrowing from somite 3 to narrow, pointed telson (Fig. 21B, C); somite 3 reaching inner margins of P5

coxae, large portion on each side of thoracic sternite 8 left exposed by closed abdomen (Fig. 21C), somite 2 transversely much shorter than somite 3. G1 (Fig. 24A, B) long, slender, sinuous, acuminate apex, with relatively few, small denticles; G2 (Fig. 24C) less than one-third of G1, straight, apex with 2 processes: one long, tip obtuse; second much shorter, tip obtuse. Male genital opening (gonopore) coxal; coxo-sternal disposition of long penis, protected by concave posterior portion of thoracic sternite 7 (Fig. 21D).

Vulva (Fig. 21F) ovoid, extending across anterior portion of sternite 6 close to median axis of thorax, sternal suture 6/7 deflected; covered by soft membrane, sternal vulvar cover absent.

Colour pattern. Unknown.



**FIGURE 21.** *Henicoplax eriochir* **n. sp.**; A–D, male holotype (5.2 mm × 8.8 mm) (MNHN-B12511), Persian Gulf; E, F, ovigerous female paratype (5.4 mm × 8.9 mm) (MNHN-B12511), Persian Gulf. A, overall view; B, E, ventral views of carapaces; C, posterior portion of male thoracic sternum and abdomen; D, male sterno-abdominal cavity; F, female thoracic sternum and vulvae. Abbreviations: a1-a3 = male abdominal somites 1, 2, 3, respectively; cx5 = coxa of fifth pereopod (P5); es7 = episternite 7; G1 = first male pleopod; G2 = second male pleopod; mg = median groove; p = penis; s4–s8 = thoracic sternites 4 to 8, respectively; tm = tuft of tomentum on cheliped merus; v = vulva.

**Etymology.** From *erios* or *erion*, Greek for "wool", and *cheir*, Greek for "hand", as a noun in apposition, in reference to the tomentum of plumose setae on the anterior margins of the cheliped propodus and merus.

**Remarks.** *Henicoplax eriochir* **n. sp.** is described as new for specimens collected from the Persian Gulf and deposited in the MNHN, and clearly different from *H. nitida* and its other congeners (Table 3).

The second abdominal somite of the male holotype of the new species is much shorter than the third abdominal somite and thus a large portion on each side of thoracic sternite 8 is left exposed by the closed abdomen (Fig. 21C). This is unique among three of its congeners, where the thoracic sternite 8 is covered by the closed abdomen because the second somite is only slightly shorter than the third (Table 3). In the remaining species, *H. trachydactylus* **n. sp.**, the abdomen of the only male known is missing (see below).

Most probably belonging to *H. eriochir* **n. sp.** are specimens that Stephensen (1946: 171) incorrectly identified as "*Goneplax maldivensis* Rathbun, 1902". His specimens, collected from soft sediments in relatively shallow water (13–23 m) from three locations in the Persian Gulf, were described as having a "great tuft of setae on the inner side" of the base of the fingers, a character neither observed in the holotype of Rathbun's species (see above) nor mentioned in Rathbun's description or figures (Rathbun 1902: 124, figs. 3, 4), but which is diagnostic of *H. eriochir* **n. sp.** *Goneplax* Leach, 1814, actually belongs in the Goneplacidae, and it was amended to receive four mostly Atlantic species (see Castro 2007: 176).

The G2 of one of Stephensen's males was described as being a quarter of the G1 length and a male abdomen that "agrees excellently with Rathbun's fig", which shows a narrow and slender abdomen. Stephensen's specimens, although not examined, clearly belong to an undescribed species of *Henicoplax* **n. gen**.

The record of "*Goneplax maldivensis*" from Indonesia (Tesch 1918: 183, pl. 9, fig. 1) does not belong to *Henicoplax* **n. gen.** (see remarks for *H. maldivensis* below), and the same probably applies to other specimens collected by T. Mortensen in Indonesia, identified as "*Goneplax maldivensis*" by T. Odhner and deposited at ZMUC (Stephensen 1946: 171).

Distribution. Only known from the Persian Gulf. Depth: 13–23 m (Stephensen 1946).

## Henicoplax maldivensis (Rathbun, 1902), new combination

(Figs. 22A-E; 24D-F)

Goneplax maldivensis Rathbun, 1902: 124, figs. 3–5 [Maldives]. — Guinot 1969b: 518 [discussion]. — Castro 2007: 686, 687 [in list].

not Goneplax maldivensis — Stephensen 1946: 171. (= Henicoplax eriochir n. sp.)

"? [Goneplax] maldivensis" Rathbun, 1902 — Guinot 1971: 1081 [in list].

Otmaroplax maldivensis Števčić 2005: 134 [nomen nudum]

"Heteroplax" maldivensis — Ng et al. 2008: 78, 79 [in list].

not Goneplax maldivensis — Tesch 1918: 183, pl. 9, fig. 1 [Indonesia]. (? = Goneplacoides marivenae Komatsu & Takeda, 2003)

**Type material.** Male holotype,  $4.8 \text{ mm} \times 7.4 \text{ mm}$  (MCZ 6695) (Fig. 22A–E).

Type locality. Maldives, Gan I., Addu Atoll, 20 fathoms [37 m].

**Material examined.** *Maldives.* Gan I., Addu Atoll, A. Agassiz coll., 5.01.1902, 37 m: male holotype, 4.8  $mm \times 7.4 mm$  (MCZ 6695).

**Diagnosis.** Chelipeds without tomentum. Apex of G1 slightly transversely cut (Fig. 24D, E) (see also Table 3).

**Remarks.** The possible inclusion of *Goneplax maldivensis* Rathbun, 1902, in the Euryplacinae was first suggested by Guinot (1969b: 511, 518), who later (Guinot 1971: 1081) included the species (as "? [*Goneplax*] *maldivensis* Rathbun, 1902") in a list of goneplacid crabs under *Autres Euryplacinae (attribution générique à préciser)*. Števčić (2005: 133) placed the species under *Otmaroplax* in a list of new genera *incertae sedis*, but it is a *nomen nudum* because no diagnosis was given (see Castro 2007: 178; Ng *et al.* 2008: 78, 79). Castro (2007: 686, 687) formally included the species among the Euryplacidae. Ng *et al.* (2008: 78, 79) recognised its placement as an independent genus in the Euryplacidae and referred to it as "*Heteroplax*" *maldivensis*.

*Henicoplax maldivensis* is very close to *H. nitida*, and a comparison of the holotypes of both species shows only small differences. The outer orbital angle and the anterolateral teeth of the small male holotype of *H. maldivensis* (Fig. 22A, B) are slightly more acute than those of the larger female holotype of *H. nitida* (6.1 mm  $\times$  9.3 mm; Fig. 23A). Although it is possible that these differences are due to size and/or sex, the wide geographical distance separating both populations suggests that both species are distinct, even if the material currently available is scant. There are also some small differences in the size and distribution of the denticles in the G1 of the two species (Fig. 24D, E for *H. maldivensis*; Fig. 24G, H for *H. nitida*) but these may be again due to differences in the size of the specimens.



**FIGURE 22.** *Henicoplax maldivensis* (Rathbun, 1914); male holotype of *Goneplax maldivensis* Rathbun, 1902 (4.8 mm  $\times$  7.4 mm) (MCZ 6695). A, dorsal view of carapace; B, third maxillipeds, anterior portion of male thoracic sternum and abdomen; C, orbit and suborbital border; D, posterior portion of male thoracic sternum and abdomen; E, male sterno-abdominal cavity, G1, and penis. Abbreviations: a1–a3 = male abdominal somites 1, 2, 3, respectively; cx5 = coxa of fifth pereopod (P5); es7 = episternite 7; G1 = first male pleopod; p = penis; s5–s8 = thoracic sternites 5 to 8, respectively.

Material from the Persian Gulf identified by Stephensen (1946: 171) as "Goneplax maldivensis", which only agreed in some respects with Rathbun's figures and those by Tesch (1918: 183, pl. 9, fig. 1) belong instead to *Henicoplax eriochir* **n. sp.** (see above). Tesch's (1918) Indonesian (Kai Is.) specimen is clearly not *H. maldivensis*, lacking a postorbital ridge and having much shorter eye peduncles and a wider male abdomen. The specimen is now destroyed but Tesch's (1918) figures show that it belongs to a goneplacid close to *Goneplacoides marivenae* (Komatsu & Takeda, 2003) (see Castro 2007: 696).

## Colour pattern. Unknown.

Distribution. Only known from the Maldives, Indian Ocean. Depth: shallow subtidal to at least 37 m.

# *Henicoplax nitida* (Miers, 1879), new combination (Figs. 23A–D; 24G, H)

"Heteroplax ? nitidus" Miers, 1879: 39, pl. 2, figs. 2, 2ª [Straits of Korea].

Heteroplax nitida — Balss 1922a: 137 [in list]. — Ng et al. 2008: 78 [in list].

Heteroplax nitidus — Sakai 1935: 184, pl. 54, fig. 2 [colour]; 1939: 560 [in key], 560, 722, pl. 67, fig. 3 [colour]; 1940: 57 [in list]; 1956: 46 [in list]; 1976: 531 [in key], 532, pl. 191, fig. 2 [colour] [Japan]. — Kim 1973: 410, 637, fig. 164, pl. 85; 1977: 206 [in list] [Korea]. — Yamaguchi *et al.* 1987: 22 [Japan]. — Miyake 1991: 220 [in list; Japan]. — Karasawa & Kato 2003b: 130 [in list].

"Heteroplax ? nitida" — Guinot 1969b: 511 [discussion]; 1971: 1080 [in list].

not *Heteroplax nitidus* — Serène & Lohavanijaya 1973: 74, 98, pl. 18, figs. B–D. — Serène & Soh 1976: 23 (as *H. nitidas* [sic]): 23, fig. 22, pl. 6, Fig. D. [Andaman Sea coast of Thailand] (= *Henicoplax pilimeles* **n. sp.**, part)

not *Heteroplax nitida* — Naiyanetr 1998: 78; 2007: 90 [Andaman Sea coast of Thailand]. — Ng & Davie 2002: 378 [Andaman Sea coast of Thailand]. (= *Henicoplax pilimeles* **n. sp.**)

**Type material.** Female holotype, 6.1 mm  $\times$  9.3 mm (NHM 78.11) (Fig. 23).



**FIGURE 23.** *Henicoplax nitida* (Miers, 1879); female holotype of *Heteroplax*? *nitidus* Miers, 1879 (6.1 mm  $\times$  9.3mm) (NHM 78.11), Straits of Korea. A, overall view; B, third maxillipeds; C, frontal view showing orbits and antennae; D, female thoracic sternum and vulvae. Abbreviations: mg = median groove; s4–s7 = thoracic sternites 4 to 7, respectively; v = vulva.



**FIGURE 24.** Gonopods of *Henicoplax* species. A–C, *Henicoplax eriochir* **n. sp.**, male holotype (5.2 mm × 8.8 mm) (MNHN-B12511), Persian Gulf; D–F, *Henicoplax maldivensis* (Rathbun, 1902), male holotype of *Goneplax maldivensis* Rathbun, 1902 (4.8 mm × 7.4 mm) (MCZ 6695), Maldives, Addu Atoll; G, H, *Henicoplax nitida* (Miers, 1879), male (2.8 mm × 4.2 mm) (ZRC 2008.1358), Hong Kong; I–K, *Henicoplax pilimeles* **n. sp.**, male holotype (4.2 mm × 6.8 mm) (ZRC 1984.7739–7740), Thailand, Andaman Sea, Phuket I. A, B, D, E, G, H, I, J, right G1, dorsal view; C, F, K, left G2, dorsal view. Scale bars: A, G, I, 0.5 mm; B, C, D, F, H, 0.2 mm; J, K, 0.1 mm; E, 0.05 mm.

**Type locality.** Straits of Korea, 33°40'N, 182°55'E.

**Material examined.** Japan. Manazuru, I. Gordon & T. Sakai coll., 1961: 1 female,  $5.1 \text{ mm} \times 8.0 \text{ mm}$  (NHM 1961.11.13.53).

Straits of Korea. 33°40'N, 182°55'E: female holotype, 6.1 mm × 9.3mm (NHM 78.11).

*Hong Kong.* 1 male, 2.8 mm  $\times$  4.2 mm, 1 ovigerous female, 3.6 mm  $\times$  5.5 mm (ex. SWIMS CRU-XX-064; ZRC 2008. 1358).

**Diagnosis.** Chelipeds with short setae along anterior margin of carpi. G1 apex transversely cut (Fig. 24G, H) (see also Table 3).

**Remarks.** Of its congeners, *Henicoplax nitida* is closest to *H. maldivensis* (Table 3), but both are treated here as separate species (see Remarks for *H. maldivensis* above).

The G1 of *H. nitida* is illustrated for the first time herein (Fig. 24G, H). It belonged to a very small male where the G2 was apparently not fully developed. It is nevertheless very similar to that of its congeners. The G1 shown by Serène & Soh (1973: fig. 22 B, B', as *Heteroplax nitidus*) belongs to *Henicoplax pilimeles* **n. sp.** (see below).

Serène & Lohavanijaya (1973: 75) inexplicably commented that *Henicoplax nitida* (as *Heteroplax nitida*) and *Heteroplax nagaskiensis* may be conspecific, although on the basis of the original descriptions, they are clearly different. In the present study, the two species are placed in separate genera.

**Colour pattern.** The female holotype was described as "whitish; brownish pink on front of carapace" (Miers 1879: 39). A colour plate in Sakai (1976: pl. 191, fig. 1) shows scattered, purplish spots on the dorsal surface of the carapace, larger purple spots on the chelipeds, and ambulatory legs banded with purple spots.

Distribution. Western Pacific: Japan and Hong Kong. Depth: shallow subtidal.

#### Henicoplax pilimeles n. sp.

(Figs. 24I-K; 25A-G; 27A, B)

Heteroplax nitidus — Serène & Lohavanijaya 1973: 74, 98, pl. 18, figs. B–D [Andaman Sea coast of Thailand]. — Serène & Soh 1976: 23 (as *H. nitidas* [sic]), fig. 22, pl. 6, Fig. D (part) [Andaman Sea coast of Thailand]. [not *Henicoplax nitida* (Miers, 1879)]

Heteroplax nitida — Naiyanetr 1998: 78; 2007: 90 [Andaman Sea coast of Thailand]. — Ng & Davie 2002: 378 [Andaman Sea coast of Thailand]. [not Henicoplax nitida (Miers, 1879)]

**Type material.** Male holotype, 4.2 mm  $\times$  6.8 mm (Figs. 24I–K; 25A–E); 1 female paratype, 4.1 mm  $\times$  6.7 mm (ZRC 1984.7739–7740) (Fig. 25F, G); 1 male paratype, 3.9 mm  $\times$  5.8 mm (ZMUC CRU-9965); 1 female paratype, 3.8 mm  $\times$  5.7 mm (ZMUC CRU-10068); 1 male paratype, 4.3 mm  $\times$  6.3 mm (NHM 1988.34).

Type locality. Thailand, Andaman Sea coast, west coast of Phuket I.

**Material examined.** *Myanmar* [= *Burma*]. Gulf of Martaban, E. W. Bates coll.: 1 male paratype, 4.3 mm  $\times$  6.3 mm (NHM 1988.34).

*Thailand.* Andaman Sea, Thai-Danish Expedition: stn.1008–5, 08°43'N, 98°11'E, 20 m, 08.01.1966: 1 male (ZMUC CRU-9963). – Stn.1010–7, 08°45'N, 98°07'E, 29 m, 09.01.1966: 1 male, 3.3 mm × 4.9 mm (ZMUC CRU-9964). – Stn.1018–2, 09°27'N, 98°016'E, 15 m, 12.01.1966: 1 female, 3.8 mm × 5.7 mm (ZMUC CRU-10068). – Stn.1018–9, 09°27'N, 98°16'E, 15 m, 12.01.1966: 1 male (ZMUC CRU-10067). – Stn.1019–7, 09°28'N, 98°07'E, 21 m, 12.01.1966: 1 male (ZMUC CRU-10071). – Stn.1019–1, 09°28.2'N, 98°07.2'E, 21 m, 12.01.1966: 1 male paratype, 3.6 mm × 5.4 mm (ZMUC CRU-10069). – Stn.1019–4, 09°28'N, 98°07'E, 20 m, 12.01.1966: 1 male, 1 male parasitized by sacculinid, 1 female parasitized by sacculinid (ZMUC CRU-10070). – Stn. 1179, 08°08'24''N, 98°16'48''E, sandy mud, 18 m, 09.03.1966: 1 male paratype, 3.9 mm × 5.8 mm (ZMUC CRU-9965).

Phuket I., west coast, off Airport Beach, 20 m, muddy sand, B. Chatananthawaj coll., 07.04.1981: male holotype, 4.2 mm  $\times$  6.8 mm, 1 female paratype, 4.1 mm  $\times$  6.7 mm (ZRC 1984.7739–7740).

**Diagnosis.** Inner margins of cheliped carpi with simple setae. G1 apex transversely cut (Fig. 24I, J) (see Table 3).



**FIGURE 25.** *Henicoplax pilimeles* **n. sp.**; A–E, male holotype (4.2 mm × 6.8 mm) (ZRC 1984.7739–7740), Andaman Sea, Phuket I.; F, G, female paratype (4.1 mm × 6.7 mm) (ZRC 1984.7739–7740), Andaman Sea, Phuket I. A, dorsal view of carapace; B, F, ventral views of carapaces; C, posterior portion of male thoracic sternum and abdomen; D, abdomen locking into sternum; E, sterno-abdominal cavity, G1, and penis; G, female thoracic sternum and vulvae. Abbreviations: a1-a3 = male abdominal somites 1, 2, 3, respectively; cx5 = coxa of fifth pereopod (P5); es7 = episternite 7; G1 = first male pleopod; mg = median groove; p = penis; pr = postorbital ridge; s4–s8 = thoracic sternites 4 to 8, respectively; v = vulva.

**Description.** Carapace (Fig. 25A; Serène & Soh 1976: fig. 22C, as *Heteroplax nitidus*) hexagonal, transversely elongated, wider than long (1.6 wider than long in male holotype), anterolateral borders nearly straight, dorsal surface without clear indication of regions; front wide, lacking median notch. Transverse depression (postorbital ridge) below each orbit extending from anterolateral tooth, becoming progressively shallower before disappearing at the level of distal portion of each eye peduncle (Fig. 25A). One short, triangular, obtuse anterolateral tooth posterior to triangular, anteriorly oriented outer orbital tooth. Orbits long (Fig.

25A, B, F), almost as long as front (0.9 frontal width); slightly sinuous, thin supraorbital border lacking notches; suborbital border sinuous, with broad median lobe, inner suborbital tooth absent (Fig. 25B, F); eye peduncles long (0.6 frontal width), much longer than corneas (1.8 times cornea length in paratype); large, spherical corneas.

Basal antennal article slightly mobile, orbital hiatus closed excluding antennal flagellum from orbit.

Posterior margin of epistome lobular; lateral lobes large, with straight margins, separated from median portion by deep fissure; median portion with 2 broadly rectangular lobes separated by shallow cleft. Anterior margin of endostome well demarcated from buccal cavern, endostomial ridges low. Pterygostomian region smooth. Third maxillipeds (Fig. 25B, F; Serène & Soh 1976: fig. 22E, as *H. nitidus*) completely closing buccal cavern; ischium rectangular with deep submedian line; merus relatively square in shape, anteroexternal angle angular, rounded; exopod long, reaching to just before anterior edge of merus with long flagellum.

Cheliped fingers moderately slender, slightly longer than swollen propodus, dorsal margin of dactylus with microscopic tubercles, distal portion light in colour. Inner margin of carpus with small triangular tooth plus sparse, long, simple setae. Dorsal, ventral margins of ambulatory legs (P2–P5) smooth, with long, sparse simple setae; dactyli long, slender; P5 (Fig. 27A, B; Serène & Soh 1976: fig. 22D, as *H. nitidus*) merus proportionally short, ventral margin slightly curved, distal end does not reach anterolateral tooth when folded against carapace; P5 propodus (1.6 mm long, 0.8 mm wide in one of 3 detached P5 from type material), proportionally stout, subcylindrical, inner margin fringed with many long, plumose setae; outer margin with scattered long, plumose setae; P5 dactylus proportionally slender (1.8 mm long, 0.3 mm maximum width in holotype), inner margin fringed with many long, plumose setae.

Thoracic sternum (Fig. 25G) wide, thoracic suture 2/3 complete, convex; 3/4 deep, short, interrupted; 4/5, 6/7, 7/8 interrupted, 5/6 complete; median groove on thoracic sternites 7, 8. Sterno-abdominal cavity of male deep, nearly reaching anterior margin of sternite 4, anterior extremity rounded (Fig. 25B). Press-button of male abdominal-locking mechanism as very small tubercle near thoracic suture 4/5.

Male abdomen narrow, slender, transversely narrow (T-shaped), lateral margins of somites 4–6 abruptly narrowing from somite 3 to narrow, pointed telson (Fig. 25B; Serène & Soh 1976: fig. 22A, as *H. nitidus*); somite 3 reaching inner margins of P5 coxae (Fig. 25C), anterior tip of outer margin of somite 3 locking under outer posterior edge of thoracic sternite 7 (Fig. 25D), only small portion of thoracic sternite 8 left exposed on each side by closed abdomen, somite 2 transversely shorter than somite 3. G1 (Fig. 24I, J; Serène & Soh 1976: fig. 22B, B', as *H. nitidus*) long, slender, slightly sinuous, transversely cut apex, with relatively few, small denticles; G2 (Fig. 24K) less than one-third of G1, straight, apex with 2 processes: one long, tip acute; second much shorter, tip obtuse. Male genital opening (gonopore) coxal; coxo-sternal disposition of long penis, protected by concave posterior portion of thoracic sternite 7 (Fig. 25E).

Vulva (Fig. 25G) ovoid, extending across anterior portion of sternite 6 close to median axis of thorax, sternal suture 6/7 deflected; covered by soft membrane, sternal vulvar cover absent.

Colour pattern. Unknown.

**Etymology.** From *pilos*, Greek for "hairy", and *melos*, Greek for "limb", as a noun in apposition, in reference to the many long, plumose setae on the inner margin of the P5 propodus and dactylus that is diagnostic of the new species.

**Remarks.** The new species is described from material collected by the 1966 Thai Danish Expedition to the Andaman Sea, which was reported by Serène & Lohavanijaya (1973: 74) and Serène & Soh (1976: 23) as belonging to *Heteroplax nitida* Miers, 1879 (= *Henicoplax nitida*), plus additional material collected from the same region. Although closely related to *H. nitida*, the inner margins of the P5 propodus and dactylus are bordered by many long, plumose setae (Fig. 27A, B; Serène & Soh 1976: fig. 22D, as *H. nitidus*), a character that separates the new species from *H. nitida* and its four congeners, where the long setae are absent (Table 3).

It can also be differentiated by the transversely cut apex of its G1 (Fig. 24I, J), which is acuminate in its congeners except in *H. nitida* (Fig. 24G, H) and *H. maldivensis* (Fig. 24D, E). The G1 of *H. pilimeles* **n. sp.**, although having a transversely cut apex as in *H. nitida*, can be differentiated from the latter by a different distribution of spinules on the distal portion of the G1. Differences observed in the material on hand may be due to differences in size. The distribution of spinules on the G1 of *H. pilimeles* **n. sp.** illustrated by Serène & Soh

(1976: fig. 22B, B', as *H. nitidus*), however, does resemble more than that of the *H. nitida* drawn here. The transversely cut apex of both species is not very distinct in Serène & Soh's (1976) figure.

**Distribution.** Andaman Sea coasts of Myanmar [= Burma] and Thailand. Depth: 15–29 m.

*Henicoplax trachydactylus* **n. sp.** (Figs. 26A–F; 27C–F)

**Type material.** Male holotype,  $3.4 \text{ mm} \times 5.3 \text{ mm}$  (MNHN-B29236) (Figs. 26A, B; 27C–E); 1 female paratype,  $4.4 \text{ mm} \times 7.2 \text{ mm}$  (MNHN-B29236) (Fig. 26C–F).

Type locality. Madagascar, northeastern coast, Nosy Iranga I., 25 m, sandy bottom.



**FIGURE 26.** *Henicoplax trachydactylus* **n. sp.**; A, B, male holotype ( $3.4 \text{ mm} \times 5.3 \text{ mm}$ ) (MNHN-B29236), Madagascar; C–F, female paratype ( $4.4 \text{ mm} \times 7.2 \text{ mm}$ ) (MNHN-B29236), Madagascar. A, C, overall views; B, D, ventral views of carapaces; C, dorsal view of carapace; E, orbit and suborbital border; F, female thoracic sternum and vulvae. Abbreviations: s4-s7 = thoracic sternites 4 to 7, respectively; v = vulva.

**Material examined.** *Madagascar.* Nosy Iranga I., 25 m, sand, R. Plante coll., 26.08.1965: male holotype, damaged,  $3.4 \text{ mm} \times 5.3 \text{ mm}$ , 1 female paratype,  $4.4 \text{ mm} \times 7.2 \text{ mm}$  (MNHN-B29236).

**Diagnosis.** Postorbital ridge of carapace absent. Chelipeds without tomentum. Cheliped dactyli granular (Fig. 27F). G1 with acuminate apex (Fig. 27C, D) (see also Table 3).

**Description.** Carapace (Fig. 26A, C) hexagonal, transversely elongated, wider than long (1.6 wider than long in male holotype), anterolateral borders nearly straight, dorsal surface without clear indication of

regions; front wide, lacking median notch. Transverse depression below orbits absent. One short, triangular, obtuse (apex of right tooth acute in male holotype) anterolateral tooth posterior to triangular, anteriorly oriented outer orbital tooth. Orbits long (Fig. 26A, C, E), slightly longer than front (1.1 frontal width); slightly sinuous, thin supraorbital border lacking notches; suborbital border (Fig. 26E) sinuous, with broad median lobe, inner suborbital tooth absent. Eye peduncles long (0.6 frontal width), much longer than corneas (1.8 times cornea length in paratype); large, spherical corneas (Fig. 26E).



**FIGURE 27.** A, B, *Henicoplax pilimeles* **n. sp.**; male holotype (4.2 mm × 6.8 mm) (ZRC 1984.7739–7740), Thailand, Andaman Sea coast; C–F, *Henicoplax trachydactylus* **n. sp.**; male holotype (3.4 mm × 5.3 mm) (MNHN-B29236), Madagascar; G–I, *Heteroplax transversa* Stimpson, 1859, male (5.8 mm × 9.5 mm) (ZRC 2008.1356), Hong Kong. A, B, P5; C, D, right G1, dorsal view; E, right G2, dorsal view; F, left cheliped, dorsal view; G, H, left G1, dorsal view; I, left G2, dorsal view. Scale bars: A, B, F, 1.0 mm; C, G, 0.5 mm; D, 0.2 mm, E, H, I, 0.1 mm.

Basal antennal article slightly mobile, orbital hiatus is closed excluding antennal flagellum from orbit.

Posterior margin of epistome lobular; lateral lobes large, with straight margins, separated from median portion by deep fissure; median portion with 2 broadly rectangular lobes separated by cleft. Anterior margin of endostome well demarcated from buccal cavern, endostomial ridges low. Pterygostomian region smooth. Third maxillipeds completely closing buccal cavern; ischium rectangular with deep submedian line; merus relatively square in shape, anteroexternal part angular, rounded; exopod long, reaching to just before anterior edge of merus with long flagellum.

Cheliped fingers moderately slender, slightly longer than swollen propodus, dorsal margin of dactylus with short, rounded tubercles (very low tubercles on outer margin of propodus, carpus) (Fig. 27F), distal portion light in colour. Inner (dorsal) margin of carpus with small triangular tooth plus sparse, long, simple setae. Dorsal, ventral margins of ambulatory legs (P2–P5) smooth, with long, sparse simple setae; dactyli long, slender; P5 merus long, moderately slender, ventral margin slightly curved, distal end does not reach anterolateral tooth when folded against carapace; P5 propodus (1.1 mm long, 0.6 mm wide in holotype), proportionally stout, subcylindrical, inner margin fringed with short, simple setae, outer margin with scattered long, simple setae; P5 dactylus (Fig. 26A–D) proportionally slender (1.2 mm long, 0.2 mm maximum width in holotype), subcylindrical, fringed with scattered simple setae .

Thoracic sternum (Fig. 26F) wide, thoracic suture 2/3 complete, convex; 3/4 deep, short, interrupted; 4/5, 6/7, 7/8 interrupted, 5/6 complete; median groove on thoracic sternites 7, 8. Sterno-abdominal cavity of male (Fig. 26B) deep, nearly reaching anterior margin of sternite 4, anterior extremity rounded. Press-button of male abdominal-locking mechanism not visible in holotype.

Male abdomen missing in holotype. G1 (Fig. 27C, D) long, slender, slightly sinuous, acuminate apex, with relatively few, small denticles; G2 (Fig. 27E) less than one-third of G1, straight, apex with 2 processes: one long, tip acute; second much shorter, tip obtuse. Male genital opening (gonopore) coxal; coxo-sternal disposition of long penis, protected by concave posterior portion of thoracic sternite 7.

Vulva (Fig. 26F) ovoid, extending across anterior portion of sternite 6 close to median axis of thorax, sternal suture 6/7 deflected; covered by soft membrane, sternal vulvar cover absent.

Colour pattern. Unknown.

**Etymology.** From *trachys*, Greek for "rough", and *dactylus*, Greek for "finger", as a noun in apposition, in reference to the granules on the dorsal surface of the cheliped dactyli that is characteristic of the new species.

**Remarks.** Two specimens from the northwestern coast of Madagascar, which included the damaged holotype male, are morphologically distinct from all known species of *Henicoplax*. **n. gen.** *Henicoplax trachydactylus* **n. sp.** can be distinguished from its four congeners by the presence of small tubercles on the outer surface of the cheliped dactylus, short granules on the cheliped propodus and merus (Fig. 27F), and the absence of postorbital ridges on the carapace (Table 3).

Distribution. Only known from Madagascar. Depth: 25 m.

#### Genus Heteroplax Stimpson, 1858

Heteroplax Stimpson, 1858: 94 (40); 1907: 94 [diagnosis] (part). — De Man 1887: 89 [discussion] (part). — Alcock 1900: 292 [in list] (part). — Balss 1922a: 136 [list of species] (part); 1957: 1656 [in list] (part). — Sakai 1934: 312 [discussion] (part); 1939: 555 [in key], 560 (part); 1976: 531 (part). — Guinot 1969b: 511 [discussion] (part); 1971: 1080 [in list] (part). — Serène & Lohavanijaya 1973: 71 [discussion] (part). — Takeda & Shimazaki 1974: 60 [discussion] (part). — Karasawa & Kato 2003a: 151 [in list] (part); 2003b: 130 [in list] (part). — Ng & Castro 2007: 44 [in list] (part). — Ng *et al.* 2008: 78, 79 [discussion] (part).

*Eucrate* — Alcock 1900: 292 [in list], 298 (part). — Tesch 1918: 157 (part). — Campbell 1969: 119 [in key of species]. [not *Cancer (Eucrate)* De Haan, 1835]

not *Heteroplax* — Poore *et al.* 2008: 46. (= *Neogoneplax* Castro, 2007 (part), *Paragoneplax* Castro, 2007 (part) [Gone-placidae])

**Diagnosis.** Carapace (Fig. 28A) transversely elongated, much wider than long (1.5–1.6 times wider); dorsal surface smooth without clear indication of regions, continuous elevation following sinuous orbital margin from each second anterolateral tooth to just below inner limit of orbits; anterolateral borders straight, nearly parallel to each other; front wide, nearly straight with long, shallow median notch (barely visible in some individuals). Three teeth posterior to triangular, anteriorly oriented outer orbital tooth: first short, obtuse, barely visible in larger individuals; second large, triangular, with anteriorly oriented, acute tip; third short, obtuse, triangular, continuing on anterolateral border as short, shallow sulcus. Orbits long (Fig. 28A-C), longer than front, small notch on inner third portion of thin supraorbital border; short, triangular median lobe, inner suborbital tooth absent on thin suborbital border (Fig. 28B, C); eye peduncles long, almost as long as front; large, spherical corneas. Basal antennal article mobile, fills orbital hiatus excluding antennal flagellum from orbit (Fig. 28B). Anteroexternal margin of third maxilliped merus angular. Cheliped fingers moderately stout (Fig. 28F), slightly longer than swollen propodus, light in colour; carpus with tooth on inner margin; long simple, plumose setae along anterior margin of carpus. Dorsal margins of ambulatory legs (P2-P5) meri, carpi, propodi unarmed, dactyli slender, smooth, setose; P5 propodus, dactylus long, slender, subcylindrical, smooth surface, fringed with scattered, long setae. Thoracic sternum (Fig. 28D) wide; thoracic suture 2/3 complete, convex, close to anterior margin of sternum (Fig. 28C); 3/4 deep, short, interrupted; 4/5, 6/7, 7/8 interrupted, 5/6 complete; median groove on thoracic sternites 7, 8. Sterno-abdominal cavity of male deep, nearly reaching anterior margin of sternite 4 (Fig. 28C, D). Press-button of male abdominal-locking mechanism as large tubercle near thoracic suture 4/5 (small tubercle present in pre-adult females). Male abdomen narrow, slender (Tshaped), lateral margins of somites 4–6 abruptly narrowing from somite 3 to narrow telson (Fig. 28D); somite 3 reaching inner margins of P5 coxae; small portion on each side of thoracic sternite 8 left exposed by closed abdomen even if somite 2 transversely almost as long as somite 3 (Fig. 28E). G1 long, slender, sinuous, acuminate apex, with relatively large denticles (Fig. 27G, H); G2 less than one-third of G1, straight, apex with 2 unequal processes (Fig. 27I). Male genital opening (gonopore) coxal; coxo-sternal disposition of long penis, protected by concave posterior portion of thoracic sternite 7. Vulva slightly transversely elongated, across anterior portion of sternite 6 close to deflected suture 5/6; margin thick, with small, triangular lip on posterior portion; covered by soft membrane, sternal vulvar cover absent.

**Type species.** *Heteroplax transversa* Stimpson, 1858. Subsequent designation by Guinot (1969b: 511), not *H. dentatus* determined by Stimpson (1858, 1907) as stated by Serène & Lohavanijaya (1973: 73); gender feminine (see Ng *et al.* 2008: 79, note 3).

**Remarks.** Serène & Lohavanijaya (1973: 71) and Ng *et al.* (2008: 78) discussed the status of *Heteroplax*. Stimpson (1858: 94 (40); 1907: 94) described the genus as "allied" to *Goneplax* "in the shape of the carapax [broadly transverse] and the form of the orbits [long]". Two new species from or near Hong Kong, *H. dentata* and *H. transversa*, were included, even if the carapace of *H. dentata* was correctly described as "narrow". Stimpson's species were not figured and his material is unfortunately no longer extant. Two new species were subsequently added, *H. nitida* Miers, 1879, from Korea, and *H. nagasakiensis* Sakai, 1934, from Japan.

Miers (1879: 39) had doubts about the inclusion of his new species, *H. nitida*, in *Heteroplax* because of Stimpson's (1858) description of the genus having a "basal antennal joint [that] is longer and occupies the orbital hiatus". The second article of Miers' specimen was described as "small, occupying the hiatus between the inner angle of the orbit and the frontal margin". Actually, both the first and second articles fill the gap in the specimens of *H. nitida* examined, including the holotype. In any case, *H. nitida* Miers does not belong in *Heteroplax* and is here referred to *Henicoplax* **n. gen.** Several authors (De Man 1888, Alcock 1900, Tesch 1918, Campbell 1969) eventually considered *Heteroplax* as a junior synonym of *Eucrate* whereas most (Balss 1922a; Sakai 1934, 1939, 1976; Guinot 1969b, 1971; Serène 1968, Serène & Lohavanijaya 1973, Serène & Soh 1976) kept them separate. Sakai (1934: 312) was nevertheless only "inclined to retain" the genus, but reiterated that the basal antennal article "differs in shape from that of "*Eucrate*" form, so that the antennal flagelum is not completely shut out from the orbit as discussed by Balss [1922a]". Guinot (1971: 1080) considered the genus as "very close" to *Eucrate* and a possible synonym (*peut-être synonyme*). The affinities between Stimpson's *Heteroplax dentata* (placed herein in *Trissoplax* **n. gen.**) and *Eucrate* were in particular pointed out by several authors (see remarks for *Henicoplax* **n. gen.** below).

Serène & Lohavanijaya (1973: 71) clarified the definition of *Heteroplax*, gave a key to its four species known at the time, and summarized the views of various authors, particularly regarding the relationship of the genus with *Eucrate*. For these authors (Serène & Lohavanijaya 1973: 71) the main differences between the two genera is that in *Heteroplax*: 1) the basal antennal article is mobile and does not fill and close the orbital hiatus (following Stimpson 1858, 1907; Alcock 1900; Sakai 1939) in contrast to being immobile, filling in the orbital hiatus in *Eucrate*, and 2) the carapace ("closer to that of *Goneplax*") and orbits are broader and the eye peduncles are longer (the "orbit breadth is as long or longer than the frontal breadth") than in *Eucrate*. Confusion about the differences in the basal antennal article may have arisen from different interpretations of the character. The article is immobile in adult *Eucrate* because of the presence of a disto-lateral process that clearly locks the article against the margin of the orbit. The process is absent in *Heteroplax* and so the article may be mobile, but the article does fill the orbital hiatus.



**FIGURE 28.** *Heteroplax transversa* Stimpson, 1858; male (5.4 mm  $\times$  8.5 mm) (CBM-CZ 7310), Japan, Seto Inland Sea. A, overall view; B, frontal view showing orbits and antennae; C, third maxillipeds; D, anterior portion of male thoracic sternum and abdomen; E, posterior portion of male thoracic sternum and abdomen; F, outer views of chelae. Abbreviations: a1-a3 = male abdominal somites 1, 2, 3, respectively; cx5 = coxa of fifth pereopod (P5).
*Heteroplax* is restricted here to *Heteroplax transversa*, its type species, on account of its wide carapace and moderately long orbits and eye peduncles (Fig. 28A–C). Another species, *Heteroplax nitida* Miers, 1879, as well as a second species sometimes assigned to *Heteroplax (Goneplax maldivensis* Rathbun, 1902), both having longer orbits and eye peduncles than *Heteroplax sensu stricto*, only one anterolateral tooth on each side of the carapace, and a postorbital ridge, are assigned to *Henicoplax* **n. gen.** *Heteroplax dentata* Stimpson, 1858, is assigned to *Trissoplax* **n. gen.** because the carapace and orbits that are narrower that those in *Heteroplax sensu stricto*.

Two "*Heteroplax*" species from Western Australia (Poore *et al.* 2008: 46) actually belong to species included in the Goneplacidae: *Neogoneplax renoculis* (Rathbun, 1914) and, shown in a colour photograph, *Paragoneplax serenei* (Zarenkov, 1972).

### Species included.

Heteroplax transversa Stimpson, 1858 = Heteroplax nagasakiensis Sakai, 1934 The genus is restricted to the Indo-West Pacific region.

Species excluded from Heteroplax Stimpson, 1858:

Heteroplax dentata Stimpson, 1858 (in Trissoplax n. gen.)

Heteroplax nitida Miers, 1879 (in Henicoplax n. gen.)

Goneplax maldivensis Rathbun, 1902 ["Heteroplax" maldivensis (Rathbun, 1902) in Ng et al. 2008] (in Henicoplax **n. gen.**)

# Heteroplax transversa Stimpson, 1858

(Figs. 27G-I; 28A-F)

- *Heteroplax transversa* Stimpson, 1858: 94 (40); 1907: 95 [Hong Kong]. Balss 1922a: 137, fig. 2 [Hong Kong]. Guinot 1969b: 511 [in list]; 1971: 1080 [in list]. Ng *et al.* 2008: 78, 79 [in list].
- (?) *Heteroplax transversa* Rathbun 1910: 342 [Gulf of Thailand]. Naiyanetr 1998: 78 [in list]; 2007: 90 [in list] [Andaman Sea coast of Thailand].
- Eucrate transversa Tesch 1918: 158 [in key, footnote]. Campbell 1969: 119 [in key], 132 [discussion].
- Heteroplax nagasakiensis Sakai, 1934: 312, fig. 21; 1935: 185, fig. 95; 1939: 560 [in key], 560, 722, fig. 65; 1940: 57 [in list]; 1956: 46 [in list]; 1976: 531 [in key], 531, fig. 283, pl. 191, fig. 2 [colour] [Japan]. Miyake 1961: 21 [in list] [Japan]. Miyake *et al.* 1962: 130 [in list] [Japan]. Guinot 1969b: 511 [footnote]; 1971: 1080 [in list]. Yamaguchi *et al.* 1987: 22 [Japan]. Miyake 1991: 220 [in list] [Japan]. Muraoka 1998: 8 [type], 47[in list] [Japan]. Watanabe & Muraoka 1999: 43, fig. 2 [Japan]. Ng *et al.* 2008: 78, 79 [in list].
- not *Heteroplax transversus* Serène & Lohavanijaya 1973: 72 [in key], 73, 98, figs. 183, 184, pl. 18, fig. A [Gulf of Thailand]. [= *Trissoplax dentata* (Stimpson, 1858)]

# Type material of Heteroplax transversa Stimpson 1858, lost.

Type locality. Hong Kong Harbour.

**Type material of** *Heteroplax nagasakiensis* **Sakai, 1974,** 1 holotype male, 7.9 mm  $\times$  12.0 mm (KPM-NH 106474); type locality: Nagasaki, Japan.

**Material examined.** *Japan.* Off Wakanoura Kishu [= Wakaura, Wakayama (?)], id. as *Goneplax maldivensis* by M. J. Rathbun: 1 female,  $5.0 \text{ mm} \times 7.6 \text{ mm}$  (USNM 45857).

Seto Inland Sea. West of Yashiro I., 33°53.80'N, 137°09'E, 18 m, TRV Toyoshio-maru, cruise 1997–05, stn. 1, S. Ohtsuka coll., 10.07.2000: 1 male, 5.4 mm  $\times$  8.5 mm, 4 females, 3.8 mm  $\times$  6.2 mm, 3.9 mm  $\times$  6.7 mm, 4.5 mm  $\times$  6.6 mm, 5.6 mm  $\times$  9.0 mm (CBM-CZ 7310); East of Hashira-jima I., 34°00'N, 137°27'E, 36 m, TRV Toyoshio-maru, cruise 2000–10, stn. 2, T. Komai coll., 27.05.2005: 1 pre-adult female, 5.3 mm  $\times$  8.8, 3 females, 5.6 mm  $\times$  8.8 mm, 5.7 mm  $\times$  8.8 mm, 6.0 mm  $\times$  9.5 mm (CBM-CZ 5603).

*Kyushu*. Nagasaki, I. Kaneko coll.: male holotype of *Heteroplax nagasakiensis* Sakai, 1974, 7.9 mm  $\times$  12.0 mm (KPM-NH 106474).

*Hong Kong*: 1 male, 5.8 mm  $\times$  9.5 mm, 2 detached chelipeds of smaller specimen, 1 ovigerous female, 7.3 mm  $\times$  12.3 mm, leg SWIMS (ZRC 2008.1356); 2 ovigerous females, 6.5 mm  $\times$  10.4 mm, 6.4 mm  $\times$  10.4 mm, 3 pre-adult females, 4.4 mm  $\times$  6.7 mm, 3.2 mm  $\times$  4.8 mm, 2.5 mm  $\times$  4.0 mm, 1 pre-adult, 1.8 mm  $\times$  2.5 mm (SWIMS CRU-XX-063). – Unknown location: 1 male, 1 ovigerous female, 1 pre-adult female, 4 pre-adults (SWIMS CRU-XX-064). – Unknown location: 27.06.1988, P. Davie coll.: female, 5.7 mm  $\times$  9.1 mm (QM W28381).

**Diagnosis.** First anterolateral tooth short, barely visible in larger individuals; second large, triangular, with anteriorly oriented, acute tip; third short, obtuse, triangular, continuing on anterolateral border as short sulcus (Fig. 28A). Eye peduncles long, almost as long as front (Fig. 28B, C).

**Remarks.** Thirteen adult and pre-adult specimens collected from Hong Kong, the type locality of *H. transversa*, agree with Stimpson's very short description (only three sentences devoted to morphology) of the species (Stimpson 1858: 94 (40); 1907: 95). The only difference is that the size of one of Stimpson's male specimens was given as  $0.26 \text{ mm} \times 0.38$  inches (6.60 mm  $\times 9.65 \text{ mm}$ ), a 1:1.5 ratio. The average ratio of the seven Hong Kong male and female specimens examined (see material examined) is of 1:1.6. It is assumed that Stimpson had more than one specimen available as he gives the carapace size "in a male". Much as a neotype for this species is needed to help stabilise the taxonomy of the species and genus, the poor condition of the specimens on hand argue against taking such an action for the moment. Certainly a neotype should be selected for the species when better preserved specimens are collected in the future.

Some slight variations were observed among the Hong Kong specimens that were examined. The outer orbital teeth, which are typically triangular, may sometimes have a rounded anterior margin. The first anterolateral teeth, the largest and the most conspicuous of the two anterolateral teeth, always have an acute apex but their anterior margins may be straight or slightly convex. In a female specimen (6.5 mm  $\times$  10.4 mm, SWIMS CRU-XX-063) the left tooth was straight and triangular in shape but the right tooth had a convex margin and thus crescent in shape. Conspicuous granules, mostly rounded but some acuminate, extended from the first anterolateral teeth along both sides of the carapace just below the long orbits. Some of the granules were located at the junction of the teeth with the carapace so that the proximal margin of the teeth appeared granular. Similar granules were found in the large male holotype of *H. nagasakiensis* Sakai, 1974, a junior synonym (see below). The carapace was otherwise smooth in most specimens, including that of the neotype. In the smallest pre-adults, and in contrast to adults, the outer orbital teeth ware longer than the first anterolateral teeth.

A character not mentioned in Stimpson's description is the presence of two short, obtuse tubercles on the outer margin of the cheliped merus. Also not mentioned is the presence of short, round tubercles across the anterior third of the carapace from the anterolateral teeth to the protogastric and branchial regions, a character found only in the largest females. The G1 and G2 are illustrated herein for the first time (Fig. 27G–I).

In addition to Stimpson's specimen, Hong Kong material of *H. transversa* was also studied by Balss (1922: 137, fig. 2). Balss' male specimen was not found in the Zoologische Staatssammlung, Munich, where many of the specimens studied by Balss were deposited. The specimen was most probably destroyed during World War II (R. Melzer, personal communication).

Examination of the male holotype (7.9 mm  $\times$  12.0 mm, KPM-NH 106474) and the abundant available material of *Heteroplax nagasakiensis* Sakai, 1974, from Japan clearly shows that it is a junior synonym of *H. transversa*. The nine Japanese specimens (CBM-CZ 5603, 7310; Fig. 28) examined here, Sakai's description of *H. nagasakiensis* (Sakai 1934: 312, fig. 21), Sakai's subsequent treatments of the species (Sakai 1935, 1939, 1976), and the photograph given by Watanabe & Muraoka (1999: 43, fig. 2), all agree with the Hong Kong material of *H. transversa* as well as Stimpson's description of the later. The G1 of *E. nagasakiensis* (see Sakai 1974: fig. 283b) is also identical to that of *H. transversa* (Fig. 27G, H). Sakai (1934: 313) remarked that his new species resembled *H. transversa* "in outer view" but the carapace was considered to be broader in *H. nagasakiensis*. A Japanese specimen examined by Sakai (1976) measured 8 mm  $\times$  12.5 mm, a carapace length to carapace width ratio of 1:1.6; the same as the ratio in the nine specimens examined here, which is identical to the ratio in *H. transversa* (see discussion of the species above) and close to the ratio of 1:1.5 given by Balss (1922a: fig. 2). One morphological difference, however, was the slightly more rounded telson of a Hong Kong

male (5.8 mm  $\times$  9.5 mm; ZRC 2008.1356) and that of the only Japanese male (5.4 mm  $\times$  8.5 mm; CBM-CZ 7310) that was examined.

The four Gulf of Thailand specimens identified by Rathbun (1910) as *H. transversa* were not available for examination. *Heteroplax transversa* is only known from Japan and Hong Kong thus far.

Campbell (1969: 132) compared *H. transversa* to his new species, *Eucrate haswelli*, a junior synonym of Stimpson's *H. dentata*, which is now being placed in *Trissoplax* **n. gen.** (see Remarks for *Trissoplax dentata* below). Campbell included both species in *Eucrate*, even when he agreed that the eye peduncles of his *E. transversa* were long. His comments, however, were based on Stimpson's descriptions and not on the examination of specimens of *H. transversa*.

The suggestion by Serène & Lohavanijaya (1973: 75) that *H. nagaskiensis* and *H. nitida* are conspecific is not correct, both species not even being congeneric.

**Colour pattern.** Stimpson described the colours in life of his Hong Kong specimens as similar to those of *H. dentata* (= *Trissoplax dentata*, see below). Very little colour remained in the preserved specimens from Japan that were examined (CBM-CZ 5603, 7310). Most of the specimens showed a few small, irregular light-orange marking on the dorsal surface of the carapace, pereopods (particularly the ventral surface of the chelipeds), and on the proximal portion of the cheliped dactylus. Sakai's colour plate (Sakai 1976: pl. 191, fig. 2) shows similar markings on the pereopods, except that the orange markings on the ambulatory legs are in the form of bands and most irregular markings on the dorsal surface of the carapace of the carapace are not shown on the plate.

**Distribution.** Japan and Hong Kong. Depth: 18–50 m.

### Genus Machaerus Leach, 1818

Machaerus Leach, 1818: 413. — Manning & Holthuis 1981: 161 [discussion]. — Karasawa & Kato 2003a: 151 [in list]; 2003b: 139 [in list]. — Ng & Castro 2007: 44 [in list]. — Ng et al. 2008: 78 [in list]. — De Grave et al. 2009: 33 [in list].

Diagnosis. Carapace (Figs. 29A, C; 30A) hexagonal, slightly wider than long, dorsal surface smooth (except granules on hepatic region, shallow sulcus extending from each third anterolateral tooth), without clear indication of regions; anterolateral borders arched; front wide, straight, with small median notch. Three obtuse to acute anterolateral teeth posterior to triangular or rounded, obtuse, anteriorly oriented outer orbital tooth. Orbits moderately long (Figs. 29A, C; 30A-C), almost as long as or slightly longer than front; 2 notches (absent in *M. atlanticus*) on thin or thick supraorbital border; obtuse, salient suborbital tooth, sinuous suborbital border (Figs. 29D; 30B, C); eye peduncles moderately long, slightly longer than large, spherical corneas (Figs. 29A; 30B, C). Basal antennal article immobile closes orbital hiatus excluding antennal flagellum from orbit (Fig. 30B, C; Monod 1956: figs. 445, 451). Anteroexternal margin of third maxilliped merus angular. Cheliped fingers moderately slender (Figs. 29A, B; 30D), shorter than propodus, light in colour; carpus with obtuse tooth on inner margin; dense tomentum (Fig. 30D) on posterior margin of propodus and anterior margin of carpus (very short in *M. atlanticus*). Dorsal margins of ambulatory legs (P2–P5) meri, carpi, propodi unarmed, dactyli slender, smooth, setose. P5 propodus subcylindrical; dactylus long, slender, fringed with long setae. Thoracic sternum (Figs. 29D; 30F) wide; thoracic suture 2/3 complete, convex (Figs. 29B, D; 30C); 3/4 deep, short, interrupted; 4/5, 6/7, 7/8 interrupted, 5/6 complete (Fig. 29D); median groove on thoracic sternites 7, 8. Sterno-abdominal cavity of male deep (Fig. 30F), reaching anterior margin of sternite 4 (Figs. 29B; 30E). Male abdomen proportionally wide, triangular (not T-shaped), proportionally narrow telson (Fig. 30E); somite 3 transversely longer than somites 4–6, reaching inner margins of P5 coxae, episternite 7 (Figs. 30G; 32A, C); small portion on each side of thoracic sternite 8 left exposed by closed abdomen (Figs. 30G; 32A, C), somite 2 slightly transversely shorter (Figs. 30G; 32C) or nearly as long as somite 3 (Fig. 32A). Press-button of male abdominal-locking mechanism as tubercle near thoracic suture 4/5 (small tubercle present in pre-adult females). G1 long, slender, slightly sinuous, acuminate apex, with many small denticles (Figs. 30F; 32B, D, E); G2 less than one-third of G1, straight, apex with 2 unequal processes (Fig. 32F). Male genital opening (gonopore) coxal (Figs. 30F; 32A, C); coxo-sternal disposition of long penis, protected by concave posterior portion of thoracic sternite 7, expanded episternite 7 (Fig. 30F). Vulva ovoid (Fig. 29D), extending across anterior third of sternite 6 close to median axis of thorax; covered by soft membrane, sternal vulvar cover absent.

**Type species.** *Pilumnoplax oxyacantha* Monod, 1956 (subsequent designation by Manning & Holthuis 1981; gender masculine)

**Remarks.** Monod (1956: 350) remarked on the similarities between *Eucrate* and both *Pilumnoplax atlantica* Miers, 1881, and his new species, *P. oxyacantha*. Guinot (1969b: 517) included both species in the Euryplacinae but left their generic status unresolved (*pour le moment ... sans attribution générique*). Manning & Holthuis (1981) revised the genus and confirmed its position in the Euryplacinae. They nevertheless concluded that the genus "appears to show closest affinities with *Neopilumnoplax* Serène" (Goneplacoidea, Mathildellidae) whereas at the same time noticing the "much slenderer male abdomen" and telson than the latter (Manning & Holthuis 1981: 162).

Although the male abdomen of *Machaerus* is relatively less slender than in *Eucrate* and other Indo-West Pacific euryplacids, it is certainly not triangular as in the Atlantic and Eastern Pacific euryplacids, *Nancyplax* and *Trizocarcinus* (Fig. 1). Despite the shape of the male abdomen, all other diagnostic characters (most especially the long and deep sterno-abdominal cavity of the male and the long and slender G1; Fig. 30F) clearly show that *Machaerus* is a euryplacid.

We should also comment on the status of what has been called "Machaerus elata" in the literature. Boone (1927: 7, fig. 1) referred a 6.0 mm  $\times$  9.0 mm male specimen from Isla de Pinos (= Isla de la Juventud) in Cuba to "Pilumnoplax elata". It was clear that Boone was identifying it with a species from west Florida, which A. Milne-Edwards (1880b: 18) had named Eucratoplax elata. Eucratoplax elata A. Milne-Edwards, 1880, is now regarded as a species of Panoplax Stimpson, 1871, and in the xanthoid family Panopeidae (see Guinot 1969a: 264; 1971: 1080; Ng et al. 2008: 189). Guinot (1969b: 512) noted that Boone's (1927) "Pilumnoplax elata" was a problem, stating On peut se demander si la Pilumnoplax elata de Cuba figurée par BOONE (1925, pp. 7–9, fig. 1), qui ne correspond nullement à l'elata typique d'A. MILNE EDWARDS, 1880, n'est pas une Euryplax: en l'absence de figure de la face ventrale et de description des régions antennaire et abdominale, il est difficile d'avoir une certitude. Mais la forme de la carapace et surtout celle du front, où l'on devine très nettement la présence de larges lobes antéro-externes ..., évoquent Euryplax et l'on pense plus particulièrement à E. polita qui, comme sur la figure de BOONE, a des dents antéro-latérales alignées et spiniformes, subégales. L' « elata » de BOONE semble malgré tout un peu moins large que polita, laquelle offre une carapace très transverse, des dents marginales plus rapprochées; par ailleurs, il faut se rappeler que polita a été récoltée à Panama et que le Crabe de BOONE vient de Cuba". Guinot (1969b: 515) added: Pilumnoplax elata de Cuba signalée par BOONE (1927, p. 7, fig. 1), qui ne correspond pas à l'elata originale d'A. MILNE EDWARDS, 1880, ni à ce que RATHBUN (1918, p. 23, pl. 23) a désigné sous ce nom, n'est bien connue que par sa face dorsale et ses appendices. Ce pourrait être un Euryplacinae: la disposition du front suggère l'existence de larges lobes externes et d'une encoche supra-orbitaire (bien sûr, en supposant que le dessin soit exact). Pour cette espèce, au sujet de laquelle nous ne pouvons pas statuer, il faut de toute façon établir une appellation spécifique nouvelle et, lorsque les caractères fondamentaux seront connues, désigner le genre qui doit la recevoir. Guinot (1969c: 714), again stated her earlier position and suggested that although similar to Trapezioplax tridentata (A. Milne-Edwards, 1880), P. elata was distinct and that it belongs to a genus other than Trapezioplax. The records of "Pilumnoplax elata" by Rathbun (1898: 281; 1918: 23, pl. 3 figs. 1, 2) from Florida were referred to two new genera and two new species, Robertsella mystica and Thalassoplax angusta, by Guinot (1969c: 716, 717). The record of "Eucratopsis elata ?" by A. Milne-Edwards & Bouvier (1923: 341, pl. 7, figs. 4, 5) remains uncertain.

Unfortunately, some authors have regarded Boone's name as a separate and valid taxon. This may have been partly due to Guinot (1971: 1081), who placed Boone's (1927) name with three other valid species for which the generic relationships she was not sure at the time (under *Autres Euryplacinae (attribution générique à préciser)*): "? [*Pilumnoplax*] *elata* de Boone, 1927 (nec A. Milne Edwards)", "[*Pilumnoplax*] *atlantica* Miers, 1881", "[*Pilumnoplax*] *oxyacantha* Monod, 1956", and "? [*Goneplax*] *maldivensis* Rathbun, 1902". *Pilumnoplax atlantica* and *P. oxyacantha* are now regarded as species of *Machaerus*, whereas *G. maldivensis* 

is being referred to a new genus, *Henicoplax* **n. gen.** (see above). Števčić (2005: 133) followed Guinot's (1969b: 512, 513, 515, 517; 1969c: 714) observations that Boone's (1927) "*Pilumnoplax elata*" was a problem but accepted it as a valid name (though incorrectly giving the year of Boone's publication as 1925) and proposed a new genus, *Henryalphonsia*, for the species. *Henryalphonsia* Števčić, 2005, is a *nomen nudum* as no description or diagnosis was provided. The supposed type species, "*Pilumnoplax elata* Boone, 1927", is not a valid name as Boone (1927) had already made it clear because her identification was based on A. Milne-Edwards' (1880) *Eucratoplax elata*. Ng *et al.* (2008: 78) also incorrectly treated it as a valid name when they listed it as an uncertain species of *Machaerus*.

The figure provided in Boone (1927: fig. 1) is relatively detailed, and although the male abdomen was neither figured nor described, it in fact bears a close resemblance to what is currently identified as *Trapezio-plax tridentata* (A. Milne-Edwards, 1880), as was been noted by Guinot (1969b, c). We examined a photograph of Boone's specimen (in the Peabody Museum of Natural History, Yale University, catalogue number YPM 42682) and we agree that it is probably *T. tridentata* or a taxon close to it. *Trapezioplax* is currently placed in the xanthoid family Pseudorhombilidae, and we tentatively refer Boone's (1927) "*Pilumnoplax elata*" to the synonymy of *Trapezioplax tridentata*.

### Species included.

Machaerus atlanticus (Miers, 1881) Machaerus oxyacanthus (Monod, 1956) The genus is restricted to the Eastern Atlantic region (West Africa).

Species excluded from Machaerus Leach, 1818:

*Pilumnoplax elata* Boone, 1927 [= *Trapezioplax tridentata* (A. Milne-Edwards, 1880), Pseudorhombilidae]

### Machaerus atlanticus (Miers, 1881)

(Figs. 29A–D; 32A, B)

Pilumnoplax sulcatifrons var. atlantica Miers, 1881: 259, 375 [in list; Senegal]; 1886: 226 [in list].

Pilumnoplax atlantica — Monod 1956: 340 [in key], 341, figs. 442—449 [Senegal, Guinea, Sierra Leone]. — Forest & Guinot 1966: 85 [Guinea, Ghana, Nigeria]. — Crosnier 1969: 531 [Congo-RC]. — Guinot 1969b: 517, 518 [discussion] [Senegal]; 1969c: 688; 1971: 1081 [in list]. — d'Udekem d'Acoz 1999: 242 [in list] [references].

"Pilumnoplax" atlantica — Guinot 1969b: 507, 508 [discussion], figs. 36, 53.

[Pilumnoplax] atlantica — Guinot 1971: 1081 [in list].

- Machaerus atlanticus Manning & Holthuis 1981: 162 [references] [Ivory Coast, Ghana]. Ng et al. 2008: 78 [in list].
- not *Pilumnoplax atlantica* Balss 1922b: 76 [Liberia, Ivory Coast, Equatorial Guinea]. Monod 1933: 533, fig. 19A, 20, 21E [Mauritania]. Capart 1951: 166, fig. 63 [Gabon, Cabinda, Congo-RC]. [= *Machaerus oxyacanthus* (Monod, 1956)]

### Type material. Unknown status (not MNHN).

Type locality. Senegal, Gorée I.

Material examined. *Mauritania*. M. Monod coll., 1923, id. as *Pilumnoplax atlantica* by M. Monod: 1 male (MNHN-B10237).

*Senegal.* Gorée I., Marche-Marchand coll., 09.01.1951: 1 ovigerous female, 6.0 mm × 8.2 mm (MNHN-B10239). – Joal, 10–11 m, 20.02.1953: 1 male 8.2 mm × 10.9 mm (MNHN-B10240); 4 m, 19.02.1953: 2 males, 6.5 mm × 8.9 mm, 6.5 mm × 9.0 mm (MNHN-B 10238).

Guinea. Calypso, stn. 7, 18 m, 17.05.1956: 2 males, 2 pre-adult females (MNHN-B10233).

**Diagnosis.** Anterolateral teeth, outer orbital teeth about same size, shape, second tooth only slightly longer than the first, third (Fig. 29A, B).

**Remarks.** *Machaerus atlanticus* appears to be sympatric with its only known congener, *M. oxyacanthus*. Both species can be easily differentiated from each other by the morphology of the anterolateral teeth. All three anterolateral teeth and the outer orbital teeth are about the same size and shape in *M. atlanticus*, with the second tooth only slightly longer than the first and third (Fig. 29A, B). The anterolateral teeth of *M. oxyacan-thus* are acute, different from the triangular outer orbital teeth, and the second anterolateral teeth much longer and more elevated than the first (Fig. 30A, B). Monod (1956: 345) provided some colour notes of a freshly preserved specimen, and there are some apparent differences between its colour pattern and that of *M. atlanticus* (see Manning & Holthuis 1981: 163).

**Distribution.** Atlantic coast of Africa from Senegal to Congo (RC). Depth: 4–100 m (Manning & Holthuis 1981).



**FIGURE 29.** *Machaerus atlanticus* (Miers, 1881); A, B, male (6.5 mm  $\times$  8.9 mm) (MNHN-B 10238), Senegal, Joal; C, D, ovigerous female (6.0 mm  $\times$  8.2 mm) (MNHN-B10239), Senegal. Gorée I. A, C, overall views; B, anterior portion of male thoracic sternum and abdomen; D, female thoracic sternum and vulvae. Abbreviations: s4–s6 = thoracic sternites 4 to 6, respectively; v = vulva.

### Machaerus oxyacanthus (Monod, 1956)

(Figs. 30A-G; 32C-F)

? Pilumnoplax sp. Cano 1889a: 91 [unknown location].

? Pilumnoplax incerta Cano, 1889b: 228, pl. 7, fig. 14 [unknown location].

Pilumnoplax atlantica — Balss 1922b: 76 [Liberia, Ivory Coast, Equatorial Guinea]. — Monod 1933: 533, fig. 19A, 20, 21E [Mauritania]. — Capart 1951: 166, fig. 63 [Gabon, Cabinda, Congo-RC]. [not Machaerus atlanticus (Miers, 1881)]

Pilumnoplax oxyacantha Monod, 1956: 340 [in key], 346, figs. 450-455 [Senegal, Ghana]. — Forest & Guinot 1966: 85

[Guinea, Sierra Leone, Liberia, (?) Equatorial Guinea]. — Guinot 1969b: 517, 518 [discussion]; 1969c: 688 [discussion].

"Pilumnoplax" oxyacantha — Guinot 1969b: 507, 508 [discussion], figs. 38, 42, 54, 55 [Senegal].

[Pilumnoplax] oxyacantha — Guinot 1971: 1081 [in list].

Machaerus oxyacantha — Manning & Holthuis 1981: 163 [references] [Ivory Coast, Ghana, Benin, Nigeria]. Machaerus oxyacanthus — Ng et al. 2008: 78 [in list].

Type material. Unknown status [given as "MP" by Monod (1956: 346) but not in MNHN].

Type locality. Senegal, unknown location.

Material examined. *Guinea. Calypso*, stn. 9, 18–30 m, 18.05.1956: 5 males, 2 pre-adult females, 7 females (MNHN-B10243).



**FIGURE 30.** *Machaerus oxyacanthus* (Monod, 1956); male (19.0 mm  $\times$  30.3 mm) (MNHN-B10242), Sierra Leone. A, overall view; B, frontal view showing orbits and antennae; C, third maxillipeds; D, outer surface of left chela; E, male thoracic sternum and abdomen; F, male sterno-abdominal cavity, G1, and penis; G, posterior portion of male thoracic sternum and abdomen. Abbreviations: a1-a3 = male abdominal somites 1, 2, 3, respectively; cx5 = coxa of fifth pereopod (P5); es7 = episternite 7; G1 = first male pleopod; G2 = second male pleopod; g = male gonopore; p = penis; s4–s8 = thoracic sternites 4 to 8, respectively.

Sierra Leone. Calypso, stn. 11, 34–30 m, 19.05.1956: 1 male, 19.0 mm  $\times$  30.3 mm, 1 male, 2 pre-adult females, 3 females (MNHN-B10242).

Gulf of Guinea. Identified as "Frevillea rosaea": 1 male, 26.1 mm × 16.9 mm (NHM 1850.32).

*Congo-RC*. Pointe Noir, 25 m, mud, A. Crosnier coll., 05.1963: 2 males, 11.6 mm  $\times$  27.2 mm, 22.5 mm  $\times$  35.8 mm (MNHN-B10231).

**Diagnosis.** Anterolateral teeth acute, different from triangular outer orbital teeth, second tooth much longer, more elevated than first (Fig. 30A, B).

**Remarks.** Differences between *M. oxyacanthus* and its only (and apparently sympatric) congener, *M. atlanticus*, are given in the Remarks for the latter. Unusual for a euryplacid, *M. oxyacanthus* has been collected in brackish water (Manning & Holthuis 1981: 163).

On the basis of the description and a rather simple figure (Cano, 1889b: 228, pl. 7, fig. 14), *Pilumnoplax incerta* Cano, 1889, is likely to be a senior synonym of *M. oxyacanthus*. This suggestion had already been made by Ahyong (2008: 54) and Ng *et al.* (2008: 84). The species is certainly not a *Pilumnoplax* Stimpson, 1858 (a junior synonym of *Eucrate* De Haan, 1835) as understood here, or a *Neopilumnoplax* Serène, 1969 (see Ahyong 2008; Tavares & Melo in press). Cano's (1889b) species is only known from the small ("6 mm × 8mm") holotype, which was obtained from an unknown location, and its whereabouts are uncertain. As Cano's (1889a, b) material was from all over the world, with the bulk from the Atlantic, it is possible that the specimen of *P. incerta* was obtained from somewhere in the western Atlantic where *M. oxyacanthus* is found. For now, we defer from synonymising the two species until more information can be obtained.

**Distribution.** Atlantic coast of Africa from Senegal to Angola (Manning & Holthuis 1981). Depth: 7–73 m (Manning & Holthuis 1981).

### Genus Nancyplax Lemaitre, García-Gómez, von Sternberg & Campos, 2001

*Nancyplax* Lemaitre *et al.* 2001: 952. — Karasawa & Kato, 2003a: 151 [in list]; 2003b: 139 [in list]. — Ng & Castro 2007: 44 [in list]. — Ng *et al.* 2008: 78 [in list]. — De Grave *et al.* 2009: 33 [in list].

**Diagnosis.** Carapace (Fig. 31A) quadrate, slightly wider than long, dorsal surface smooth (except granules on hepatic region) without clear indication of regions; anterolateral borders arched; front wide, with small median notch. One conspicuous, acute anterolateral tooth posterior to simple, unarmed outer orbital angle. Orbits short, shorter than front (Fig. 31B, C); 2 notches on thin supraorbital border; thin, sinuous suborbital border, inner suborbital tooth absent (Fig. 31C); eye peduncles short, nearly as long as corneas; large, spherical corneas (Fig. 31B, C). Basal antennal article immobile, disto-lateral process absent but orbital hiatus is closed excluding antennal flagellum from orbit (Fig. 32B, C; Lemaitre et al. 2001: fig. 2a). Anteroexternal margin of third maxilliped merus angular. Stridulating ridge on pterygostomian region (Lemaitre et al. 2001: fig. 2a). Cheliped fingers moderately slender, slightly shorter than propodus, light in colour (Fig. 31E); carpus with acute tooth on inner margin; sparse setae on outer margin of propodus, carpus (Lemaitre et al. 2001: fig. 3f); stridulating ridge on proximal margin of merus (Lemaitre et al. 2001: figs. 2a, 3f). Dorsal margins of ambulatory legs (P2-P5) meri, carpi, propodi unarmed, dactyli slender, smooth, setose. P5 propodus, dactylus long, slender, fringed with long setae (Lemaitre et al. 2001: fig. 4d). Thoracic sternum (Fig. 31D, F, G) wide; thoracic suture 2/3 complete, straight (Fig. 31D); 3/4 deep, short, interrupted; 4/5, 5/6, 6/7, 7/8 interrupted (Fig. 31F, G); median groove on thoracic sternites 7, 8. Sterno-abdominal cavity of male deep, reaching anterior margin of sternite 4 (Fig. 31D, F). Press-button of male abdominal-locking mechanism as large tubercle near thoracic suture 4/5 (Fig. 31D) (presence in pre-adult females unknown). Male abdomen proportionally wide, triangular (not T-shaped), telson wider than long (Fig. 32G); somite 3 only slightly transversely wider than somites 4–6, somite 3 not reaching inner margins of P5 coxae or episternite 7, small portion on each side of thoracic sternite 8 left exposed by closed abdomen ((Lemaitre et al. 2001: fig. 2b), somite 2 transversely shorter than somite 3 (Lemaitre et al. 2001: fig. 2b). G1 long, slender, slightly sinuous, thin distal part, acuminate apex, with small, relatively few denticles (Fig. 32H, I); G2 less than one-third of G1, straight, apex with 2 processes, one much longer, larger (Fig. 32J, K). Male genital opening (gonopore) coxal (Fig. 31F); coxosternal disposition of long penis, protected by slightly convex posterior portion of thoracic sternite 7. Vulva relatively large, ovoid, transverse on median portion of sternite 6, extending across median half of sternite (Fig. 31G); covered by soft membrane, sternal vulvar cover absent.

**Type species.** *Nancyplax vossi* Lemaitre, García-Gómez, von Sternberg & Campos, 2001 (by original designation, gender feminine).

**Diagnosis.** One long, acute tooth on each anterolateral border of carapace (Fig. 31A–C). Outer orbital tooth absent (Fig. 31B, C).



**FIGURE 31.** *Nancyplax vossi* Lemaitre, García-Gómez, von Sternberg & Campos, 2001; A–D, male paratype (12.1 mm  $\times$  17.2 mm) (USNM 308994), Suriname; E–G, female paratype (12.1 mm  $\times$  17.9 mm) (USNM 308994), Suriname. A, overall view; B, frontal view showing orbits and antennae; C, third maxillipeds; D, anterior portion of male thoracic sternum and sterno-abdominal cavity; E, outer surface of right chela; F, male sterno-abdominal cavity and penis; G, female thoracic sternum and vulvae. Abbreviations: cx5 = coxa of fifth pereopod (P5); es7 = episternite 7; g = male gonopore; mg = median groove; p = penis; pb = press-button of male abdominal-locking mechanism; s4–s8 = thoracic sternites 4 to 8, respectively; v = vulva.

**Remarks.** As in some of the other Western Atlantic and tropical Eastern Pacific genera of euryplacids, the male abdomen of *Nancyplax* is triangular in shape (Fig. 32G), not narrow and T-shaped (see Remarks for Euryplacidae). The G2 departs from the typical euryplacid G2 by having an apex that consists of one large process and a much smaller one (Fig. 32J) in contrast to other euryplacids, where the two processes are

unequal but not as dissimilar as in *Nancyplax*. The sterno-abdominal cavity, however, is deep and relatively narrow, and the G1 slender as in other euryplacids. With the exception of sternal suture 5/6, which is interrupted as in *Systroplax* **n. gen.** and *Xenocrate* whereas complete in the remaining euryplacid genera, the other defining characters of *Nancyplax* agree with those of the family.

**Species included.** *Nancyplax vossi* Lemaitre, García-Gómez, von Sternberg & Campos, 2001 The genus is restricted to the Western Atlantic region.



**FIGURE 32.** A, B, *Machaerus atlanticus* (Miers, 1881) (after Guinot 1969b: figs. 36, 53, as "*Pilumnoplax*" *atlantica*); C–F, *Machaerus oxyacanthus* (Monod, 1956) (after Guinot 1969b: figs. 38, 54a, 54b, 55, as "*Pilumnoplax*" *oxyacantha*); G–K, *Nancyplax vossi* Lemaitre, García-Gómez, von Sternberg & Campos, 2001 (after Lemaitre *et al.* 2001: figs. 5b–e). A, C, posterior portion of male thoracic sternum, abdomen, and gonopore; B, D, E, H, I, G1; F, J, K, G2. Abbreviation: a1–a3 = male abdominal somites 1, 2, 3, respectively; g = male gonopore.

# *Nancyplax vossi* Lemaitre, García-Gómez, Von Sternberg & Campos, 2001 (Figs. 31A-G; 32G-K)

**Type material.** Male holotype,  $10.7 \text{ mm} \times 15.7 \text{ mm}$  (USNM 308995); 1 male paratype (USNM 308996); 2 males paratypes (USNM 308993); 1 male, 1 female paratypes (USNM 308994); 2 ovigerous female paratypes (UMML 32.8776); 2 males paratypes (UMML 32.9079); 4 males paratypes (UMML 32.9078); 1 male, 2 female paratypes (UMML 32.8775); 1 male paratype (INVEMAR-CRU 2926).

**Type locality.** Off Venezuela, 11°06.3'N, 68°14.6'W, 95–132 m.

**Material examined.** *Suriname.* North of Paramaribo,  $07^{\circ}07$ 'N,  $55^{\circ}08$ 'W, *Pillsbury*, 11.07.1968: 1 male paratype, 12.1 mm × 17.2 mm, 1 female paratype, 12.1 mm × 17.9 mm (USNM 308994).

**Remarks.** See Remarks for genus.

**Distribution.** Western Atlantic, only known from the Caribbean Sea coasts of Colombia to Suriname. Depth: 55–155 m.

## Genus *Platyozius* Borradaile, 1902

Pseudozius (Platyozius) Borradaile, 1902: 243. Eucrate — Tesch 1918: 158 (part). — Ng et al. 2008: 78 [in list] (part).

**Diagnosis.** Carapace (Figs. 33, 34) trapezoidal, almost as wide as long, dorsal surface smooth without clear indication of regions except continuous, curved postorbital ridge between second anterolateral teeth parallel to front, orbits (Fig. 34E; dark colour in live specimens [Fig. 33A-E]; ridge less distinct in small individuals); anterolateral borders arched; front wide, straight, with small median notch, truncate margin but slight transverse sulcus in largest individuals. Three short, triangular teeth posterior to short, obtuse outer orbital angle; second anterolateral teeth largest, dorsally oriented, third smallest, particularly in largest individuals. Orbits moderately short (shorter than front), oblique, spherical (Fig. 35A); thin supraorbital border without notches (small notch may be present in small individuals); inner suborbital lobe, nearly straight margin without notches on thin suborbital border (Fig. 35C); eye peduncles short; large, spherical corneas (Fig. 35A, C). Basal antennal article mobile in small individuals, slightly mobile in larger ones, with disto-lateral process so that orbital hiatus is closed excluding antennal flagellum from orbit (Fig. 35A, C). Merus of third maxilliped auriculiform (Fig. 35A, C). Cheliped fingers moderately stout, slightly longer than swollen propodus (Fig. 35B), tips dark in live individuals (Fig. 33); carpus with tooth on inner margin; scattered setae, no tomentum on anterior margin of carpus. Dorsal margins of ambulatory legs (P2-P5) meri, carpi, propodi unarmed, dactyli slender, smooth, setose; P5 propodus, dactylus proportionally short, flattened (Figs. 33; 34), fringed with scattered, long setae, short spines. Thoracic sternum (Fig. 35D, F, G) wide; thoracic suture 2/3 complete, convex (Fig. 35C, D); 3/4 deep, short, interrupted; 4/5, 6/7, 7/8 interrupted, 5/6 complete (Fig. 35G); median groove on thoracic sternites 7, 8. Sterno-abdominal cavity of male deep, reaching only to median portion of sternite 4 (Fig. 35F). Press-button of male abdominal-locking mechanism as large tubercle near thoracic suture 4/5 (small tubercle present in pre-adult females). Male abdomen narrow, slender (T-shaped), lateral margins of somites 4–6 abruptly narrowing from somite 3 to narrow, pointed telson wide (Fig. 35D, E); somite 3 reaching inner margins of P5 coxae (Fig. 35E), outer margin with semi-circular projection that fits under thoracic sternite 7; no portions of thoracic sternite 8 exposed by closed abdomen, somite 2 transversely slightly shorter than somite 3. G1 long, slender, slightly sinuous, acuminate apex, with small denticles (Figs. 35F; 38A, B); G2 less than one-third of G1, straight, apex with 2 processes: one long, tip obtuse; second much shorter, tip obtuse (Fig. 38C). Male genital opening (gonopore) coxal; coxo-sternal disposition of long penis (Fig. 35F), protected by concave posterior portion of thoracic sternite 7. Vulva ovoid, extending across anterior portion of sternite 6 close to median axis of thorax (Fig. 35G); covered by soft membrane, sternal vulvar cover absent.

Type species. Pseudozius (Platyozius) laevis Borradaile, 1902 (by monotypy, gender feminine).

**Remarks.** The only species in the genus was described as *Pseudozius (Platyozius) laevis* by Borradaile (1902: 243). The species, however, is clearly not a member of *Pseudozius* Dana, 1851 (family Pseudoziidae Alcock, 1898), as noted by Rathbun (1906: 861), who noticed the diagnostic "ridge above, behind, and parallel to the margin", and adding that the anterior margin of the third maxilliped merus is not notched "as in typical *Pseudozius*". Its affinities with the Euryplacidae were recognized by Tesch (1918: 158), who synonymised *Platyozius* with *Eucrate* on account of its "general appearance". Barnard (1950: 295) synonymised the species, without any comments, with *Eucrate sulcatifrons* Stimpson, 1858, a junior synonym of *E. crenata* (De Haan, 1835). This position was followed by Edmondson (1962: 4), whereas Dai *et al.* (1996: 247) and Ng *et al.* (2008: 78) treated it as a separate species of *Eucrate*. The genus *Platyozius* Borradaile, 1902, is hereby resurrected and a diagnosis is given for the first time.

Species included. Platyozius laevis (Borradaile, 1902)

The genus is restricted to the Indo-West Pacific region.

## Platyozius laevis (Borradaile, 1902)

(Figs. 33A–F; 34A–F; 35A–G; 38A–C)

Pseudozius (Platyozius) laevis Borradaile, 1902: 243, fig. 45. — Garth 1971: 185 [in list].

Platyozius laevis - Rathbun 1906: 861, pl. 11, fig. 7 [Hawaiian Is.].

*Eucrate sulcatifrons* — Edmondson 1962: 4, figs. 1 b, 2a-c [Hawaiian Is.] — McLaughlin *et al.* 2005: 257 [in list]. [not *Eucrate sulcatifrons* (Stimpson, 1858) = *Eucrate crenata* (De Haan, 1835)]

*Eucrate laevis* — Dai *et al.* 1996: 247, fig. 10 [South China Sea]. — Ng *et al.* 2008: 78 [in list]. — Yang *et al.* 2008: 770 [in list] [China].

Eucrate sp. — Kawamoto & Okuno 2003: 149 [colour photograph] [Japan].



**FIGURE 33.** *Platyozius laevis* (Borradaile, 1902), colours in life. A, female (12.5 mm  $\times$  16.0 mm) (UF 1534), French Polynesia, Tuamotu Archipelago, Rangiroa Atoll; B, female (9.5 mm  $\times$  12.1 mm) (UF 1534), same location; C, specimen not located (LACM), Hawaiian Is., Northwest Hawaiian Islands, French Frigate Shoals; D, specimen not located, male, Vanuatu; E, F, male (6.9 mm  $\times$  8.6 mm) (LACM), Hawaiian Is., Northwest Hawaiian Is., Northwest Hawaiian Islands, French Frigate Shoals; A–E, overall views; F, ventral view. Photo credits: A, B by Florida Museum of Natural History (UF); C–F by J. Martin (LACM).



**FIGURE 34.** *Platyozius laevis* (Borradaile, 1902); A, male holotype of *Pseudozius (Platyozius)* Borradaile, 1902 (5.0 mm × 6.0 mm) (UMZC), Maldives, Suvadiva Atoll (after Borradaile 1902: fig. 45); B, male holotype of *Pseudozius (Platyozius)* Borradaile, 1902 (5.0 mm × 6.0 mm) (UMZC), Maldives, Suvadiva Atoll; C, topotypic female of *Pseudozius (Platyozius)* Borradaile, 1902 (7.5 mm × 9.5 mm) (UMZC), Maldives; D, male (6.0 mm × 7.5 mm) (MNHN-B30534), Seychelles; E, female (12.5 mm × 16.0 mm) (UF 1534), French Polynesia, Tuamotu Archipelago, Rangiroa Atoll; F, female (6.3 mm × 7.7 mm) (MNHN-B30534), Seychelles. Abbreviation: pr = postorbital ridge. Photo credits: B, C by T.-Y. Chan (NTOU).

**Type material.** Male holotype, 5.0 mm  $\times$  6.0 mm (UMZC) (Fig. 34A); 1 female, 7.5 mm  $\times$  9.5, 1 male, 7.0 mm  $\times$  8.5 mm (UMZC) not mentioned in the description.

Type locality. Maldives, Suvadiva Atoll, 36 m.

Material examined. *Madagascar*. North of Nosy Be, 12°26'N, 48°16'E, 200 m, G. Casellato coll., 10.1971: 1 male (MNHN-B30524).

*Seychelles.* REVES 2: stn.18, 05.09.1980: 1 female, 4.4 mm  $\times$  4.8 mm (MNHN-B30539); stn. 32, 57 m, 09.09.1980: 1 female, 4.2 mm  $\times$  4.3 mm (MNHN-B30535); stn. 51, 42 m, coral and sand, 15.09.1980: 1 male 6.4 mm  $\times$  7.7 mm, 1 female, 5.3 mm  $\times$  6.2 mm (MNHN-B30537); stn. 60, 41 m, 19.09.1960: 1 male, 6.0 mm

 $\times$  7.5 mm, 4 pre-adults females, 6.3 mm  $\times$  7.7 mm, 6.4 mm  $\times$  7.7 mm, 6.0 mm  $\times$  7.2 mm, cw 7.8 mm, 1 pre-adult 4.5 mm  $\times$  5.2 mm (MNHN-B30534).

*Maldives.* Suvadiva Atoll, 36 m.: male holotype, 5.0 mm  $\times$  6.0 mm; same location: 1 female, 7.5 mm  $\times$  9.5, 1 male, 7.0 mm  $\times$  8.5 mm (UMZC). – Laamu Atoll, under boulders in reef, A. Anand J. K. coll., 1 male, 6.1 mm  $\times$  7.8 mm (ZRC 2007.0707).

*Japan*. Ogasawara Is., off Chichi-jima I., 27°06.35'N, 142°10.48'E, 59–55 m, coral sand and rock, TRV *Shin'yo-maru*, 1997 cruise, stn. 10, T. Komai coll.: 2 males, 5.0 mm  $\times$  5.6 mm, 4.6 mm  $\times$  5.2 mm (CBMZC 6531).

Hong Kong. No data: 1 female (SWIMS SML-Z-159.1).

*Philippines*. Sulu Archipelago, Basilan Straits, SW Malanipa I., 48–51 m, *Pele*, B. R. Wilson coll., 12.02.1964: 1 male, 5.4 mm × 7.0 mm (MNHN-B10342).

Bohol, Panglao I., Balicasag I., tangle nets of local fishermen, 12.2003: 1 female, 11.0 mm  $\times$  14.0 mm (ZRC 2004.0806); 02.05.2004: 1 female, 9.5 mm  $\times$  11.9 mm (ZRC 2004.0732).

*Indonesia*. Ceram, Mariel King Memorial Expedition: stn. CP I, haul 1, Piru Bay,  $03^{\circ}15$ 'S,  $128^{\circ}8$ 'E, 59-64 m, 01.06.1970: 1 male, 4.5 mm × 4.8 mm (MNHN-B30773); stn. CP III, 01.06.1970: 1 male, 5.7 mm × 6.6 mm (MNHN-B30774).

Kai Is., Mariel King Memorial Expedition: stn. KR VI, haul 3–10, north of Du Rowa I.,  $05^{\circ}32$ 'S,  $132^{\circ}41$ 'E, 27–37 m, 11.06.1970: 1 female, 5.1 mm × 6.3 mm (MNHN-B30840).

*Solomon Is.* SALOMON 1: stn. DW 1822, 09°51.8'S, 160°51.8'E, 51–54 m: 1 male, 4.2 mm × 4.7 mm (MNHN-B30777); 1 male, 4.6 mm × 4.8 mm (MNHN-B32011).

*Vanuatu*. SANTO 2006: stn. DB29, west of Malo I., 15°38.9'S, 167°05.1'E, 15 m, 17.09.2006: 1 male, 6.9 mm × 8.5 mm (ZRC).

*Australia*. Queensland, Wreck Reef near Porpoise Cay,  $22^{\circ}11$ 'S,  $155^{\circ}20$ 'E, outer reef flat under dead coral boulders at base of live coral heads, low tide, J. Short & S. Mullens coll., 14.05.1988: 1 female, 12.3 mm  $\times$  15.0 mm (QM W15174). – Flinders Reef, off Cape Moreton,  $26^{\circ}59$ 'S,  $155^{\circ}29$ 'E, fringing reef under rock, scuba, 20 m, N. Coleman coll., 09.07.1997: 1 male, 10.9 mm  $\times$  13.5 mm (QM W24144).

*Chesterfield Is.* CORAIL 2: stn.DW1, 20°55.9'S, 161°40.7'E, 59 m, 20.07.1988: 1 female, 6.5 mm  $\times$  7.7 mm (MNHN-B30801). – Stn. DW 11, 20°59'S, 161°41'E, 58 m, 20.07.1988: 1 male, 5.5 mm  $\times$  6.9 mm (MNHN-B30779).

*New Caledonia*. LAGON: stn. 229, Ile Ouen, Baie du Prony,  $22^{\circ}39$ 'S,  $166^{\circ}39$ 'E, 41 m: 1 male,  $6.6 \text{ mm} \times 8.0 \text{ mm}$  (MNHN-B30778).

LAGON EST: stn. 748, 21°16.9'S, 165°49.9'E, 35 m, 06.01.1987: 1 pre-adult female, 6.1 mm × 7.4 mm, photograph CB 392 (MNHN-B30782).

MUSORSTOM 5: stn. DW 264, 25°19.69'S, 159°44.33'E, 56 m, 08.10.1986: 1 male, 7.0 mm × 8.5 mm, photograph (MNHN-B30780)

NORFOLK 2: stn. DW 2135, 23°02'S, 168°21'E, 295–330 m, 03.11.2003: 1 female, 5.4 mm × 6.7 mm (MNHN-B30781).

*Loyalty Is.* Ouvéa I., Mouli, diving, 11 m, J.-P. Menou coll., 13.11.1991: 1 male, 10.1 mm  $\times$  12.5 mm, photograph CB 1070 (MNHN-B30608).

*Micronesia*. Yap I., Y–251, R. Hiatt coll., 1952: 1 male, 8.5 mm × 10.7 mm (MNHN-B24496).

Marshall Is. Enewetak Atoll, #090351-B: 1 male, 1 pre-adult female, 1 female (LACM).

*Hawaiian Is.* Northwest Hawaiian Is, French Frigate Shoals, stn. FFS 114, 23.699°N, 166.058°W, fore reef, 16.8 m, G. Paulay *et al.* coll., 19.10.2006: 1 male, photograph 1JMO166, 6.9 mm × 8.6 mm (LACM); 23.699°N, 166.0575°W, under coral rubble, 16.7 m: 1 male, photograph, 5.0 mm × 6.5 mm (UF 12194). – Stn FFS 192, 23.699°N, 166.058°W, fore reef, under coral rubble, 25.7 m, G. Paulay *et al.* coll., 26.10.2006: 1 male, photograph, 7.7 mm × 9.7 mm (UF 12283); 23.8633°N, 166.1877°W: 1 male, photograph, 4.4 mm × 4.9 mm (UF 12284). – Stn FFS 193, 23.8445°N, 166.3348°W, back reef, under coral rubble, 18.1 m, G. Paulay *et al.* coll., 26.10.2006: 1 male, photograph, 13.5 mm × 10.4 mm (UF 12282).

Oahu, Halona Blowhole, 17 m, 21°26'N, 157°58'W, under surface of rubble, R. Holcom coll., 2.08.1997: 1 male, 7.7 mm  $\times$  9.5 mm (QM W28380).

*French Polynesia*. Tuamotu Archipelago, Rangiroa Atoll, ca. 1 km S of NW point of atoll off Motu Maeherahonae, stn. BRNG–31, 14°55.72'S, 147°51.47'W, reef flat, under coral rubble, Liu *et al.* coll., 13.10.2001: 2 females, 9.5 mm × 12.1 mm, 12.5 mm × 16.0 mm, photographs GP909: 5–7 and 912: 9–11 (UF 1534).

Society Is., Moorea, offshore between Motu Tiahura and Fareone, outer reef slope, 17.4848°N, 149.9172°W, S. McKeon *et al.* coll., 14.10.2008: 1 ovigerous female, 7.8 mm  $\times$  9.4 mm (UF 15510).



**FIGURE 35.** *Platyozius laevis* (Borradaile, 1902); A, female (11.0 mm  $\times$  14.0 mm) (ZRC 2004.0806), Bohol, Panglao Is., Balicasag I.; B, C, F, male (7.7 mm  $\times$  9.5 mm) (QM W28380), Hawaiian Is., Oahu, Halona Blowhole; D, E male (6.0 mm  $\times$  7.5 mm) (MNHN-B30534), Seychelles; F, female (12.5 mm  $\times$  16.0 mm) (UF 1534), French Polynesia, Tuamotu Archipelago, Rangiroa Atoll. A, frontal view showing orbits and antennae; B, outer surface of left chela; C, third maxillipeds; D, anterior portion of male thoracic sternum and abdomen; E, posterior portion of male thoracic sternum and abdomen; F, male sterno-abdominal cavity, G1, and penis; G, female thoracic sternum and vulvae. Abbreviations: a2, a3 = male abdominal somites 2 and 3, respectively; cx5 = coxa of fifth pereopod (P5); es7 = episternite 7; G1 = first male pleopod; p = penis; s4–s7 = thoracic sternites 4 to 7, respectively; v = vulva.

**Diagnosis.** Anterolateral borders of carapace each with three short, triangular teeth (Figs. 33A–E; 34); postorbital ridge along entire anterior portion of carapace (Fig. 34E); obtuse outer orbital angle (Figs. 34; 35A–C). Dorsal surface of carapace with brightly coloured pattern of irregular lines (Fig. 33).

**Remarks.** Unique among euryplacids is a postorbital ridge that curves along the entire anterior portion of the carapace between the second anterolateral teeth and parallel to the front and orbits of *Platyozius*. In small individuals (e.g. male, 5.5 mm  $\times$  6.9 mm, MNHN-B30779; male, 7.0 mm  $\times$  8.5 mm MNHN-B30780; female, 5.4 mm  $\times$  6.7 mm, MNHN-B30781) the ridge, as well as the third anterolateral teeth, are only slightly evident.

Also diagnostic is the unique colour pattern (Fig. 33). The details of the colour pattern (see below) vary, even among specimens collected from the same locality. This relative variation is not correlated with any morphological differences suggesting that these differences are not species specific.

Other details of the morphology of the species are given in the diagnosis of *Platyozius* (see above) and in Table 1.

*Platyiozius laevis* shows a very wide geographical distribution across the Indo-West Pacific, wider than any known euryplacid. It has been collected from under coral rubble or rocks at low tide in the Maldives, Australia, the Hawaiian Islands, and French Polynesia as well as dredged in water as deep as 200 m.

Colour pattern. The colourful pattern diagnostic of *P. laevis* rapidly disappears in alcohol-preserved specimens. It is still discernible in a photograph of a specimen from the Hawaiian Is. given by Rathbun (1906: pl. 11, fig. 7). A colour photograph of a specimen from the type locality, the Maldives (male,  $6.1 \text{ mm} \times 7.8$ mm; ZRC 2007.0707), shows irregular, red-brown spots and wavy lines across the carapace, an almost continuous, wavy, thin, red-brown band around the anterior and lateral borders of the carapace, and a large irregular spot of the same red-brown colour on the gastric region. There are three red-brown bands across each of the ambulatory legs and one on dactylus of the chelipeds. All carapace and pereopod markings are on a light pink background, except on the anterior half of the carapace, which is yellowish orange. A colour photograph of a specimen from the Ryukyu Is., Japan (Kawamoto & Okuno 2003: 149, as Eucrate sp.) shows an almost identical colour pattern to that of the Maldives specimen. There are variations of this colour pattern, however. A specimen from New Caledonia (male,  $7.0 \text{ mm} \times 8.5 \text{ mm}$ ; MNHN-B30780) shows the dark red-brown pattern across the anterior and anterolateral portions of the carapace and a cross-like pattern along the front, bound by two pink circles. The rest of the carapace and the percopods are pink, with red-brown bands on the ambulatory legs. The colour pattern of two females from French Polynesia (9.5 mm × 12.1 mm, 12.5 mm × 16.0 mm; UF 1534; Fig. 33A, B) is similar to that of the New Caledonia male except that the red-brown markings on the carapace show slightly different patterns, the carapace having an orange background except six greyish spots, the bands on the ambulatory legs thicker and four in number, and there are irregular spots on each of the chelipeds. Specimens from the Northwest Hawaiian Islands (Fig. 33C, E, F) and Vanuatu (Fig. 33D) show an orange or white carapace background and variations in the spotting of the chelipeds and banding of the ambulatory legs.

**Distribution.** Wide distribution across the Indo-West Pacific region: Indian Ocean from Madagascar, Seychelles, the Maldives, and India (unpublished manuscript by M. Deb, Zoological Survey of India); western Pacific from southern Japan to Indonesia (photographic evidence from Sulawesi), New Caledonia, and Queensland, Australia; Micronesia, Marshall Is., Hawaiian Is., and French Polynesia. Depth: intertidal to 200 m.

#### Genus Psopheticoides Sakai, 1969

Psopheticoides Sakai, 1969: 272; 1976: 523 [in key], 528. — Serène & Vadon 1981: 127 [discussion]. - Karasawa & Kato 2003a: 151 [in list]; 2003b: 139 [in list]. — Castro 2007: 618, 620 [discussion]. — Ng & Castro 2007: 44 [in list]. — Ng et al. 2008: 78, 79 [in list]. — De Grave et al. 2009: 33 [in list].

**Diagnosis.** Carapace (Figs. 36A; 39C) trapezoidal, almost as wide as long, dorsal surface smooth without clear indication of regions, large orange-red, circle on cardiac region (remains visible in preserved specimens); anterolateral borders arched; front wide, straight with small median notch (absent in large individuals),

transverse sulcus along margin. Two teeth posterior to triangular outer orbital angle, first short, elongated with rounded outline following arched anterolateral border, second acute, dorsally salient. Orbits long, wide, spherical (Fig. 36B), 2 weak notches on supraorbital border, raised lobe immediately before inner notch; small, low inner suborbital tooth on broad, suborbital border (Fig. 36C); eye peduncles short, large reniform (dorsoventrally flattened) corneas (Fig. 36B, C). Basal antennal article slightly mobile, completely closing orbital hiatus so that antennal flagellum is excluded from orbit (Fig. 36B, C). Anteroexternal margin of third maxilliped merus auriculiform (Fig. 36C). Cheliped fingers (Fig. 36D) stout, slightly longer than swollen propodus, light in colour; carpus with tooth on inner margin, merus with acute anterodorsal tooth; row of short setae along anterior margin of carpus. Dorsal margins of ambulatory legs (P2-P5) meri, carpi, propodi unarmed, dactyli slender, smooth, setose; P5 propodus, dactylus proportionally short, flattened (Fig. 36A), fringed with many short setae. Thoracic sternum (Fig. 36E, G) wide; thoracic suture 2/3 complete, straight (Fig. 36E); 3/4 deep, short, interrupted; 4/5, 6/7, 7/8 interrupted, 5/6 complete (Fig. 36G); median groove on thoracic sternites 7, 8. Sterno-abdominal cavity of male deep, nearly reaching anterior margin of sternite 4 (Fig. 36E). Press-button of male abdominal-locking mechanism as large tubercle near thoracic suture 4/5 (presence in pre-adult females unknown). Male abdomen narrow, slender (T-shaped), lateral margins of somites 4-6 abruptly narrowing from somite 3 to transversely narrow, pointed telson (Fig. 36E); somite 3 reaching inner margins of P5 coxae; no portions of thoracic sternite 8 exposed by closed abdomen, somite 2 transversely slightly shorter than somite 3 (Fig. 36F), somite 1 conspicuous. G1 long, slender, slightly sinuous, arrowhead-shaped apex, relatively large denticles (Fig. 38D, E); G2 less than one-third of G1, straight, apex with 2 processes: one long, tip obtuse; second much shorter, tip obtuse (Fig. 38F). Male genital opening (gonopore) coxal; coxosternal disposition of long penis with greatly expanded proximal portion, protected by concave posterior portion of thoracic sternite 7. Vulva crescent shaped, extending across anterior, median portion of sternite 6 close to median axis of thorax (Fig. 36G); thick, transverse, ventrally projecting sternal vulvar cover on outer margin in large females (Fig. 36G).

Type species. Psopheticoides sanguineus Sakai, 1969 (by original designation, gender masculine).

**Remarks.** The inclusion of the genus in the subfamily Euryplacinae of the Goneplacidae was first suggested (*conduisent à l'inclure*) by Serène & Vadon (1981: 127), although Sakai (1969: 272) had noted the similarities in the male abdomen and gonopods of his new species with those of *Eucrate*. Karasawa & Kato (2003a: 151; 2003b: 139) formally included *Psopheticoides* in the Euryplacinae and ultimately in the Euryplacidae (Castro 2007: 618, 620; Ng *et al.* 2008: 78, 79).

Unusual among euryplacids are the dorsoventrally flattened reniform eyes in this species (Fig. 36B), a character also found in *Frevillea* (Figs. 18E, F; 19A, B) and in some members of the Goneplacidae (Castro 2007). The G1 is unusual in featuring an arrowhead-shaped apex (Fig. 38D, E; Sakai 1969: fig. 17a, a'). Also unusual among euryplacids is the presence of a fully sclerotised sternal vulvar cover (Fig. 36G). *Psopheticoides* shares such a structure with only one euryplacid genus, *Trissoplax* **n. gen.** (Fig. 41G). The typical euryplacid vulva has simple margins and the opening itself is covered by a soft membrane (e.g. Figs. 3G, 19H). The role of such a sclerotised vulvar cover, in goneplacoids remains unknown (see Castro 2007: 755).

Species included. Psopheticoides sanguineus Sakai, 1969

The genus is restricted to the Indo-West Pacific region.

# Psopheticoides sanguineus Sakai, 1969

(Figs. 36A–G; 38D–F; 39C)

Psopheticoides sanguineus Sakai, 1969: 274, figs. 16b, 17a, a', b, 18b, c; 1976: 528, fig. 282, pl. 192, fig. 3 [Japan]. —
Serène & Vadon 1981: 120, 123, 127 [Philippines] — Takeda 1982: 19 [list]; 2001: 248 (as Propheticoides [sic]), 251, 258 [list] [Japan]. — Miyake 1991: 220 [in list] [Japan]. — Castro 2007: 620 [discussion] [Philippines, Tonga] — Ng et al. 2008: 78, fig. 63 [colour photograph] [in list].

Type material. Male holotype (USNM 125888); 1 female paratype (unknown status)

Type locality. Japan, Kyushu, Tosa Bay, off Mimase, 100–150 m.

**Material examined.** *Philippines. Bohol.* Balicasag I., off Panglao I., 200–300 m, tangle nets of local fishermen, 12.2000: 2 females (ZRC 2001.0366); 50–500 m, 28.11.2001: 4 males, 1 female, 2 ovigerous females (ZRC 2001.0539); 200–300 m, 06.2002: 1 male, 1 female (ZRC 2002.0651); 25–30.07.2003: 8 males, 1 female, 17.7 mm  $\times$  22.3 mm (ZRC 2004.0752); 02.03.2004: 2 ovigerous females (ZRC 2004.0713); 11.2003: 1 male, 2 females, 3 ovigerous females (ZRC); 12.2003: 1 male (ZRC 2008.1359); 02.2004: 1 ovigerous female (ZRC 2008.1360); 05.2004: 2 males (ZRC).

Panglao I., Maribojoc Bay, 100–300 m, T. J. Arbasto coll., 11.2003–04.2004: 1 ovigerous female (ZRC 2008.1361); 28.05.2004: 1 male, 21.9 mm  $\times$  27.8 mm (ZRC 2008.1357); 07.2004–05.2005: 1 ovigerous female, 1 female (ZRC 2008.1362).



**FIGURE 36.** *Psopheticoides sanguineus* Sakai, 1969; male (21.3 mm  $\times$  26.5 mm) (ZRC 2004.0752), Philippines, Bohol, Panglao. A, overall view; B, frontal view showing orbits and antennae; C, third maxillipeds; D, outer surface of right chela; E, anterior portion of male thoracic sternum and abdomen; F, posterior portion of male thoracic sternum and abdomen; G. female sternum and vulvae. Abbreviations: a1-a3 = male abdominal somites 1, 2, 3, respectively; cx5 = coxa of fifth pereopod (P5); s4–s7 = thoracic sternites 4 to 8, respectively; vc = sternal vulvar cover.

PANGLAO 2004: stn. P1, Nato coll., 30.05.2004: 1 male, 22.0 mm × 26.7 mm, 1 female, 20.1 mm × 25.3 mm (MNHN-B29728).*Vanuatu.* SANTO 2006: no data: 1 male, 7.8 mm × 9.8 mm (ZRC 2009.0974).

*Tonga*. BORDAU 2: stn. DW 1634, 21°45'S, 175°20'W, 321–322 m, 20.06.2000: incomplete specimen (MNHN-B29808).

Diagnosis. Reniform eyes (Fig. 36B). Orange-red circle on dorsal surface of carapace (Fig. 39C).

**Remarks.** A large but damaged and incomplete specimen from Tonga (MNHN-B29808) clearly shows the characteristic carapace, including the colour spot.

**Colour pattern.** A distinctive orange-red circle fringed by a yellow-white border located on the cardiac region of the carapace (Fig. 39C; Ng *et al.* 2008: fig. 63). The rest of the carapace and the ambulatory legs are orange-red.

Distribution. Western Pacific from Japan to the Philippines, Vanuatu, and Tonga. Depth: 50–322 m.

## Genus Systroplax n. gen.

Carcinoplax — Tesch 1918: 154 (part). — Rathbun, 1914b: 142. — Serène 1968: 89 [in list] (part). — Sakai 1969: 269 (part). — Serène & Lohavanijaya 1973: 62, 63 [key to species] (part). — Guinot 1989: 273 (part). — Chen 1998: 266 [key to species] (part). [not Carcinoplax H. Milne Edwards, 1852]

Diagnosis. Carapace (Fig. 37A) suboctagonal, nearly round; front long, nearly straight (outer edges slightly arched in large individuals), marked by small median notch; transverse sulcus along margin; notch between front, supraorbital border. Orbits short, spherical (Fig. 37B); supraorbital borders short, arched, with 2 notches; suborbital borders arched, 2 very small notches in larger individuals; large, granular, ventrally oriented inner suborbital tooth (Fig. 37B, C); eve peduncles short, granular; large, spherical corneas. Anterolateral borders arched, 2 short, obtuse anterolateral teeth; posterolateral borders long, arched. Dorsal, ventral surface of carapace with short, spherical granules (Fig. 37B, C), strongly convex, without clear indication of regions. Outer orbital angle with very short, triangular tooth; 2 obtuse, small anterolateral teeth on each side of carapace, first larger (much reduced or absent in large individuals, particularly second tooth; Fig. 38I, J). Basal antennal article immobile, with distolateral process so that orbital hiatus is closed excluding antennal flagellum from orbit (Fig. 37B, C). Outer (ventral) surface of third maxilliped carpus, merus granular, anteroexternal margin of merus auriculiform (Fig. 37C). Subhepatic, pterygostomian regions, pterygostomian crest granular. Thoracic sternum (Fig. 37E, G) wide, granular outer margins; thoracic suture 2/3 complete, straight (Fig. 37E, G); 3/4 deep, short, interrupted; 4/5, 5/6, 6/7, 7/8 interrupted (Fig. 37G); median groove on thoracic sternites 7, 8 (Fig. 37G). Sterno-abdominal cavity of male deep, reaching median portion of sternite 4 (Fig. 37E). Press-button of male abdominal-locking mechanism as tubercle near thoracic suture 4/5 (presence in pre-adult females unknown). Anteroexternal margin of third maxilliped merus auriculiform. Cheliped (P1) propodus, carpus, merus granular (inner surface of propodus relatively smooth); fingers moderately stout, slightly shorter than swollen propodus, tips darker in colour (Fig. 37D). Carpus with long, blunt tooth on distal, inner margin; merus with large, blunt tooth on inner surface near anterior margin. Dorsal margins of ambulatory legs (P2–P5) meri, carpi, propodi unarmed, dactyli slender, smooth, setose; P5 dactyli, propodi proportionally short, flattened, fringed with scattered, long setae, spines. Male abdomen narrow, slender (Tshaped), lateral margins of somites 4-6 abruptly narrowing from somite 3 to transversely narrow, pointed telson (Fig. 37E); somite 3 reaching inner margins of P5 coxae, outer end fitting under episternite 7; somite 2 transversely shorter than somite 3 but no portions of thoracic sternite 8 exposed by closed abdomen (Fig. 37F). G1 long, slender, slightly sinuous, acuminate apex, with small denticles (Fig. 38G). G2 less than onethird of G1, straight, with 2 processes: one long, tip acute; second much shorter, small, lobe-like (Fig. 38H). Male genital opening (gonopore) coxal; coxo-sternal disposition of long penis with very broad, soft proximal expansion, protected by concave posterior portion of thoracic sternite 7. Female abdomen relatively narrow, not covering outer portions of thoracic sternum, with six freely-mobile somites. Telson broadly triangular, wider than long. Somites 1, 2 cover space between P5 coxae, only small portion of each P5 condyle of sternite 8 left exposed by closed abdomen (Fig. 37F). Vulva of mature females ovoid, extending across median portion of thoracic sternite 6 close to median axis of thorax (Fig. 37G); covered by soft membrane, sternal vulvar cover absent.



**FIGURE 37.** *Systroplax angusta* (Rathbun, 1914); A–C, G, female (27.8 mm  $\times$  31.4 mm) (MNHN-B29377), Fiji; D–F, male (32.3 mm  $\times$  37.2 mm) (MNHN-B29377), Fiji. A, overall view; B, frontal view showing orbits and antennae; C, third maxillipeds; D, outer surface of left chela; E, anterior portion of male thoracic sternum and abdomen; F, posterior portion of male thoracic sternum and abdomen; female sternum and vulvae; G, female sternum and vulvae. Abbreviations: a1-a3 = male abdominal somites 1, 2, 3, respectively; cx5 = coxa of fifth pereopod (P5); es7 = episternite 7; mg = median groove; s4–s7 = thoracic sternites 4 to 8, respectively; v = vulva.

Type species. Carcinoplax angusta Rathbun, 1914 (by present designation, gender feminine).

**Etymology.** From *systremma*, Greek for anything aggregated, generally a ball or round object, in reference to the diagnostic round shape of the carapace of the type species, and *plax*, Greek for "plate" or "tablet", which is derived from the generic name *Carcinoplax* (from *karkinos*, Greek for crab), to denote that the species included in the new genus was formerly included in the latter.

**Remarks.** Although the carapace shape is superficially similar to two species assigned to the family Goneplacidae *sensu stricto* (i.e. *Carcinoplax tenuidentata* Castro, 2007, and *Pycnoplax bispinosa* (Rathbun,

1914); Castro 2007: figs. 5, 13B), *Systroplax* **n. gen.** clearly belongs to the Euryplacidae (Castro 2007: 623). The male abdomen is slender, with a narrow and pointed telson (Fig. 37E), and the G1, also slender, is much longer than the G2. Although the shape of the abdomen of goneplacids varies, it is typically broad and triangular and a similarly shaped telson (i.e. Castro 2007: figs. 4B, 16B), never narrow as in the Euryplacidae. The G1 in *Carcinoplax* H. Milne Edwards, 1852, is never as slender as in euryplacids and the apex is much wider, never acuminate (e.g. Castro 2007: fig. 2), or thick and stout as in *Pycnoplax* Castro, 2007 (e.g. Castro 2007: fig. 16C). A G2 much shorter than the G1, however, is present in three goneplacid genera (Castro 2007). The vulva of *Systroplax* **n. gen.** is typical of euryplacids, relatively small with thick margins and no sternal vulvar cover, in contrast to the much expanded vulva of *Carcinoplax* (e.g. Castro 2007: fig. 1), or the vulva covered by a sternal vulvar cover of *Pycnoplax* (e.g. Castro 2007: fig. 15).

In contrast to most euryplacids, thoracic suture 5/6 is interrupted, a character nevertheless shared with *Nancyplax* and *Xenocrate* (Table 1).

### Species included. Systroplax angusta (Rathbun, 1914)

The genus is restricted to the Indo-West Pacific region.

### Systroplax angusta (Rathbun, 1914)

(Figs. 37A–G; 38G–J)

*Carcinoplax angusta* Rathbun, 1914b: 142 [Philippines]. — Tesch 1918: 154 [in list]. — Estampador 1937: 533 [in list]; 1959: 89 [in list] [Philippines]. — Serène 1968: 90 [in list]. — Sakai 1969: 269 [in list], fig. 15b [holotype]. — Zarenkov 1972: 241, fig. 4–4, 6–4 [South China Sea]. — Serène & Lohavanijaya 1973: 62 [in list], 64 [in key]. — Guinot 1989: 309 [discussion], fig. 39, pl. 12, figs. A–E [holotype]. — Castro 2007: 623, 624 [discussion]. — Yang *et al.* 2008: 770 [in list] [China].

Carcinoplax angustata [sic] — Chen 1998: 266 [in key], 273, 310 [in list], fig. 6 [South China Sea].

"Carcinoplax" angusta — Ng et al. 2008: 79 [in list].

(?) Carcinoplax cf. angusta — Naderloo & Sari 2007: 344, 335, 347 [Persian Gulf].

**Type material.** Female holotype, 23.7 mm  $\times$  26.9 mm; 1 male paratype, 10 mm  $\times$  10.8 mm (USNM 46166).

**Type locality.** Philippines, Verde Island Passage between Luzon and Mindoro, *Albatross*, stn. 5376, 13°42.8'S, 121°51.5'E, 165 m.

Material examined. *South China Sea. Dampier*, stn. DD19, 05°26.0'S, 111°13.5'E, 210–201 m, 1963: 1 female (NHM).

*Philippines. Verde Island Passage. Albatross*, stn. 5376, 13°42.8'S, 121°51.5'E, 165 m, 02.03.1909: female holotype (USNM 46166).

Solomon Is. SALOMON 2: stn. CP 2284, 8°38,4' S , 157°21,5' E, 195–197 m, 06.11.2004: 2 males, 10.7 mm  $\times$  11.8 mm, 8.3 mm  $\times$  8.8 mm (MNHN-B30100). – No stn. no. : 1 female, 14.6 mm  $\times$  16.5 mm (MNHN-B30074).

*Vanuatu*. MUSORSTOM 8: stn. CP 1117, 15°09.91'S, 166°53.37'E, 170–220 m, 09.10.1994: 1 male (MNHN-B29404). – Stn. CP 1123, 15°07.19'S, 166°55.20'E, 262–552 m, 09.10.1994: 2 males, 28.0 mm × 31.6 mm, 18.9 mm × 21.4 mm (MNHN-B29402).

BOA1: stn. CP22447, 15°07.20'S, 166°52.0'E, 10.09.2005: 1 male, 27.8 mm × 31.1 mm (MNHN-B30135). *Fiji*. MUSORSTOM 10: stn. CAS 1321, 17°17.3'S, 177°47.7'E, 200 m, 07.08, 1998: 1 male, 32.3 mm × 37.2 mm, 1 female 27.8 mm × 31.4 mm (MNHN-B29377). – Stn. CP 1322, 17°17.1'S, 177°47.9'E, 210–282 m, 07.08, 1998: 1 male, 22.1 mm × 24.6 mm (MNHN-B29378). – Stn. CP 1328, 17°16.8'S, 177°50.4'E, 248–277 m, 07.08.1998: 1 male (MNHN-B29488).

BORDAU 1: stn. CP 1403, 16°40'S, 179°36'E, 220–224 m, 25.02.1999: 2 males, 19.9 mm  $\times$  22.5 mm, 13.5 mm  $\times$  14.8 mm (MNHN-B29470); 1 pre-adult male, cl 9.9 mm [rest of carapace damaged] (MNHN-B29489).

**Diagnosis.** Carapace suboctagonal, almost round, granular, with two short teeth on each anterolateral border (Fig. 37A).



**FIGURE 38.** Gonopods of *Platyozius, Psopheticoides*, and *Systroplax*; carapace of *Systroplax*. A–C, *Platyozius laevis* (Borradaile, 1902), male (6.1 mm × 7.8 mm) (ZRC 2007.0707), Maldives, Laamu Atoll; D–F, *Psopheticoides sanguineus* Sakai, 1969, male (21.9 mm × 27.8 mm) (ZRC 2008.1357), Philippines, Bohol, Balicasag I.; G–J, *Systroplax angusta* (Rathbun, 1914); G, G1 (after Guinot 1989: fig. 39D); H, male (32.3 mm × 37.2 mm) (MNHN-B29377), Fiji; I, J, variation in anterolateral borders of carapace (after Guinot 1989: fig. 39A, C). A, B, D, E, right G1, dorsal view; C, F, H, right G2, dorsal view. Scale bars: A, D, 1.0 mm; B, E, 0.5 mm; C, F, H, 0.2 mm; G, 0.1 mm.

**Remarks.** *Carcinoplax angusta* Rathbun, 1914, was described from two specimens from the Philippines, the female holotype (23.8 mm  $\times$  27.6 mm, USNM 46166) and a pre-adult male (10 mm  $\times$  10.8 mm, same catalogue number). Most of the characters that separate this species from *Carcinoplax sensu stricto* were nevertheless clearly listed by Rathbun (1914b: 142) and discussed by Castro (2007: 624), who formally placed the species "in a yet undescribed genus in the family Euryplacidae" (Castro 2007: 623). These characters, plus the very slender G1 of relatively small specimens, were illustrated by Zarenkov (1972: figs. 4–4, 6–4, as *C. angusta*), and particularly Chen (1998: fig. 6, as *C. angustata* [sic]), who also showed the short G2.

In large specimens (e.g. male, 22.1 mm  $\times$  24.6 mm, MNHN-B29378; male, 27.8 mm  $\times$  31.1 mm, MNHN-B30135) the second anterolateral tooth is hardly noticeable (Fig. 38I, J).



**FIGURE 39.** Colours in life. A, *Euryplax nitida* Stimpson, 1871; male neotype (7.1 mm × 11.3 mm) (UF 15166), Gulf of Mexico; B, *Euryplax nitida* Stimpson, 1871; male (4.4 mm × 7.0 mm) (UF 15168), Gulf of Mexico; C, *Psopheticoides sanguineus* Sakai, 1969, male (22.2 mm × 26.7 mm) (MNHN-B29728), Philippines, Bohol, Panglao; D, *Trissoplax dentata* (Stimpson, 1858), male (6.2 mm × 8.3 mm) (NHM), Thailand, Andaman Sea; E, *Trissoplax dentata* (Stimpson, 1858), young male, not preserved, Singapore, Changi; F, *Trissoplax dentata* (Stimpson, 1858), female (8.7 mm × 11.5 mm) (ZRC 2000.2240), Singapore. Photo credits: A, B by Florida Museum of Natural History (UF); D by P. F. Clark (NHM).

**Distribution.** Southwestern Pacific from the South China Sea to Fiji. A record from the Persian Gulf (Naderloo & Sari 2007; as *Carcinoplax angusta*) is highly questionable. Depth: 165–282 m (also from a station at depths of 226-552 m).

## Genus Trissoplax n. gen.

Heteroplax Stimpson, 1858: 94 (40); 1907: 94 [diagnosis] (part). — Balss 1922a: 136 [list of species] (part). — Campbell 1969: 117 (part). — Guinot 1969b: 511 [discussion] (part). — Serène & Lohavanijaya 1973: 71 [discussion] (part). — Ng et al. 2008: 78, 79 [discussion] (part).

**Diagnosis.** Carapace (Figs. 39D–F; 40A–E; 42A) hexagonal, transversely elongated, wider than long, convex; anterolateral borders nearly straight, only slightly arched in small individuals, progressively arched with increasing carapace size in T. dentata; dorsal surface smooth without clear indication of regions (larger individuals of T. dentata with short sulcus on each branchial region extending laterally from third anterolateral tooth, short elongated boss on each branchial region near second anterolateral tooth); front wide, straight with median notch, transverse sulcus along margin (continuing as a short vertical groove in large individuals of T. *dentata*). Three anterolateral teeth (first triangular, obtuse; second acute, dorsally salient [particularly in T. *dentata*]; third small, obtuse) posterior to triangular, anteriorly-oriented outer orbital angle (variations in Tirmizi & Ghani 1988: fig. 3A-G'; 1996: fig. 30A-G', as E. haswelli). Orbits moderately long, about as long as front (Fig. 41B), sinuous to slightly sinuous, one notch on inner third portion of thin to thick supraorbital border (second notch on outer portion more noticeable in larger individuals of T. dentata); triangular inner suborbital tooth, short median lobe, outer notch on thick suborbital border (Fig. 41A, B) (suborbital border sinuous, granular, without inner suborbital tooth or median lobe in T. tuberosa n. sp.; Fig. 42E); eye peduncles moderately long, nearly half of frontal width, much longer than large, slightly elongated corneas (Figs. 41A, B; 42E). Basal antennal article immobile (slightly mobile in small specimens), with small disto-lateral process so that orbital hiatus is closed excluding antennal flagellum from orbit (Fig. 41A, B; Campbell 1969: fig. 3E, as E. affinis; fig. 5D, as E. haswelli; Yang & Sun 1979: fig. 3-1, as Eucrate costata). Anteroexternal margin of third maxilliped merus angular (Fig. 41A). Cheliped fingers moderately stout, slightly longer than swollen propodus, light in colour (Figs. 41E; 42E); carpus with tooth on inner margin; dense tomentum consisting of plumose setae on anterior margin of carpus (Figs. 40A, C, E; 41E) (clumps of plumose setae in T. tuberosa n. sp.; smallest individuals of T. dentata). Dorsal margins of ambulatory legs (P2-P5) meri, carpi, propodi unarmed, dactyli slender, smooth, setose; P5 propodus long, slender, subcylindrical, fringed with many long setae (Campbell 1969: fig. 3I, as E. affinis; fig. 5E, as E. haswelli). Thoracic sternum (Fig. 41C, F, G) wide, thoracic suture 2/3 complete, convex (Figs. 41C; 42C); 3/4 deep, short, interrupted; 4/5, 6/7, 7/8 interrupted, 5/6 complete (Fig. 41G); median groove on thoracic sternites 7, 8. Sterno-abdominal cavity of male deep, only reaching median portion of sternite 4. Press-button of male abdominal-locking mechanism as small tubercle near thoracic suture 4/5 (small tubercle present in pre-adult females). Male abdomen narrow, slender, transversely narrow (T-shaped), lateral margins of somites 4–6 abruptly narrowing from somite 3 to transversely narrow, pointed telson (Figs. 41D; 42C); somite 3 reaching inner margins of P5 coxae, somite 2 transversely slightly shorter or as long as somite 3; no portions of thoracic 8 exposed by closed abdomen or small portion of each side exposed (T. tuberosa n. sp.). G1 long, slender, slightly sinuous to nearly straight, acuminate apex, with small denticles (Figs. 41F; 43A, B, D, E); G2 less than one-third of G1, straight, apex with 2 processes: one long, tip acute; second much shorter, tip acute (Fig. 43C, F). Male genital opening (gonopore) coxal; coxo-sternal disposition of long penis (Fig. 41F), protected by concave posterior portion of thoracic sternite 7. Female abdomen relatively narrow, not covering outer portions of thoracic sternum, with 6 freely-mobile somites (Serène & Lohavanijaya 1973: fig. 179, as Heteroplax dentatus, fig. 184, as H. transversus; Tirmizi & Ghani 1988: fig. 3H; 1996: fig. 30H, as E. haswelli). Vulva ovoid, extending transversely across anterior portion of sternite 6 close to median axis of thorax; short, transverse, triangular sternal vulvar cover on posterior margin (Fig. 41G).

Type species. Heteroplax dentata Stimpson, 1858 (by present designation, gender feminine).

**Etymology.** From the Greek *trissos* for "threesome", in reference to the three conspicuous teeth (the outer orbital tooth and the first two anterolateral teeth) on each side of the carapace, which is characteristic of the new genus, and *plax*, Greek for "plate" or "tablet", which is derived from the generic name *Heteroplax* to denote that the type species of the new genus was formerly included in *Heteroplax sensu lato*.

**Remarks.** Stimpson (1858: 94 (40); 1907: 94) described two species of *Heteroplax* from or near Hong Kong, *H. transversa* and *H. dentata*, but his descriptions were brief, no illustrations were given, and the type material of both species is presumably lost (see Evans 1967; Deiss & Manning 1981; Manning 1993; Manning & Reed 2006). A specimen from the type locality that closely follows Stimpson's description of *H. transversa* has been selected as its neotype and the genus *Heteroplax* Stimpson 1858, is being re-described herein, with *H. transversa* as its only species, *H. nagasakiensis* Sakai, 1934, being a junior synonym (see above).

*Trissoplax* **n. gen.** is described herein for the second of Stimpson's (1858) Hong Kong species, *H. dentata*. Stimpson compared his two new species, describing *H. dentata* as having a "carapax narrow" in contrast to the "much broader carapax" of *H. transversa*. Indeed, the Hong Kong male specimen herein selected as the neotype of *H. dentata* Stimpson, 1858 (16.4 mm  $\times$  21.5 mm; QM W27400), the type species of *Trissoplax* **n. gen.** (see below), has a much narrower carapace than *H. transversa*. Whereas the carapace-length to carapace-width ratio of *H. transversa* given by Stimpson is 1:1.5 (1:1.6 ratio for the neotype and other Hong Kong specimens; see above), the ratio given by Stimpson for his *H. dentata* is 1:1.27 (1: 1.3 for the neotype and additional Hong Kong specimens listed here; 1:1.3–1.4 for specimens from other locations). A second species of *Trissoplax* **n. gen.** being described as new, *T. tuberosa* **n. sp.**, also has a narrow carapace (1:1.3 in the holotype, see below).

Stimpson (1858: 94 (40); 1907: 94, 95) mentioned three additional characters in contrasting between the two species. One was the presence in his *H. dentata* of "four unequal teeth" (including the outer orbital tooth) in contrast to only two teeth that were described posterior to the outer orbital tooth in *T. transversa*, the third always being very small so that Stimpson possibly overlooked it. A third difference was the presence of "a tuft of pubescence" in *H. dentata*, which he did not mention for *H. transversa*, a character that is found in the neotype and all the remaining specimens of *T. dentata* that were examined except the pre-adults. A final difference was in the length of the eye peduncles, being proportionately longer in *H. transversa* than in *H. dentata*. Alcock (1900), Balss (1922b), and Guinot (1969) commented on the obvious affinities between Stimpson's *H. dentata* and *Eucrate*. In fact, Alcock (1900: 299, 301) erroneously regarded *H. dentata* as a subspecies of *Eucrate crenata*, although large specimens of both species may be confused (see Remarks for *H. dentata* below). *Eucrate* is clearly different from both *Heteroplax* and *Trissoplax* **n. gen.** (Table 1) but the confusion unfortunately developed as a result of authors only relying on the short description with no illustrations and, most probably, the absence of specimens of Stimpson's *H. dentata*. Specimens from other localities were described as new species, thus adding to the confusion (see Remarks for *H. dentata* below).

The most obvious difference between *Trissoplax* **n**. gen. and *Eucrate* is that in *Eucrate* the carapace is trapezoidal and with relatively short orbits and eye peduncles (e.g. Fig. 3B), whereas in *Trissoplax* **n**. gen. (as in *Heteroplax*) the carapace is slightly more elongated and with longer orbits and eye peduncles (e.g. Fig. 41B) (see Table 1). The anterolateral borders of the carapace of *T. dentata* nevertheless become arched with increasing size and as such they may be superficially similar to large individuals of *Eucrate* species. These large specimens of *Eucrate* can still be easily distinguished from *T. dentata* in having proportionately much longer eye peduncles and orbits, a higher and more conspicuous inner suborbital tooth, and thinner orbital margins than in *Eucrate*. Both *Eucrate* and *Trissoplax* **n**. gen., however, share the presence of a conspicuous setous patches along the anterior margin of the cheliped carpus, which is absent in *Heteroplax*.

#### Species included.

Trissoplax dentata (Stimpson, 1858)

- = Eucrate affinis Haswell, 1882
- = Pseudorhombila sulcatifrons var. australiensis Miers, 1884
- = Eucrate haswelli Campbell 1969
- = Eucrate costata Yang & Sun 1979

Trissoplax tuberosa **n. sp.** 

The genus is restricted to the Indo-West Pacific region.

#### Trissoplax dentata (Stimpson, 1858), new combination

(Figs. 39D–F; 40A–F; 41A–G; 43A–C)

- Heteroplax dentata Stimpson, 1858: 94 (40); 1907: 94 [China]. Balss 1922a: 137 [in list]. Guinot 1969b: 511 [in list]. Dai et al. 1986: 371, fig. 194 [China]. Dai & Yang 1991: 400, fig. 194 [China]. Naiyanetr 1998: 78; 2007: 90 [Andaman Sea coast of Thailand]. Ng et al. 2008: 78, 79 [in list]. Yang et al. 2008: 770 [in list] [China]. Clark et al. 2008: 52 [western Thailand].
- Eucrate affinis Haswell, 1882a: 547; 1882b: 86 [Australia]. Stebbing 1920a: 238; 1921b: p. 458, pl. 15 (110) [South Africa]. Campbell 1969: 118 [in key], 122, figs. 2, 3 [Australia]. Guinot 1971: 1080 [in list]. Springthorpe & Lowry 1994: 92 [type material]. Davie 2002: 198 [fig.], 199. Thoma 2007: 299 [Western Australia.] Hutchins & Gomez 2007: 331 [in list] [Western Australia]. Ng et al. 2008: 78 [in list].
- Pseudorhombila sulcatifrons var. australiensis Miers, 1884: 242, pl. 24, fig. C, c [Australia].
- (?) Eucrate affinis De Man 1887: 89, pl. 5, figs. 5–7 [Myanmar = Burma].
- Heteroplax dentatus Walker 1887: 110 [in list] [Singapore].
- (?) Eucrate crenata var. affinis Alcock 1900: 299 [in key], 300.
- Eucrate crenata var. dentata Nobili 1906b: 297 [Gulf of Aden].
- Eucrate crenata dentata Chhapgar 1957: 437, pl. 11, fig. j-l. [west coast of India].
- not *Eucrate crenata* var. *dentata* Alcock 1900: 299 [in key], 301 [India, Hong Kong]. Sankarankutty 1966: 350 [in list] [India] (? = *Eucrate alcocki* Serène, in Serène & Lohavanijaya, 1973; *E. indica* **n. sp.**)
- not Heteroplax dentata Rathbun 1910: 342 [Gulf of Thailand]. [not Trissoplax dentata (Stimpson, 1858)]
- Eucrate dentata Tesch 1918: 158 [in key, footnote]. Campbell 1969: 119 [in key], 132 [discussion].
- Eucrate sulcatifrons Stephensen 1946: 167, fig. 45 A, B [Persian Gulf].
- not *Eucrate sulcatifrons* —Barnard 1950: 282 [in key], 295, fig. 54 d, e. [not *Eucrate sulcatifrons* Stimpson, 1858 = *Eucrate crenata* (De Haan, 1835)]
- *Eucrate haswelli* Campbell 1969: 119 [in key], 130, figs. 2, 5 [Australia]. Guinot 1971: 1080 [in list]. Tirmizi & Ghani 1988: 139, figs. 2, 3; 1996: 77 [in key], 77, figs. 29, 30 [Pakistan]. Springthorpe & Lowry 1994: 101 [type material]. Davie 2002: 199 [in list]. Apel 2001: 102 [Persian Gulf]. Ng *et al.* 2008: 78 [in list]. Naderloo & Sari 2007: 344, 347 [Persian Gulf]. Yang *et al.* 2008: 770 [in list] [China].
- not "? *Heteroplax dentatus*" Serène & Lohavanijaya 1973: 73, 98, figs. 178–182, pl. 17, figs. A-D [Philippines]. [not *Trissoplax dentata* (Stimpson, 1858) = *Heteroplax tuberosa* **n. sp**]
- Heteroplax transversus Serène & Lohavanijaya 1973: 72 [in key], 73, 98, figs. 183, 184, pl. 18, fig. A [Gulf of Thailand].

*Eucrate costata* Yang & Sun 1979: 4, 10, fig. 3, plate, figs. 5, 6, 9 [China]. — Dai & Yang 1991: 401 [in key], 404, fig. 197(1), pl. 54, fig. 5 [China]. — Ng *et al.* 2008: 78 [in list]. — Yang *et al.* 2008: 770 [in list] [China].

Type material of Heteroplax dentata Stimpson 1858, lost.

Type locality. "among the islands on the coast of China near Hong Kong", "shelly bottoms, in 10–15 fath-oms" (18–27 m).

Neotype (see Remarks below): male, 16.4 mm  $\times$  21.5 mm (QM W27400) (Figs. 40A; 41); type locality. Hong Kong, New Territories, Tolo Harbour, stn. 64, 22°45'N, 114°20'E.

**Type material of** *Eucrate affinis* **Haswell, 1882,** dry male lectotype, 6.6 mm  $\times$  8.7 mm, 1 dry female paralectotype (AM P2972) (Fig. 40D), designated by B. M. Campbell; type locality: Australia, Port Denison, off Holborn I., 36 m (see Springthorpe & Lowry 1994: 92).

**Type material of** *Pseudorhombila sulcatifrons* **var.** *australiensis* **Miers, 1884,** pre-adult female holotype, 8.4 mm  $\times$  6.0 mm (NHM 1882.93) (Fig. 40F); type locality: Australia, Port Molle, 26 m, HMS *Alert*.

**Type material of** *Eucrate haswelli* **Campbell, 1969,** male holotype, 15.0 mm × 19.5 mm (AM P6991) (Fig. 40B); type locality: Australia, Queensland, Port Denison, intertidal (see Springthorpe & Lowry 1994: 101).

**Type material of** *Eucrate costata* **Yang & Sun 1979,** male holotype (BMNH J79149), 1 male paratype, 25.0 mm × 19.0 mm (BMNH J79140) (Fig. 40E); type locality: China, Fujian Province, Dongshan.

**Material examined.** *Gulf of Aden. Djibouti*, F. P. Jousseaume coll., 1897, id. as "*Eucrate crenata* var. *dentata* Stm" by G. Nobili, 1905: 2 females (MNHN-B12514).

*Persian Gulf.* Det. as *E.* aff. *haswelli* by M. Apel, 2 males, cl 6.5 [rest of carapace damaged], 8.1 mm  $\times$  11.4 mm, 2 females 6.5 mm  $\times$  9.2 mm, 6.7 mm  $\times$  9.3 mm, 1 ovigerous female, 7.7 mm  $\times$  10.6 mm (MNHN-B12513).

*Pakistan.* Korangi Creek, south of Karachi, N.M. Tirmizi leg., 15.03.1992: 2 males, 15.0 mm  $\times$  19.5 mm, 15.5 mm  $\times$  20.9 mm, 1 female, 14.9 mm  $\times$  19.9 mm (RMNH D46768).

(?) *India*. Leg. Marine Research Station, Ratnagiri, jetty Mirya: 1 female [incomplete], 17.9 mm × 23.0 mm (MNHN-B10559).

*Thailand*. Andaman Sea coast, Ranong, stn. 126, offshore, TILS project, P. Clark coll., 29.11.2007: 1 male,  $6.2 \text{ mm} \times 8.3 \text{ mm}$  (NHM).

China. Amoy, 07.1932, leg. National Wu-Han University, no. 80: 1 female, 16.1 mm  $\times$  20.6 mm (MNHN-B10149).

*Hong Kong.* Unknown locations, T49, sp. 38, 1992: 1 ovigerous female, 14.8 mm  $\times$  19.0 mm (SWIMS CRU-P12-015); T4/2, sp. 46: 1 female, 13.7 mm  $\times$  18.4 mm (SWIMS); T10, sp. 60: 3 males, 1 female (SWIMS CRU-92-011); 1 male (SWIMS CRU-92-049). – New Territories, Tolo Harbour, 22°45'N, 114°20'E, stn. 64, P. Davie coll.: male neotype (here designated), 16.4 mm  $\times$  21.5 mm (QM W27400). – GO 788, 5A: 1 male, 3.1 mm  $\times$  4.1 mm, 1 male, 3.8 mm  $\times$  4.9 mm (QM W28382).

*Thailand*. Gulf of Thailand, off Pattaya, L. B. Holthuis & P. K. L. Ng coll., 25.12.1991: 2 males, 4.6 mm  $\times$  6.4 mm, 6.9 mm  $\times$  9.6 mm (ZRC 1992.10297–10298).

Gulf of Thailand, stn. GVF 53, channel between Songkhla and Ko Nu I.,  $07^{\circ}14$ 'N,  $100^{\circ}36$ 'E, 03.11.1957: 1 ovigerous female, 7.3 mm × 9.1 mm (ex USNM access no. 230087, MNHN-B24502).

*Singapore*. Southern islands, 1992: 1 male, 15.2 mm × 19.4 mm (ZRC 1992.7922).

Tuas Basin, P. K. L. Ng et al. coll., 15.01.1994: 1 pre-adult male, 3.5 mm  $\times$  4.9 mm, 2 males, 5.6 mm  $\times$ 

7.3 mm, 6.5 mm  $\times$  8.8 mm, 1 pre-adult female, 5.7 mm  $\times$  7.5 mm, 3 females, 5.9 mm  $\times$  8.3 mm, 6.5 mm  $\times$  8.4 mm, 8.7 mm  $\times$  11.5 mm (ZRC 2000.2240).

Off Changi, dredging, P. K. L. Ng coll., 17.12.1998: 1 female, 7.7 mm  $\times$  10.6 mm (ZRC 1998.1231). – Changi Beach, beach seine, P. K. L. Ng coll., 02.04.2003: 1 male, 6.9 mm  $\times$  9.1 mm (ZRC 2004.0758).

SAF jetty, Changi Point, washed dead on shore, Chan S. Y. coll., 11.03.2005: 2 males, 20.0 mm  $\times$  26.2 mm, 21.5 mm  $\times$  28.9 mm (ZRC 2008.1236).

Semekau, H. H. Tan coll., 18.02.2009: 1 female (ZRC 2009.0048).

Unknown location, J. C. Y. Lai coll., 15.09.07: 1 male, 14.1 mm × 18.4 mm (ZRC 2009.0375).

Indonesia. Kai Is. Danish Kai Expedition, stn. 116, 05°57" S, 136°34"E, 22 m, 07.08.1922, id. as *Heteroplax dentata* by T. Odhner, 1924: 1 female (ZMUC CRU-1519).

*Australia*. Queensland, Port Denison, intertidal: male holotype of *Eucrate haswelli* Campbell, 1969, 15.0  $\text{mm} \times 19.5 \text{ mm}$  (AM P6991).

Queensland, Port Molle, HMS *Alert*, 26 m, 1882: pre-adult female holotype of *Pseudorhombila sulcatifrons* var. *australiensis* Miers, 1884, 8.4 mm × 6 mm (NHM 1882.93).

"*Eastern Seas*". Identified as "*Pilumnoplax sulcatifrons*": 2 males, 9.4 mm  $\times$  7.5 mm, 8.9 mm  $\times$  6.8 mm (NHM 1847.21).

Unknown location. Loc. 0047, stn. 003-5, 17.02.1983: 2 males, 3 pre-adult females, 3 females (LACM).

**Diagnosis.** Suborbital border with triangular inner suborbital tooth, short median lobe (Fig. 41A, B). Conspicuous tomentum on chelipeds (Fig. 39D–F; 40A–C, E; 41E). Smooth chelipeds, without tubercles (Fig. 41E).

**Remarks**. The status of *H. dentata*, one of the two species of *Heteroplax sensu lato* described by Stimpson (1858) from Hong Kong, had remained problematic until now. The clarification of Stimpson's (1858) description (see Remarks for *Trissoplax* **n. gen.**) and the designation of a neotype (see below) now permits settling the status of several other species that were described by other authors who were not aware of the real identity of Stimpson's *H. dentata*, or even the case where a new species was not recognized because both of Stimpson's species were confused with each other. Nevertheless, authors such as Walker (1887), Nobili

B

(1906), and T. Odhner (see Material examined above) correctly identified their material as belonging to Stimpson's species.

**FIGURE 40.** *Trissoplax dentata* (Stimpson, 1858); A, male neotype of *Heteroplax dentatus* Stimpson, 1858 (16.4 mm × 21.5 mm) (QM W27400), Hong Kong, Tolo Harbour; B, male holotype of *Eucrate haswelli* Campbell, 1969 (15.0 mm × 19.5 mm) (AM P6991), Australia, Queensland, Port Denison; C, male (20.0 mm × 26.2 mm) (ZRC 2008.1236), Singapore, Changi Point; D, male lectotype of *Eucrate affinis* Haswell, 1882 (6.6 mm × 8.7 mm) (AM P2972), Australia, Queensland, Port Denison; E, male paratype of *Eucrate costata* Yang & Sun, 1979 (25.0 mm × 19.0 mm) (BMNH J79140), China, Dongshan, Fujian Province; F, pre-adult female holotype of *Pseudorhombila sulcatifrons* var. *australiensis* Miers, 1884 (8.4 mm × 6.0 mm) (NHM 1882.93), Australia, Queensland, Port Molle. A–C, E, F, overall views; D, dorsal view of carapace. Photo credits: D by R.T. Springthorpe © (AM), F by P. Crabb (NHM).

A series of seven specimens from Singapore (ZRC 2000.2240) ranging from a pre-adult male (3.5 mm  $\times$  4.9 mm) to an adult female (8.7 mm  $\times$  11.5 mm), plus additional specimens of various sizes from other locations, drew light on the ontogeny of the diagnostic characters of *T. dentata*. The smallest pre-adult male barely shows a third anterolateral tooth, only a short tubercle, and, as in the remaining small individuals, does not show the characteristic tomentum on the distal margin of the cheliped carpi, only many short plumose setae that increase in number with carapace size. The short tufts of setae of two pre-adult Hong Kong specimens (3.1 mm  $\times$  4.1 mm, 3.8 mm  $\times$  4.9 mm; QM W28382) do indeed correspond to Stimpson's "tuft of pubes-

cence". Another character, the shape of the anterolateral borders of the carapace, changes from being almost parallel to each other in small individuals (Fig. 39D–F) to arched in the largest ones (Fig. 40A–E).



**FIGURE 41.** *Trissoplax dentata* (Stimpson, 1858); A–D, F, male neotype of *Heteroplax dentatus* Stimpson, 1858 (16.4 mm  $\times$  21.5 mm) (QM W27400), Hong Kong, Tolo Harbour; E, male (20.0 mm  $\times$  26.2 mm), Singapore, Changi Point; G, female (8.7 mm  $\times$  11.5 mm) (ZRC 2000.2240) (ZRC 2008.1236), Singapore. A, frontal view showing third maxillipeds; B, frontal view showing orbits and antennae; C, anterior portion of male thoracic sternum; D, posterior portion of male thoracic sternum and abdomen; E, outer surface of right chela; F, male sterno-abdominal cavity, G1 and penis; G, female thoracic sternum and vulvae. Abbreviations: a1–a3 = male abdominal somites 1, 2, 3, respectively; cx5 = coxa of fifth pereopod (P5); es7 = episternite 7; G1 = first male pleopod; G2 = second male pleopod; mg = median groove; p = penis; s4–s7 = thoracic sternites 4 to 7, respectively; vc = sternal vulvar cover.

The carapace and single cheliped of two pre-adult males (3.1 mm  $\times$  4.1 mm, 3.8 mm  $\times$  4.9 mm; QM W28382) from Hong Kong also agree with Stimpson's (1858) description of *H. dentata*. The smallest specimen, however, lacks the third anterolateral tooth, which was described (Stimpson 1907: 94) as "inconspicuous, formed only by a slight emargination". The only available cheliped has a short tuft of setae on the distal margin of the carpus.

The many specimens examined agree with the characters given in Stimpson's description of his Hong Kong specimens. An exception is the presence of a median notch in the front. It was indicated as absent in Stimpson's material (Stimpson 1907: 94) but this character may have been missed as the notch is small and may be obscured by sediment.

Eucrate affinis Haswell, 1882, described from Queensland, Australia (Haswell, 1882a: 547; 1882b: 86), was among the species of *Eucrate* revised by Campbell (1969: 118, 122, fig. 3). Campbell's illustrations of Haswell's type material (male lectotype and a female paralectotype (AM P2972) selected as such by Campbell from two syntypes) show strong similarities to T. dentata in the general shape of their carapaces and, most especially, orbits and eye peduncles that are much longer than those of *Eucrate*. Campbell unfortunately did not discuss Haswell's species in detail and concluded that the most "characteristic feature of this species is probably the presence of the short strong ridges at the bases of the third and fourth anterolateral teeth", a feature that is shown in his figures (Campbell 1969: fig. 3b, H) but without mentioning the long orbits and eye peduncles, which are also shown in his figures. Haswell's species is only known from the relatively small male lectotype and female paralectotype (AM P2972) as selected by Campbell. Their carapace widths were measured by Campbell as 8.7 mm and 12.4 mm, respectively. Both specimens are dry and fragile but photographs (one of which is reproduced as Fig. 40D) confirm that Haswell's specimens belong to T. dentata (Stimpson, 1858). Campbell, however, provided a drawing of the abdomen of the male lectotype (Campbell 1969: fig. 3F), which shows a telson that is slightly shorter than that of T. dentata. The specimen drawn by Campbell was a small male so it is possible that the telson was not fully developed. It is also possible that the abdomen was not fully extended and straight when drawn. Not mentioned by Stimpson in his description of H. dentata, but observed by Campbell in Haswell's holotype, and by us in specimens of T. dentata is a slight, granular elevation on the branchial region parallel to each posterolateral margin. These are indicated in Campbell's figure of *E. affinis* (Campbell 1969: fig. 3B, H) but they are not as evident in larger individuals such as the male holotype of E. haswelli (15.0 mm  $\times$  19.5 mm, AM P6691; Fig. 40B), another junior synonym of T. dentata (see below), or in the neotype of T. dentata (16.4 mm × 21.5 mm, QM W27400; Fig. 40A).

Campbell (1969: 119) regarded Stimpson's *H. dentata* as a species of *Eucrate* and included it in his key to species. He discussed in detail Stimpson's description (Campbell 1969: 132) and pointed out six similarities and three differences between it and his new species *E. haswelli*. One difference was in the carapace length to width ratio, 1.34 in the male holotype of *E. haswelli* against 1.46 in Stimpson's specimen. As pointed out in the case of Stimpson's *H. transversa* (see Remarks above), the difference may be due to the possibility that Stimpson's specimen, whose sex was not indicated, being a female. A second difference resulted after errone-ously concluding from Stimpson's description that the second anterolateral tooth (first tooth below the outer orbital tooth) was "almost obsolete" in *H. transversa*. He finally presumed ("by inference") that a median frontal notch was absent in *H. transversa* because its presence was not mentioned by Stimpson. A colour photograph of the male holotype of *E. haswelli* Campbell, 1969 (15.0 mm × 19.5 mm, AM P6691; Fig. 40B) confirms that Campbell's species is indeed a junior synonym of *T. dentata* (Stimpson, 1858).

Other authors referred specimens collected elsewhere to *Eucrate affinis* Haswell, 1882. Such is the case of four specimens from the Mergui Archipelago, Andaman Sea identified "with some hesitation" as *E. affinis* by De Man (1887: 89, pl. 5, figs. 5–7), as well as the single specimen of the same collection identified by Alcock (1900: 300) as *E. crenata* var. *affinis*. Campbell (1969: 128) referred to *E. tripunctata* Campbell, 1969, the four specimens identified "with some hesitation" as *E. affinis* by De Man (1887: 89, pl. 5, figs. 5–7), as well as the single specimen of the same collection identified by Alcock (1900: 300) as *E. crenata* var. *affinis*. Campbell's decision was made on account of the restriction of the cheliped tomentum to "the upper border of the wrist of the cheliped", the proportions of the P5 propodus, and the similarity between the outer orbital teeth and the first two anterolateral teeth. Based solely on De Man's description and his figures, however, it is clear that the specimens do not belong to *E. tripunctata*. The anterolateral teeth, described by De Man (1887: 90, pl. 5, fig. 5) as "rather acute", do not resemble the conspicuously short teeth of *E. tripunctata*, a feature that is observed even in pre-adults (Campbell 1969: fig. 4K, L). Furthermore, the male telson (De Man 1887: pl. 5, fig. 6) is shorter than that in *E. tripunctata*. Alcock's specimen was described as being "more sculptured" than that of *E. crenata*, which is in sharp contrast to the smoother carapace of *E. tripunctata*.

The similarities between De Man's material and *T. dentata* are evident from his figures, most especially the long orbits and eye peduncles but there are some differences. Assuming that the figures are accurate, the anterolateral teeth are subequal, the orbits are slightly transverse, and the P5 dactylus relatively shorter than in *T. dentata*. The identity of the material, as well as Alcock's *E. crenata* var. *affinis* thus remains unknown.

Also referred to *E. affinis* were specimens from South Africa (Stebbing 1920a: 238; 1921b: p. 458, pl. 15). Stebbing's illustration of the carapace shows the elongated orbits and eye peduncles and what appear to be a granular elevation parallel to the left posterolateral margin. Nevertheless, the tomentum on the cheliped carpi is not illustrated, the P5 propodus is proportionally short and wide, the anterolateral teeth show acute tips, and the male telson is shorter than in *T. dentata*. Stebbing's material from South Africa is referred to as *Eucrate sulcatifrons* Stimpson, 1858, a junior synonym of *E. crenata* (De Haan, 1835), by Barnard (1950: 295, fig. 54d, e), who mentions that the "distal end of wrist [is] more or less covered with thick fur". His figure shows orbits and eye peduncles that are longer than in *Eucrate* and the relatively large outer orbital and anterolateral teeth characteristic of *T. dentata*.

Often placed in synonymy with Haswell's *Eucrate affinis* (e.g. Campbell 1969: 122), *Pseudorhombila sulcatifrons* var. *australiensis* Miers, 1884 (Miers 1884: 242, pl. 24, fig. C, c) agrees with some of the diagnostic characters of *T. dentata* as defined here. Miers compared his female specimen from Queensland, Australia with Stimpson's *H. dentata* and stated that his variety differs "it would appear, [by] the shorter thicker eye-peduncles", which is not readily apparent from Miers' figure, and a first anterolateral tooth that is "as long as the preceeding [sic]" (the outer orbital tooth). Campbell (1969: 126) examined photographs of the dry holotype (deposited at NHM) and found that there are some errors in Miers' representation of, among other structures, the anterolateral teeth and the P5. Nevertheless, absent from Miers' specimen is the tomentum on the cheliped carpi, although short setae instead of a conspicuous tomentum has been observed in small specimens of *T. dentata* like that of Miers', which was only 6 mm × 8 mm (Miers 1884: 242). Examination of the pre-adult female holotype of *Pseudorhombila sulcatifrons* var. *australiensis* Miers, 1884 (8.4 mm x 6.0 mm, NHM 1882.93; Fig. 40F) confirms it is a junior synonym of *T. dentata* (Stimpson, 1858).

The photographs of a Gulf of Thailand specimen identified as "*Heteroplax transversus*" by Serène & Lohavanijaya (1973: figs. 183, 184, pl. 18, fig. A) is clearly identifiable as *T. dentata*. The specimen identified as "*Heteroplax dentatus*" (Serène & Lohavanijaya (1973: 73, 98, figs. 178-182, pl. 17), however, belongs to *Trissoplax tuberosa* **n. sp.** (see below). The authors were, like many others, obviously confused by Stimpson's ((1858, 1907) descriptions of the two species.

*Eucrate costata* Yang & Sun, 1979, described from southern China can also be referred to *T. dentata*. This synonymy is clearly apparent in the photographs of the carapace (broad carapace, characteristic shape of the anterolateral teeth) and long orbits and eye peduncles (Yang & Sun 1979: plate, figs. 5, 6, 9), particularly since the photographs are side by side to photographs of two species of *Eucrate*. Also characteristic of *T. dentata* is the elongated male telson and the proportionally slender P5 propodus and dactylus (Yang & Sun 1979: figs. 3, 4). The species was described as resembling more *Eucrate haswelli* and *E. affinis* but a table contrasting the three species (Yang & Sun 1979: 11) listed five characters, three of which involved the sculpturing of the carapace and cheliped, and two slight differences in the morphometry of the P5 propodus and male abdomen. The authors did not mention their examination of material of the two "*Eucrate*" species so their data was taken from Campbell's rather incomplete illustrations. As mentioned above, there is a slight difference in the shape of the male telson of *E. affinis* as figured by Campbell (1969: fig. 3F) and the more slender telson of *E. costata* (19.0 mm × 25.0 mm, BMNH J79140; Fig. 40E) confirm the synonymy.

In view of the complex and confusing taxonomic history of the species and in the interest of long-term nomenclatural stability, we hereby designate a male (16.4 mm × 21.5 mm; QM W27400) from Hong Kong, the type locality of Stimpson's species, as the neotype of *Heteroplax dentata* Stimpson, 1858. This action effectively makes *Eucrate affinis* Haswell, 1882, *E. costata* Yang & Sun, 1979, *E. haswelli* Campbell, 1969, and *Pseudorhombila sulcatifrons* var. *australiensis* Miers, 1884, junior subjective synonyms of *Heteroplax dentata* Stimpson, 1858.

The specimen figured by Dai *et al.* (1986: fig. 194) and Dai & Yang (1991: fig. 194) of a specimen from Guandong, southern China conforms to *T. dentata*. It shows three anterolateral teeth in addition of an obtuse but conspicuous outer anterolateral tooth, and a smooth chelipeds propodus.

The "*Eucrate crenata* var. *dentata*" records of Alcock (1900) (see Remarks for *E. alcocki*) probably refer to either *E. alcocki* Serène, in Serène & Lohavanijaya, 1973, or *E. indica* **n. sp.** The record of "*Eucrate crenata dentata*" by Chhapgar (1957: 39, pl. 11, figs. j, k, l), however, is clearly *T. dentata* as presently defined here as his figures leave no doubt about its identity. Material from the Iranian Gulf identified by Stephensen (1946: 167, fig. 45) as *Eucrate sulcatifrons*, a junior synonym of *E. crenata* De Haan, 1835, was examined by Apel (2001: 102) and according to him, is actually *E. haswelli*; which is here regarded as a junior synonym of *T. dentata*.

The specimen photographed by Serène & Lohavanijaya (1973: pl. 17, fig. C) does show four teeth (in addition of acuminate outer orbital tooth) but their specimen does not conform to Stimpson's description. The chelipeds propodus of their specimen has conspicuous tubercles whereas Stimpson (1907) described the chelipeds as "smooth, and glossy".

Two pre-adult specimens from the Gulf of Thailand (1.8 mm  $\times$  1.8 mm, 2.6 mm  $\times$  3.0 mm; USNM 39740), which belong to a batch of four females and one male recorded by Rathbun (1910: 342), do not belong to *H. dentata*. Their small size makes a conclusive identification impossible but they have clear affinities to *Carcinoplax* and *Psopheticus* Wood-Mason, 1892, both included in the Goneplacidae *sensu stricto*.

Differences between *T. dentata* and its only known congener are given in the description of *T. tuberosa* **n. sp.** (see below).

**Colour pattern.** There is considerable variation in the colour pattern of *T. dentata*. Stimpson's Hong Kong live specimens were described as having a gray or brown carapace, "whitish posteriorly, and with a transverse narrow white band being the eyes ... frontal region and feet punctuate with red" (Stimpson 1905: 95). Pakistan specimens were described by Tirmizi & Ghani (1996: 80, as *Eucrate haswelli*) as "pale with purple dots, chelipeds white with purple dots". Two preserved male specimens from Singapore (14.1 mm × 18.4 mm, ZRC 2009.0375; 15.2 mm × 19.4 mm, ZRC 1992.7922) showed small dots on the dorsal surface of the chelipeds and the anterior third of the carapace. The same colour pattern is observed in a photograph of a fresh specimen from the Persian Gulf provided by R. Naderloo (Forschunginstitut Senckenberg, Frankfurt). A recently preserved, small male ( $6.2 \text{ mm} \times 8.3 \text{ mm}$ ; NHM) from the Andaman Sea coast of Thailand showed a broad purplish band across the carapace just below the orbits. The front and the posterior half of the carapace were pinkish (Fig. 39D). Small specimens photographed live in Singapore, however, show light-coloured carapaces with an irregular pattern of dots, some of which take the form of two spots on the dorsal surface (Fig. 39E, F).

The Indian specimen illustrated by Chhapgar (1957: pl. 11, fig. j, as *Eucrate crenata* var. *dentata*) shows two small, round spots on the carapace, but specimens were described as "bright yellow, with minute red spots scattered throughout. One of the specimens has two black square patches on the outer sides of the gastric region". A similar colour in life colour pattern has also been observed among some specimens, including some preserved ones from an unknown location (LACM).

**Distribution.** Wide Indo-West Pacific distribution: South Africa (Stebbing 1920a), Gulf of Aden, Persian Gulf, Pakistan, India (Chhapgar 1957), Thailand (Andaman Sea and Gulf of Thailand coasts), China (including Hong Kong), Singapore, Australia (Queensland). Depth: shallow subtidal to 40 m.

### Trissoplax tuberosa n. sp.

(Figs. 42A–E; 43D–F)

*"?Heteroplax dentatus"* — Serène & Lohavanijaya 1973: 72 [in key], 73, 98, figs. 178–182, pl. 17 [Gulf of Thailand]. *Heteroplax nitidas* [sic] — Serène & Soh 1976: 23 (part) [Andaman Sea]. [not *Henicoplax nitida* (Miers, 1879)]

**Type material.** Male holotype, 7.6 mm × 10.2 mm (MNHN-B10340) (Fig. 42). **Type locality.** Indonesia, Moluccas, Ceram, Piru Bay, Tanjung Ani, 03°14'50" S, 128°04'20"E. **Material examined.** *Thailand.* Andaman Sea, Thai-Danish Expedition: stn.1047-8, 05°43'N, 100°13'E, 15 m, 26.01.1966, id. as *Heteroplax dentata* by R. Serène: 1 feminised male parasitized by sacculinid, 3.8 mm  $\times$  4.4 mm, 1 juv. male (ZMUC CRU-10066).

*Indonesia. Moluccas.* Rumphius 1 Expedition: Ceram, Piru Bay, Tanjung Ani, stn. D1,  $03^{\circ}14'50''$  S,  $128^{\circ}04'20''E$ , sand with mixed dead shells and dead corals, 23.01.1973: male holotype, 7.6 mm × 10.2 mm (MNHN-B10340).

**Diagnosis.** Suborbital border straight, without inner suborbital tooth or median lobe (Fig. 42E). Outer surface of chelipeds with spherical tubercles (Fig. 42E).



**FIGURE 42.** *Trissoplax tuberosa* **n. sp.**; male holotype (7.6 mm  $\times$  10.2 mm) (MNHN-B10340), Indonesia, Moluccas. A, overall view; B, ventral view of carapace; C, anterior portion of male thoracic sternum and abdomen; D, male sterno-abdominal cavity and G1; E, frontal view showing orbits, antennae and outer surfaces of chelae. Abbreviations: G1 = first male pleopod; sc = sterno-abdominal cavity. Photo credits: A, B by H. H. Tan (ZRC).

**Description.** Carapace (Fig. 42A) hexagonal, transversely elongated, wider than long (1.3 wider than long in male holotype), anterolateral borders nearly straight, dorsal surface without clear indication of regions; front

wide, with shallow median notch, transverse sulcus along margin. Three anterolateral teeth posterior to triangular outer orbital tooth (first well developed, triangular, obtuse tip; second largest, triangular, acute tip; third short, obtuse tip); margin of teeth slightly granular, margin between outer orbital tooth, first anterolateral teeth curved, margin between first, second anterolateral teeth straight. Orbits moderately long (Fig. 42A, E), nearly as long as front (0.8 times frontal width in holotype); small notch on inner third portion of slightly sinuous, thin, granular (from notch to outer orbital tooth) supraorbital border; suborbital border granular, sinuous, without inner suborbital tooth or median lobe (Fig. 42E); eye peduncles moderately long (0.4 frontal width in holotype), much longer than corneas (2.6 times cornea length in holotype); large, spherical corneas.

Basal antennal article slightly mobile, with small disto-lateral process so that orbital hiatus is closed excluding antennal flagellum from orbit (Serène & Lohavanijaya 1973: pl. 17, fig. A, as *Heteroplax dentatus*).

Posterior margin of epistome lobular; lateral lobes large, with straight margins, separated from median portion by deep fissure; median portion with 3 lobes separated by very weak clefts, with median lobe broadly rectangular. Anterior margin of endostome well demarcated from buccal cavern, endostomial ridges low. Pterygostomian region with coarse granules. Third maxillipeds completely closing buccal cavern; ischium rectangular with deep submedian line; merus relatively square in shape but anteroexternal part angular, rounded, auriculiform; exopod long, reaching to just before anterior edge of merus with long flagellum (Serène & Lohavanijaya 1973: fig. 178, pl. 17, fig. A, as *Heteroplax dentatus*).

Cheliped fingers moderately stout, slightly longer than swollen propodus, distal portion light in colour. Outer (dorsal) surface of carpus, propodus, dactylus covered with large, spherical, mammillate tubercles (Fig. 42E; Serène & Lohavanijaya 1973: pl. 18, figs. C, D, as *Heteroplax dentatus*). Inner (dorsal) margin of carpus with large tooth; clump of short setae on anterior margin of carpus, long plumose setae on ventral margin; outer (dorsal) margin of merus with large, obtuse, distal tooth with few, long, simple setae; median portion of ventral surface with 3, 4 rows of large, spherical tubercles. Dorsal, ventral margins of ambulatory legs (P2–P5) smooth, with long, sparse simple setae; dactyli long, slender; P5 merus long, moderately slender (4.1 mm long in holotype), ventral margin slightly arched, distal end reaches past third anterolateral tooth but not second anterolateral tooth when folded against carapace; P5 propodus (1.8 mm long, 0.8 mm wide in holotype), proportionally stout, subcylindrical, inner margin fringed with row of numerous short, simple setae, outer margin with scattered long, simple setae; P5 dactylus (2.2 mm long, 0.2 mm maximum width in holotype) proportionally slender, subcylindrical (Fig. 42A, B), fringed with short, simple setae.

Thoracic sternum (Fig. 42C, D) wide, thoracic suture 2/3 complete, convex; 3/4 deep, short, interrupted; 4/5, 6/7, 7/8 interrupted, 5/6 complete; median groove on thoracic sternites 7, 8. Sterno-abdominal cavity of male deep, nearly reaching anterior margin of sternite 4 (Fig. 42D). Press-button of male abdominal-locking mechanism not visible in holotype.

Male abdomen (Fig. 42C; Serène & Lohavanijaya 1973: fig. 180, as *Heteroplax dentatus*) narrow, slender, transversely narrow (T-shaped), lateral margins of somites 4–6 abruptly narrowing from somite 3 to narrow, pointed telson; somite 3 reaching inner margins of P5 coxae; small portion on each side of thoracic sternite 8 left exposed by closed abdomen, somite 2 transversely almost as long as somite 3 (Serène & Lohavanijaya 1973: fig. 180, as *Heteroplax dentatus*). G1 (Fig. 43D, E; Serène & Lohavanijaya 1973: figs. 181, 182, as *Heteroplax dentatus*) long, slender, sinuous, acuminate apex, with small denticles; G2 (Fig. 43F) less than one-third of G1, straight, with 2 processes: one long, tip obtuse; second much shorter, tip acute. Male genital opening (gonopore) coxal; coxo-sternal disposition of long penis, protected by concave posterior portion of thoracic sternite 7.

Female not examined (female abdomen illustrated by Serène & Lohavanijaya (1973: fig. 179, as *Heteroplax dentatus*).

**Etymology.** From *tuber*, Latin for "swelling" or "bulb", in reference to the conspicuous, spherical tubercles on the outer and dorsal surface of the chelipeds (P1) that is diagnostic of the species.

**Remarks.** Photographs and drawings of specimens from Manila Bay, Philippines that were identified as "*Pheteroplax dentatus*" by Serène & Lohavanijaya (1973: figs. 178–182, pl. 17) clearly show that their two specimens, a male and a female, are referable to the new species. These authors did not realize that their Philippine specimens were actually different from either of Stimpson's two species of *Heteroplax*, even after not-

ing that *H. dentata* lacks the coarse cheliped granules found in their Philippine specimens, that the carapace of Stimpson's *H. dentata* was narrower than that of the Philippine specimens, and that the conspicuous tomentum on the cheliped meri of Stimpson's *H. dentata* was missing in the Philippine specimens.



**FIGURE 43.** Gonopods. A–C, *Trissoplax dentata* (Stimpson, 1859); male neotype of *Heteroplax dentata* Stimpson, 1859 (16.4 mm × 21.5 mm) (QM W27400); D–F, *Trissoplax tuberosa* **n. sp.**, male holotype (7.6 mm × 10.2 mm) (MNHN-B10340), Indonesia, Moluccas. A, B, D, E, right G1, dorsal view; C, F, right G2, dorsal view. Scale bars: A, 1.0 mm; B, D, 0.5 mm; C, E, F, 0.2 mm.

One difference between Serène & Lohavanijaya's specimens and the holotype is that in their male specimen the cheliped granules were "less numerous and more worn out" than in their female specimen, a situation that is evident from their photograph (Serène & Lohavanijaya 1973: pl. 17, fig. B, D, as "?*Heteroplax denta-tus*").

Two of a number of specimens from the Andaman Sea identified by Serène & Soh (1976: 23) as *Heteroplax nitida* (the remaining belong to *Henicoplax pilimeles* **n. sp.**, see above) are also referred to *T. tuberosa* **n. sp.** The detached chelipeds of one of the two specimens (a male feminised by a sacculinid,  $3.8 \text{ mm} \times 4.4 \text{ mm}$ ; ZMUC CRU-10066) are characteristic of the new species. The second, a very small juvenile male, had no chelipeds but both specimens are clearly conspecific and differ from *T. dentata* because the suborbital border lacks teeth, but possesses a defined median lobe in contrast to *T. dentata* (Fig. 41A, B).

Although close to *T. dentata* in the general shape of the carapace, *T. tuberosa* **n. sp.** is easily distinguished from its sole congener by the presence of coarse tubercles on the outer surface of its chelipeds (smooth in *T. dentata*; Fig. 41E), the absence of the conspicuous tomentum of *T. dentata* (Fig. 39D–F; 40A–E; 41E), and, as mentioned above, the absence of both, an inner suborbital tooth and a median lobe on each suborbital border (both present in *T. dentata*; Fig. 41A, B).

**Distribution.** Andaman Sea coast of Thailand, Philippines (Serène & Lohavanijaya 1973, as "?*Heteroplax dentatus*"), Indonesia (Moluccas). Depth: shallow subtidal of at least 15 m depth.

### Genus Trizocarcinus Rathbun, 1914

*Trizocarcinus* Rathbun, 1914a: 117; 1918: 16 [in key], 17 [diagnosis]. — Balss 1957: 1656. — Guinot 1969b: 517, 518 [discussion]; 1971: 1081 [list of species]. — Karasawa & Kato, 2003a: 151 [in list]; 2003b: 139 [in list] [part]. — Ng & Castro 2007: 44 [in list] [part]. — Ng *et al.* 2008: 78 [in list] [part]. — De Grave *et al.* 2009: 33 [in list].

**Diagnosis.** Carapace (Figs. 44A; 45A) nearly quadrate, slightly wider than long, dorsal surface granular (T. dentatus) or smooth (T. tacitus), without clear indication of regions; anterolateral borders slightly arched; front wide, straight or slightly bilobed, with small median notch. Two triangular anterolateral teeth with acute tips posterior to triangular, anteriorly oriented outer orbital tooth on outer orbital angle. Orbits (Figs. 44B; 45A) moderately transversely long (shorter than front) or long (almost as long as front in *T. tacitus*); thin supraorbital margin, granular or smooth, with 2 notches; inner suborbital tooth absent (only slightly elevated margin), sinuous median lobe, outer notch on granular or smooth suborbital border (Figs. 44C; 46A, G); eye peduncles moderately long, shorter than front, approximately as long as corneas; large, spherical corneas (Figs. 44B, C; 46G). Stridulating ridge on pterygostomian region in T. dentatus (Rathbun 1918: fig. 3). Basal antennal article immobile, orbital hiatus is closed excluding antennal flagellum from orbit (Figs. 44B, C; 46A, G). Anteroexternal margin of third maxilliped merus auriculiform (Figs. 44C). Cheliped fingers slender, dorsoventrally flattened, slightly shorter than propodus, light in colour (Fig. 44D); carpus with acute, curved tooth on inner margin; conspicuous tomentum on outer surface of propodus, carpus (plus anterior margin of merus in T. tacitus; Figs. 44A, D; 45A). Dorsal margins of ambulatory legs (P2–P5) meri, carpi, propodi unarmed, dactyli slender, smooth, setose; P5 propodus, dactylus long, slender, fringed with many short setae (Figs. 44A; 45A). Thoracic sternum (Figs. 44F; 45B; 46C; 46I) wide; thoracic suture 2/3 complete, slightly convex (Fig. 45B); 3/4 deep, short, interrupted; 4/5, 6/7, 7/8 interrupted, 5/6 complete (Fig. 45B); median groove on thoracic sternites 7, 8. Ovoid concavity on anterior portion of sternite 1–2. Sterno-abdominal cavity of male deep, reaching anterior margin of sternite 4 (Fig. 46C, I); sterno-abdominal cavity of female with deep, wide depression along median portion of sternite 4 (Fig. 45B). Press-button of male abdominal-locking mechanism as large tubercle near thoracic suture 4/5 (small tubercle present in pre-adult females). Male abdomen proportionally wide, triangular (not T-shaped), telson longer than wide (Figs. 1A; 44E); somite 3 only slightly transversely shorter than somites 4–6, reaching inner margins of P5 coxae, fitting under episternite 7 (Fig. 44G; 46D; 46J); small portion on each side of thoracic sternite 8 left exposed by closed abdomen, somite 2 transversely shorter than somite 3 (Fig. 44G). G1 long (particularly in *T. dentatus*, which has long, thin distal part), slender, slightly sinuous, with many small denticles, acuminate apex (Figs. 44F; 46E, K); G2 less than onethird of G1, apex with 2 unequal processes (Fig. 46F, M). Male genital opening (gonopore) coxal (Fig. 46B, H); coxo-sternal disposition of long penis, protected by slightly convex posterior portion of thoracic episternite 7 (Fig. 44F). Vulva relatively large, ovoid, transversely near median portion of sternite 6, extending across median half of sternite (Fig. 45B); thick, elevated outer-posterior margin; covered by soft membrane, sternal vulvar cover absent.

Type species. Carcinoplax dentatus Rathbun, 1893 (by monotypy, gender masculine).

**Remarks.** The proportionally wide, triangular male abdomen of *Trizocarcinus* (Figs. 1A, 44E) contrasts with the T-shaped abdomen of most other euryplacids, a character shared with *Nancyplax* and *Villoplax* **n. gen.** (see Remarks for Euryplacidae). The G1 is particularly long, with a narrow distal part, in *T. dentatus* (Figs. 44F; 46E), longer than in its congener *T. tacitus* and all other euryplacids except one (see below). All other characters, however, clearly argue for its inclusion in the Euryplacidae (see Guinot 1969b: 518).

*Trizocarcinus peruvianus* Garth, 1973, like *T. dentatus* also described from the Tropical Eastern Pacific region, is being referred to *Villoplax* **n. gen.** (see below). *Trizocarcinus dentatus* appears to be sympatric with *V. peruvianus* (Garth, 1973), along its southernmost distribution in northern Perú. Both species share a conspicuous tomentum and a G1 with a long, narrow apex. Other characters, most importantly the shape of the carapace, nevertheless provide evidence of their inclusion in separate genera (see Remarks for *Villoplax* **n. gen.** and Table 1).
# Species included.

*Trizocarcinus dentatus* (Rathbun, 1893) *Trizocarcinus tacitus* Chace, 1940 The genus is restricted to the Western Atlantic and Tropical Eastern Pacific regions.

## Species excluded from Trizocarcinus:

Trizocarcinus peruvianus Garth, 1973 (= Villoplax peruvianus (Garth, 1973))



**FIGURE 44.** *Trizocarcinus dentatus* (Rathbun, 1893); male (14.7 mm  $\times$  20.2 mm) (MNHN-B20990), Mexico, Gulf of California. A, overall view; B, frontal view showing orbits and antennae; C, third maxillipeds; D, outer surface of right chelae; E, anterior portion of male thoracic sternum and abdomen; F, posterior portion of male thoracic sternum and abdomen; G, male sterno-abdominal cavity, G1, and penis. Abbreviations: a1-a3 = male abdominal somites 1, 2, 3, respectively; cx5 = coxa of fifth pereopod (P5); es7 = episternite 7; G1 = first male pleopod; mg = median groove; p = penis; s6–s8 = thoracic sternites 6 to 8, respectively.

## Trizocarcinus dentatus (Rathbun, 1893)

(Figs. 44A–G; 46A–F)

Carcinoplax dentatus Rathbun, 1893: 243 [Gulf of California].

Trizocarcinus dentatus Rathbun 1914a: 118, fig. 1, pl. 1; 1918: 18, fig. 3, pl. 1 [Gulf of California]. — Garth 1948: 52
[Ecuador]; 1960: 113. — Guinot 1969b: 518 [discussion], figs. 37, 44, 46, 48, 49 [holotype]; 1971: 1081 [in list]. — Chirichigno 1970: 61, fig. 151. — del Solar 1970: 44 [Perú]. — del Solar *et al.* 1970: 27 [Perú]. — Hendrickx 1990: 49 [Gulf of California]; 1992: 9 [in list]; 1993a: 314 [in list]; 1995: 139 [in list] [Pacific coast of Mexico]. — Lemaitre & Álvarez-León 1992: 56 [in list]. — Ng *et al.* 2008: 78 [in list].

Type material. Male holotype (USNM 17462); 1 male paratype (USNM 123310).

Type locality. Mexico, Gulf of California, Sonora, off Cabo Lobos, 54-137 m.

**Material examined.** *Mexico.* Bahía de San Ignacio, Gulf of California, 30.03.1980: 1 male, 14.7 mm  $\times$  20.2 mm (MNHN-B20990). – Gulf of California, *Albatross*, stn. 3017, 29°54.5'N, 113°01.0'W, 104 m, 24.03, 1889: 1 pre-adult female, 10.0 mm  $\times$  12.4 mm (USNM 17463); stn. 3035, 1 pre-adult female, 7.3 mm  $\times$  8.7 mm (USNM 17464). – Roca Consag, Gulf of California, 31°7'N, 114°29'W 09.05.1982: 1 male, 15.3 mm  $\times$  20.3 mm (MNHN-B20987).

**Diagnosis.** Dorsal, ventral surface of carapace granular (Fig. 44B, C, F, G). Granular stridulating ridge on pterygostomian region (Rathbun 1918: fig. 3). G1 apex exceptionally long (Fig. 46E).

**Remarks.** *Trizocarcinus dentatus*, which is restricted to the Tropical Eastern Pacific region, shares with the Western Atlantic *T. tacitus* Chace, 1940, a carapace with curved anterolateral borders each armed with two teeth (Figs. 44A; 45A) as well as the other characters that define the genus *Trizocarcinus*. Its carapace, however, is granular in contrast to the smooth carapace of *T. tacitus*. The conspicuous, granular stridulating ridge along the pterygostomian region of *T. dentatus* (Rathbun 1918: fig. 3) is absent in *T. tacitus*, and the cheliped tomentum (Fig. 44D) is generally more conspicuous than that of *T. tacitus*.

**Distribution.** Tropical Eastern Pacific region from the Gulf of California to northern Perú. Depth: 36–126 m.

## Trizocarcinus tacitus Chace, 1940

(Figs. 45A, B; 46G–M)

*Goneplax tridentata* — Boone 1927: 10, figs. 2–4 [Belize]; 1930: 194, pl. 66, fig. A [Florida]. [not *Trapezioplax tridentata* (A. Milne-Edwards, 1880); Pseudorhombilidae]

*Trizocarcinus tacitus* Chace, 1940: 41, figs. 15, 16 [Barbados]; 1956: 20 [Gulf of Mexico]. — Guinot 1969b: 518, 522 [discussion], figs. 34, 43, 45, 50, 51 [holotype]; 1971: 1081 [in list]. — Soto 1985: 484, 495; 1986: 3, 4, 36; 1991: 626, 627 [Florida]. — McLaughlin *et al.* 2005: 257 [in list]. — Ng *et al.* 2008: 78 [in list].

Type material. Male holotype (MCZ 5646).

Type locality. West Indies, Barbados, 272 m.

**Material examined**. *Bahamas*. Grand Bahama, *Gerda*, stn. 696, 26°28'N, 78°43'W, 22.07.1965: 1 male, 14.0 mm  $\times$  18.0 mm (RMNH D 26876).

*Florida*. Florida Straits, SW of Dry Tortugas, 24.3629°N, 83.2277°W, F. F. Snelson coll., 9.05.2006: 1 male, 11.5 mm  $\times$  15.2 mm (UF 11583).

*Gulf of Mexico. Oregon*, stn. 273, U.S. Fish & Wildlife Service, 1951: 1 female, 23.3 mm  $\times$  31.5 mm (USNM 92164).

*Guadeloupe*. Mission ORSTOM, IRPM, SMCB: stn. C34, off Basse Terre,  $16^{\circ}22.49$ 'N,  $61^{\circ}48.99$ 'W, 405 m, G. Leblond & J. Poupin, 04.1993: 1 female, 20.6 mm × 29.4 mm (MNHN-B30602).

*St. Vincent. Pillsbury*, stn.876, 13°18.9'N, 61°04.7'W, 231–258 m, 06.07.1969: 1 female, 18.5 mm × 26.3 mm (RMNH D 26875).

**Diagnosis.** Dorsal, ventral surface of carapace smooth, not granular (Fig. 45). Stridulating ridge absent on pterygostomian region. G1 apex not particularly long (Fig. 46K, L).

**Remarks.** *Trizocarcinus tacitus*, which is Western Atlantic in distribution, can be differentiated from its Tropical Eastern Pacific congener, *T. dentatus*, by having a characteristically smooth carapace, not granular as in the latter. Other characters separating the two species are given in the Remarks for *T. dentatus*.

**Distribution.** Western Atlantic from the Bahamas and the Gulf of Mexico to St. Vincent, West Indies. Depth: 187–462 m.



**FIGURE 45.** *Trizocarcinus tacitus* Chace, 1940; female (20.6 mm  $\times$  29.4 mm) (MNHN-B30602), West Indies, Guadeloupe. A, overall view; B, female thoracic sternum and vulvae. Abbreviations: mg = median groove; md = median depression; s4–s7 = thoracic sternites 4 to 7, respectively; v = vulva.



**FIGURE 46.** A–F, *Trizocarcinus dentatus*, (Rathbun, 1893) (after Guinot 1969b: figs. 37, 44, 46, 48, 49); G–M, *Trizocarcinus tacitus* Chace, 1940 (after Guinot 1969b: figs. 34, 43, 45, 50a, 50b, 51). A, G, frontal view showing orbits and third maxillipeds; B, H, posterior portion of male thoracic sternum, abdomen, and gonopore; C, I, anterior portion of male thoracic sternum and abdomen; D, J, posterior portion of male thoracic sternum and abdomen; E, K, L, G1; F, M, G2. Abbreviation: a2, a3 = male abdominal somites 2 and 3, respectively; g = gonopore.

#### Genus Villoplax n. gen.

*Trizocarcinus* — Karasawa & Kato, 2003a: 151 [in list]; 2003b: 139 [in list] [part]. — Ng & Castro 2007: 44 [in list] [part]. — Ng *et al.* 2008: 78 [in list] [part]. (not *Trizocarcinus* Rathbun, 1914)

Diagnosis. Carapace (Figs. 47A, B; 48A) quadrate, slightly wider than long, dorsal surface minutely granular, without clear indication of regions; anterolateral borders nearly straight; front wide, straight or slightly bilobed, with small median notch. One triangular anterolateral tooth with acute tips posterior to narrowly triangular, acute, anteriorly oriented outer orbital tooth. Orbits (Figs. 47C; 48B) moderately transversely long (nearly as long as front); thin supraorbital margin, with 2 notches; short inner suborbital tooth, sinuous median lobe, outer notch on granular suborbital border (Figs. 47C; 48B); eye peduncles moderately long, shorter than front, approximately as long as corneas; large, spherical corneas. Basal antennal article immobile, orbital hiatus is closed excluding antennal flagellum from orbit (Fig. 47C). Anteroexternal margin of third maxilliped merus auriculiform (Figs. 47C; 48B). Cheliped fingers slender, dorsoventrally flattened, slightly shorter than propodus, light in colour; carpus with acute, curved tooth on inner margin; tomentum long, conspicuous, on outer surface of propodus, carpus, anterior margin of merus (Figs. 47A; 48A, C). Dorsal margins of ambulatory legs (P2–P5) meri, carpi, propodi unarmed, dactyli slender, smooth, with conspicuous tomentum along margins; P5 propodus, dactylus long, slender, fringed with many short setae (Figs. 47A; 48A). Thoracic sternum wide; thoracic suture 2/3 complete, convex, close to anterior margin (Figs. 47D; 48B); 3/4 deep, short, interrupted; 4/5, 6/7, 7/8 interrupted, 5/6 complete; median groove on thoracic sternites 7, 8. Sterno-abdominal cavity of male deep, reaching anterior margin of sternite 4 (Fig. 47D). Press-button of male abdominallocking mechanism as large tubercle near thoracic suture 4/5 (small tubercle present in pre-adult female holotype). Male abdomen proportionally wide, triangular (not T-shaped), telson longer than wide (Figs. 47D; 48D); somite 3 only slightly transversely shorter than somites 4–6, reaching inner margins of P5 coxae, fitting under episternite 7; no portions of thoracic 8 exposed by closed abdomen, somite 2 transversely almost as long as somite 3 (Fig. 48D). G1 long, slender, slightly sinuous, thin distal part, acuminate apex, with many denticles (Fig. 48E, F); G2 less than one-third of G1, apex with 2 unequal processes (Fig. 48G). Male genital opening (gonopore) coxal; coxo-sternal disposition of long penis, protected by slightly convex posterior portion of thoracic sternite 7. Vulva of adult female unknown but, ovoid, transversely near median portion of sternite 6 in pre-adult female.

Type species. Trizocarcinus peruvianus Garth, 1973 (by present designation, gender feminine).

**Etymology.** From *villosus* Latin for "hairy", in reference to the thick tomentum on the chelipeds of the only species included in the new genus, *Villoplax peruvianus*, and *plax* Greek for "plate" or "tablet", a common suffix also used for many related goneplacoid genera.

**Remarks.** The only species included in the new genus, *V. peruvianus* (Garth, 1973) was described as a species of *Trizocarcinus*. Although sharing with *Trizocarcinus* a triangular male abdomen, the new genus departs from the two species included in *Trizocarcinus* by several characters related to carapace shape (straight anterolateral border each with one anterolateral tooth but arched with two teeth in *Trizocarcinus*), morphology of the orbits (thin, acute outer orbital tooth and an inner suborbital tooth in contrast to a triangular outer orbital tooth and the absence of an inner suborbital tooth in *Trizocarcinus*), and thoracic suture 2/3 (close to the thoracic margin but broad space between suture and margin in *Trizocarcinus*) (also see Remarks for *Trizocarcinus* and Table 1).

#### Species included. Trizocarcinus peruvianus (Garth, 1973)

The genus is restricted to the Tropical Eastern Pacific region.

# Villoplax peruvianus (Garth, 1973), new combination

(Figs. 47A-D; 48A-G)

Goneplax sp. — Chirichigno 1970: 61, fig. 150.

*Trizocarcinus peruvianus* Garth, 1973: 9, fig. 5 [Perú]. — Wicksten 1989: 303 [in list], 316 [in list]. — Ng *et al.* 2008: 78 [in list].

**Type material.** Pre-adult female holotype, 13.4 mm  $\times$  19.1 mm (AHF 699, now LACM) (Fig. 47A, B); 1 male paratype, 19.9 mm  $\times$  28.7 mm (AHF 705; now LACM) (Fig. 47C, D).

**Type locality.** Perú, off Paita, 144 m.

**Material examined.** *Perú*. Off Paita, stn. 106, 144 m, E. N. del Solar coll.: 1 male paratype, 19.9 mm × 28.7 mm (AHF 705, now LACM), pre-adult female holotype, 13.4 mm × 19.1 mm (AHF 699, now LACM).

**Diagnosis.** Carapace with one short, acute tooth on each anterolateral border (Figs. 47A, B; 48A). Ambulatory legs with long, conspicuous tomentum (Fig. 48A).

**Remarks.** The holotype, regarded as a female by Garth (1973) is actually a pre-adult specimen where the vulvae are barely visible and closed.

**Distribution.** Only known from northern Perú, Tropical Eastern Pacific region. Depth: subtidal to at least 144 m.



**FIGURE 47.** *Villoplax peruvianus* (Garth, 1973); A, B, female holotype of *Trizocarcinus peruvianus* Garth, 1973 (13.1 mm  $\times$  19.1 mm) (AHF 699; now LACM); C, D, male paratype of *Trizocarcinus peruvianus* Garth, 1973 (19.9 mm  $\times$  28.7 mm) (AHF 705; now LACM); Perú, off Paita. A, overall view; B, dorsal view of carapace; C, frontal view showing orbits and antennae; D, ventral view of carapace. Abbreviations: a3 = male abdominal somite 3; es7 = episternite 7; s4–s7 = thoracic sternites 4 to 7, respectively; t = telson. Photo credits: J. Martin (LACM).



**FIGURE 48.** *Villoplax peruvianus* (Garth, 1973); male paratype of *Trizocarcinus peruvianus* Garth, 1973 (10.0 mm  $\times$  28.9 mm) (LACM), Perú, off Paita. A, overall view; B, frontal view showing third maxillipeds, orbits, and antennae; C, outer surface of right chela; D, male abdomen; E, F, G1; G, G2 (after Garth 1973: fig. 5). Abbreviations: a2, a3 = male abdominal somites 2 and 3, respectively.

## Genus Xenocrate Ng & Castro, 2007

Xenocrate Ng & Castro, 2007: 45. - Ng et al. 2008: 78 [in list]. - De Grave et al. 2009: 33 [in list].

Diagnosis. Carapace (Fig. 49A) subhexagonal, almost as wide as long, dorsal surface granular without clear indication of regions; anterolateral borders arched; front wide, nearly straight with median notch, transverse sulcus along margin. Two short teeth (second acute, dorsally salient; small third tooth in small individuals) posterior to short, rounded outer orbital angle. Orbits (Fig. 49C) short, shorter than front, wide, spherical; 2 notches, large, thick inner suborbital tooth, shorter, thick median tooth, outer notch on thick suborbital border (Fig. 49B, C); eye peduncles short, about as long as cornea (Fig. 49C); large, spherical corneas. Basal antennal article immobile, orbital hiatus is closed excluding antennal flagellum from orbit (Fig. 49B, C). Anteroexternal margin of third maxilliped merus auriculiform (Fig. 49B). Cheliped fingers (Fig. 49D) moderately stout, slightly longer than swollen propodus, dark in colour; carpus with tooth on inner margin; glabrous. Dorsal margins of ambulatory legs (P2-P5) meri, carpi, propodi unarmed, dactyli slender, smooth, setose; P5 propodus, dactylus proportionally short, flattened, fringed with many short setae (Fig. 49A). Thoracic sternum (Fig. 49G, H) wide; thoracic suture 2/3 complete, straight (Fig. 49G); 3/4 deep, short, interrupted; 3/4 deep, short, interrupted; 4/5, 6/7, 7/8 interrupted, 5/6 complete (Fig. 49G, H); median groove on thoracic sternites 7, 8. Sterno-abdominal cavity of male deep, nearly reaching anterior margin of sternite 4 (Fig. 49G). Press-button of male abdominal-locking mechanism as large tubercle near thoracic suture 4/5 (Fig. 49G) (presence in preadult females unknown). Male abdomen narrow, slender (T-shaped), lateral margins of somites 4-6 abruptly narrowing from somite 3 to transversely narrow, pointed telson (Fig. 49E); somite 3 transversely reaching inner margins of P5 coxae; no portions of thoracic 8 exposed by closed abdomen, somite 2 transversely shorter than somite 3 (Fig. 49F). G1 long, slender, slightly sinuous, acuminate apex, with small denticles (Fig. 50A-C); G2 less than one-third of G1, apex flattened, with obtuse tip (Fig. 50D). Male genital opening (gonopore) coxal; coxo-sternal disposition of long penis, protected by concave posterior portion of thoracic sternite 7 (Ng & Castro 2007: fig. 3B). Female abdomen relatively narrow, not covering outer portions of thoracic sternum (Ng & Castro 2007: fig. 5B). Vulva ovoid, with thick borders, extending across anterior portion of sternite 6 close to median axis of thorax (Fig. 49H); covered by soft membrane, sternal vulvar cover absent.

**Remarks.** This monotypic genus was recently described from specimens collected in the Philippines (Ng & Castro 2007: 45, figs. 1–5). It is herein reported for the first time from the Solomon Is. and Vanuatu, which suggests a more extensive geographical distribution.

The G2 has a unique flattened apex with an obtuse tip instead of the two unequal processes characteristic of most euryplacids, with the basal, much shorter process missing (Fig. 50D). Other characters of *Xenocrate* are summarized in Table 1.

Species included. Xenocrate peculiaris Ng & Castro, 2007

The genus is restricted to the Indo-West Pacific region.

Xenocrate peculiaris Ng & Castro, 2007

(Figs. 49A–H; 50A–D)

*Xenocrate peculiaris* Ng & Castro, 2007: 45, figs. 1–5. – Ng *et al.* 2008: 79 [in list].

**Type material.** Male holotype, 34.0 mm  $\times$  39.1 mm (NMCR); 1 male paratype, 39.6 mm  $\times$  45.8 mm (ZRC 2008.0428), 1 female paratype, 36.9 mm  $\times$  42.2 mm (ZRC 2008.0427).

Type locality. Philippines, Bohol, Panglao I., Maribojoc Bay, 100–300 m.

**Material examined**. *Philippines*. *Bohol*. Panglao I., Maribojoc Bay, tangle nets, 100–300 m, T. J. Arbasto coll., 11.2003–04.2004: male holotype 34.0 mm  $\times$  39.1 mm (NMCR); 06.2004–05.2005: 1 male paratype, 39.6 mm  $\times$  45.8 mm (ZRC 2008.0428).

PANGLAO 2005: stn. L45, tangle nets, T. J. Arbasto coll., 80–90 m, 03.07.2004: 1 female paratype, 36.9 mm  $\times$  42.2 mm (ZRC 2008.0427).

*Solomon Is.* SALOMON 1: stn. DW 1823, 09°50.4'S, 160°53.2'E, 82–83 m, 04.10.2001: 1 male, 10.5 mm  $\times$  12.7 mm (MNHN-B830609).

*Vanuatu.* SANTO 2006: stn.EP40, west Tutuba I., 15°33.1/33.6'S, 167°16.4/16.5'E, tangle net, 125–156 m, 18.10.2006: 1 male, 30.8 mm × 36.8 mm (MNHN-B).

**Diagnosis.** Dorsal, ventral surface of carapace granular, carapace subhexagonal, with two short teeth on each anterolateral border (Fig. 49A–C). Orbits short, shorter than front, wide, spherical (Fig. 49C).

Distribution. Western Pacific: Philippines, Solomon Is., and Vanuatu. Depth: 80-300 m.



**FIGURE 49.** *Xenocrate peculiaris* Ng & Castro, 2007; A–G, male holotype ( $34.0 \text{ mm} \times 39.1 \text{ mm}$ ) (NMCR), Philippines, Bohol; H, female paratype ( $36.9 \text{ mm} \times 42.2 \text{ mm}$ ) (ZRC 2008.0427), Philippines, Bohol. A, overall view; B, third maxillipeds; C, frontal view showing orbits and antennae; D, outer surface of left chelae; E, anterior portion of male thoracic sternum and abdomen; F, posterior portion of male thoracic sternum and abdomen; G, male sterno-abdominal cavity and G1; H, female thoracic sternum and vulvae. Abbreviations: a1-a3 = male abdominal somites 1, 2, 3, respectively; cx5 = coxa of fifth pereopod (P5); G1 = first male pleopod; mg = median groove; pb = press-button of male abdominal-locking mechanism; s4-s7 = thoracic sternites 4 to 7, respectively; v = vulva.



**FIGURE 50.** *Xenocrate peculiaris* Ng & Castro, 2007; male holotype (34.0 mm × 39.1 mm) (NMCR). A–C, G1; D, G2 (after Ng & Castro 2007: fig. 4). Scale bars: 1.0 mm.

## **Biogeography of the Euryplacidae**

Of the 30 species of euryplacids reported here, 19 are restricted to the Indo-West Pacific region (including one, *Eucrate crenata*, introduced in the Mediterranean Sea, most probably by way of the Suez Canal). Six species are restricted to the Western Atlantic, three to the Tropical Eastern Pacific, and two to the Eastern Atlantic regions respectively. Of the 13 genera, only *Euryplax* and *Trizocarzinus*, include species that cross major biogeographic regions, with each having representatives in both the Tropical Eastern Pacific and Western Atlantic regions.

The significant morphological differences between New World euryplacids (those in the Western Atlantic and Tropical Eastern Pacific regions) and those in the Indo-West Pacific have been previously discussed in the Remarks section for the Euryplacidae.

## Evolution of penial protection in the Euryplacidae

The protection of the penis in the Euryplacidae is provided by the closed abdomen (specifically by somites 2 and 3, which typically reach the inner margins of the P5 coxae), an expansion of episternite 7, and, as evidence for its categorization as a coxo-sternal condition, a concavity in sternite 7 at the level of suture 7/8, which may extend into sternite 8 (Guinot *et al.* in prep.).

Variations of this pattern, most notably in the width of the male abdomen (Fig. 1), have already been noted (see Remarks for Euryplacidae). In *Euryplax*, the type genus of the family, penial protection involves a relatively wide abdomen but one in which abdominal somite 3 does not actually reach the inner margins of the P5 coxae and where small portions on each side of thoracic sternite 8 are left exposed (Figs. 16F; 17F; 18D). Another peculiarity of *Euryplax*, in contrast to nearly all euryplacid species, is the protection of the proximal portion of the penis by the partial closure of thoracic sternites 7 and 8 (Figs. 16E; 17G; see also Guinot 1969b: fig. 39; Castro *et al.* 2010: 8C, D).

Such additional penial protection by this partial closure may be interpreted as a compensation for the rather incomplete protection by the abdomen, even if the relative width of somites 4-6 and the telson are not directly involved in penial protection as do somites 2 and 3. It could be suggested that a wide, triangular male abdomen similar to that in many goneplacoid families such as the Goneplacidae, is plesiomorphic for the Euryplacidae, the slender abdomen a derived character. If the wide abdomen is plesiomorphic, then penial protection by the partial closure of sternites 7 and 8 in *Euryplax* can be interpreted as an adaptation to a more complete protection of the penis.

Another modality of protection evolved, one which resulted in the typical T-shaped abdomen of most euryplacids, where the penis is protected by transversely wide abdominal somites 2 and 3, a concavity in thoracic sternite 7, and an expanded episternite 7. Such adaptations do not require the need for a closure in thoracic sternites 7 and 8 over the penis. Such a T-shaped abdomen over the deep sterno-abdominal cavity enclosing the long, slender G1 could then be interpreted as the derived condition of penial protection in the Euryplacidae.

An alternate hypothesis is that the T-shaped abdomen of most euryplacids, all of which are Indo-West Pacific in distribution, is plesiomorphic, and that the wider male abdomen, together with the partial closure of thoracic sternites 7 and 8 in *Euryplax*, is a derived modality, a condition that has evolved only in the Atlantic and Eastern Pacific genera, not only *Euryplax* but in *Nancyplax* (Fig. 32G), *Trizocarcinus* (Figs. 1A; 44E), and *Villoplax* **n. gen.** (Fig. 48D), where the abdomen is even wider than in *Euryplax*. This would require the evolution of a secondary re-widening, which seems unlikely given the diversification and success of the narrow abdominal condition in the Indo-West Pacific genera.

Fossil euryplacids, unfortunately, do not provide any clues as to the evolution of the male abdomen in the family. Although eight fossil genera have been placed in the Euryplacidae (Karasawa & Schweitzer 2006: 57) their inclusion in the family is based almost entirely on the morphology of the dorsal surface of the carapace because the male abdomen and external reproductive structures are very rarely preserved in fossil crabs (see Ng *et al.* 2008: 9). The inclusion of these eight fossil genera in the Euryplacidae is therefore a matter for conjecture because the morphologies of the abdomen and G1 are indispensable for the correct inclusion of a genus in the Euryplacidae, a dilemma that nevertheless is recognized by palaeontologists (see Karasawa & Schweitzer 2004: 148).

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