Revision of the genus *Ocypode* with the description of a new genus, *Hoplocypode* (Crustacea: Decapoda: Brachyura)

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ABSTRACT

A taxonomic revision of *Ocypode* Weber, 1795, has resulted in the recognition of a new genus, *Hoplocypode* containing a single species *H. occidentalis* (Stimpson, 1860) that is endemic to the East Pacific. *Ocypode* is now recognised to contain 21 valid species. Of these, one eastern Pacific, one western Atlantic, and two eastern Atlantic species tend to have widespread distributions within their respective regions. Conversely, many of the 17 Indo-Pacific species exhibit relatively restricted ranges. Only three of them, *O. cordimanus*, *O. ceratophthalma* and *O. pallidula* are widespread. Morphological features and their importance in identification are discussed, and a key to all species is provided. ❑ Ocypode, *taxonomy, new genus, biogeography, Indian Ocean, Pacific Ocean, Atlantic Ocean.*

Species in the genus *Ocypode* are a common and conspicuous feature of tropical and subtropical sandy beaches worldwide. This is the reason why specimens have been collected since early times, and there has been so much interest in studying them. However, there have long been problems in identifying some species, and there has been considerable confusion over the correct names to use. Some species were described from very few specimens and types have been subsequently lost, some have had confusion over their original labeling, or were attributed to vague or even wrong localities. Thus, the present world revision has, by necessity, attempted to carefully re-examine all earlier published specimens, including the types, as well as the extensive collections of the Senckenberg Forschungsinstitut und Naturmuseum in Frankfurt am Main, and a number of other museums from around the world. We give complete keys, descriptions, and figures of all the species of the genus known to date to finally resolve problems in identification. Detailed descriptions and figures of the male Go1, and the female genital opening, have been provided for the first time for many species, and these have proved very important in helping to define species and genera, and in helping to understand their phylogenetic relationships.

Abbreviations. *c.* = *ca.*; Car = carapace; Go1 = Gonopod 1; Mxp3 = Maxilliped 3; P1 = pereiopod 1; P2–5 = pereiopods 2–5. The measurements of carapace length and width (CL/CW) in the descriptions of the species and the material lists are given in mm. AMS = Australian Museum, Sydney; IRSNB = Institut Royal des Sciences Naturelles de Belgique, Bruxelles; MCM = Museo Civico di Storia Naturale di Milano; MCG = Museo Civico di Storia Naturale di Genova; MZT = Museo e Istituto di Zoologia sistematica dell'Univesitá di Torino; MBL = Museu Bocage Lisboa; MCZ = Museum of Comparative Zoology, Cambridge, Massachusets; MHNG = Museum d'Histoire naturelle, Genève; MI = Mauritius-Institute, Port Louis, Mauritius;

MNHN = Muséum national d'Histoire naturelle, Paris; MW = Museum Wiesbaden, Naturwissenschaftliche Sammlungen; MZUT = Zoological Museum of the Turin University; NHM = Natural History Museum, London; NHMB = Naturhistorisches Museum Basel; NHCY = National Natural History Collection Yemen (collection presently at Senckenberg, Frankfurt); NHMW = Naturhistorisches Museum Wien; NHRS = Naturhistoriska Riksmuseet Stockholm; QM = Queensland Museum, Brisbane; RMNH = Rijksmuseum van Natuurlijke Historie, Leiden [now 'Naturalis']; SMF = Senckenberg Museum, Frankfurt am Main; SNMNH = Saudi National Museum of Natural History (collection presently at Senckenberg, Frankfurt am Main); USNM = U.S. National Museum, Washington, D.C.; UZMK = Universitetets Zoologiske Museum, København; WAM = Western Australian Museum, Perth; ZRCNUS = Zoological Reference Collections, National University of Singapore; ZSI = Zoological Survey of India, Calcutta; ZSM = Zoologische Staatssammlung, München; ZMA = Zoologisch Museum Universiteit van Amsterdam; ZMG = Zoologisches Museum Göttingen (on Permanent loan to Senckenberg); ZMH = Zoologisches Museum Hamburg; ZMK = Zoologisches Museum Kiel.

TERMINOLOGY

The terminology we use for the body-parts is based on the thorough descriptions of Balss (1940, 1941), and Pesta (1918) and is explained in detail by Sakai *et al.* (2006).

Morphological features and their importance

A number of characters can be used for discriminating species within this genus, however these are not necessarily useful for creating natural groupings, and a discussion of their adaptive and phylogenetic value is necessary. In *Ocypode*, classifications simply based on the most obvious morphological characters result in different groupings depending on the primary feature used. This was the case in the past, and very different and incompatible relationships have been suggested. Therefore, the character complexes used in this paper are here discussed one by one, with regard to their usefulness in defining a natural phylogenetic classification.

Stridulating ridge. A stridulating ridge is found on the inner surface of the palm of the larger cheliped in all species except for *O. cordimanus*, and its morphology differs among species. It may be composed of tubercles, of tubercles with striae, of tubercles and tubercles with striae, of tubercles and striae, or solely of striae. It is one of the most important characters for distinguishing species, because it can be found even in juveniles. The difference in the structure of the stridulating ridge is closely related to the sound produced for communication, on which interspecific separations are based (Popper *et al.* 2001).We have observed that the stridulating ridge is often absent on regenerated claws (easily recognisable as abnormal because the larger cheliped is similar in size to the smaller one). As this would make sound production impossible, normal communication with other individuals must be severely impaired.

As stated, the morphology of the stridulating ridge is very useful for separating species, however this feature may not be useful in helping to define relationships between species. Selection pressures may actually promote diversification between species in order to avoid introgression. Furthermore the detection of plesiomorphies and apomorphies is rendered difficult, as even species without stridulating ridges exhibit a similar mode of sound production (Horch 1975; for *Gecarcinus*, see Klassen 1973). Von Hagen (1975) postulated that the existence of a stridulating ridge is a synapomorphy, however the one species lacking this character, *Ocypode cordimanus*, stridulates quite efficiently (Horch 1975), so it is difficult to know if the lack of a stridulating ridge in *O. cordimanus* is plesiomorphic, or if the ridge has been secondarily lost.

The suggestion that diversification plays a major role in determining the morphology, and sound patterns generated, is further supported by the fact that stridulating ridges of sympatric species are typically very different, while geographically distant species can be very similar. For example, the stridulating ridge of *O. occidentalis* (= *H. occidentalis*) from the eastern Pacific is

almost identical with that of *O. convexa* from Western Australia, though those two species are now classified under different genera according to the form of Go1. Thus it is apparent that a classification based on the shape of the stridulating ridge would be artificial.

The stridulating ridges of *Hoplocypode* and *Ocypode* species are characterised as follows:

1. *Hoplocypode occidentalis* (Fig. 1A). Stridulating ridge composed of *c.* 21–22 tubercles.

2. *Ocypode africana* (Fig. 1B). Stridulating ridge composed of 11–13 interspaced tubercles with striae in dorsal half and 21–26 closely spaced tubercles with striae in ventral half.

3. *Ocypode brevicornis* (Fig. 1C). Stridulating ridge composed of 23–28 tubercles.

4. *Ocypode ceratophthalma* (Figs 1D–I). Stridulating ridge composed of 10–11 interspaced tubercles in dorsal third, 8 thick striae in middle third, and 20–30 closely spaced striae in ventral third.

5. *Ocypode convexa* (Fig. 2A). Stridulating ridge composed of 19–24 tubercles.

6. *Ocypode cordimanus*. Stridulating ridge absent.

7. *Ocypode cursor* (Fig. 2B). Stridulating ridge composed of 69–96 tubercles with striae [*c.* 23 tubercles with striae in dorsal third and *c.* 46 closely pressed tubercles with fine striae in ventral two-thirds (SMF 9296)].

8. *Ocypode fabricii* (Fig. 2C). Stridulating ridge composed of 126–133 regularly and closely spaced fine striae.

9. *Ocypode gaudichaudii* (Fig. 2D). Stridulating ridge composed of 18 tubercles in dorsal half and 36–38 striae in ventral half.

10. *Ocypode jousseaumei* (Fig. 3A). Stridulating ridge composed of at least 41 (SMF 24530), 72 (NHMW) or at most 79 (Holotype) elements [15 tubercles in dorsal third and 26 closely spaced tubercles with striae in ventral two thirds (SMF 24530)].

11. *Ocypode kuhlii* (Fig. 3B). Stridulating ridge composed of *c.* 10 interspaced tubercles.

12. *Ocypode macrocera* (Fig. 3C). Stridulating ridge composed of 36–56 elements [9 slightly interspaced tubercles with striae in dorsal third and 27 closely pressed elongate tubercles with striae in ventral two-thirds (SMF 6772)]

13. *Ocypode madagascariensis* (Fig. 3D). Stridulating ridge composed of 20–30 closely spaced tubercles with striae.

14. *Ocypode mortoni* (Fig. 3E). Stridulating ridge composed of 35–71 striae.

15. *Ocypode nobilii* (Fig. 4A). Stridulating ridge composed of 99–120 closely spaced fine striae.

16. *Ocypode pallidula* (Fig. 4B). Stridulating ridge composed of 30–42 interspaced thick striae.

17. *Ocypode pauliani* (Fig. 4C). Stridulating ridge composed of 7–13 irregularly spaced tubercles.

18. *Ocypode quadrata* (Fig. 4D). Stridulating ridge composed of 15–18 interspaced tubercles.

19. *Ocypode rotundata* (Fig. 5A). Stridulating ridge composed of 10–15 irregularly spaced elongate tubercles with striae.

20. *Ocypode ryderi* (Fig. 5B). Stridulating ridge composed of *c.* 15 irregularly arranged tubercles.

21. *Ocypode saratan* (Fig. 5C). Stridulating ridge composed of 67–87 fine striae.

22. *Ocypode stimpsoni* (Fig. 5D). Stridulating ridges composed of 44–57 narrow striae, extending ventrally over midline of fixed finger to near ventral margin.

Eyestalks. Eyestalks are elongate throughout *Ocypode*, with the cornea located distally. In seven species the eyestalks are prolonged beyond the cornea (exophthalmy), and this appears to occur randomly within the genus. Its function is not yet known (von Hagen 1970). All species with exophthalmy have an associated reduction of the external orbital tooth, and the anterolateral corner of the carapace is more or less rounded. Exophthalmy is clearly apomorphic, but it is not clear if it can be regarded as a synapomorphic relationship among all species in which it occurs. Instead, it may have developed several times independently. In consequence, we feel this feature cannot be used, on its own, to define monophyletic groups within the genus.

Carapace, pereiopods and thoracic sternum. Most of these features are relatively homogeneous in morphology. This applies especially to the carapace which shows only minor variation in shape, although the granulation may vary among species. This is also true of the shape of the front. The sternum is that of a typical thoracotreme crab (see Guinot 1969), and again there are only minor variations in granulation

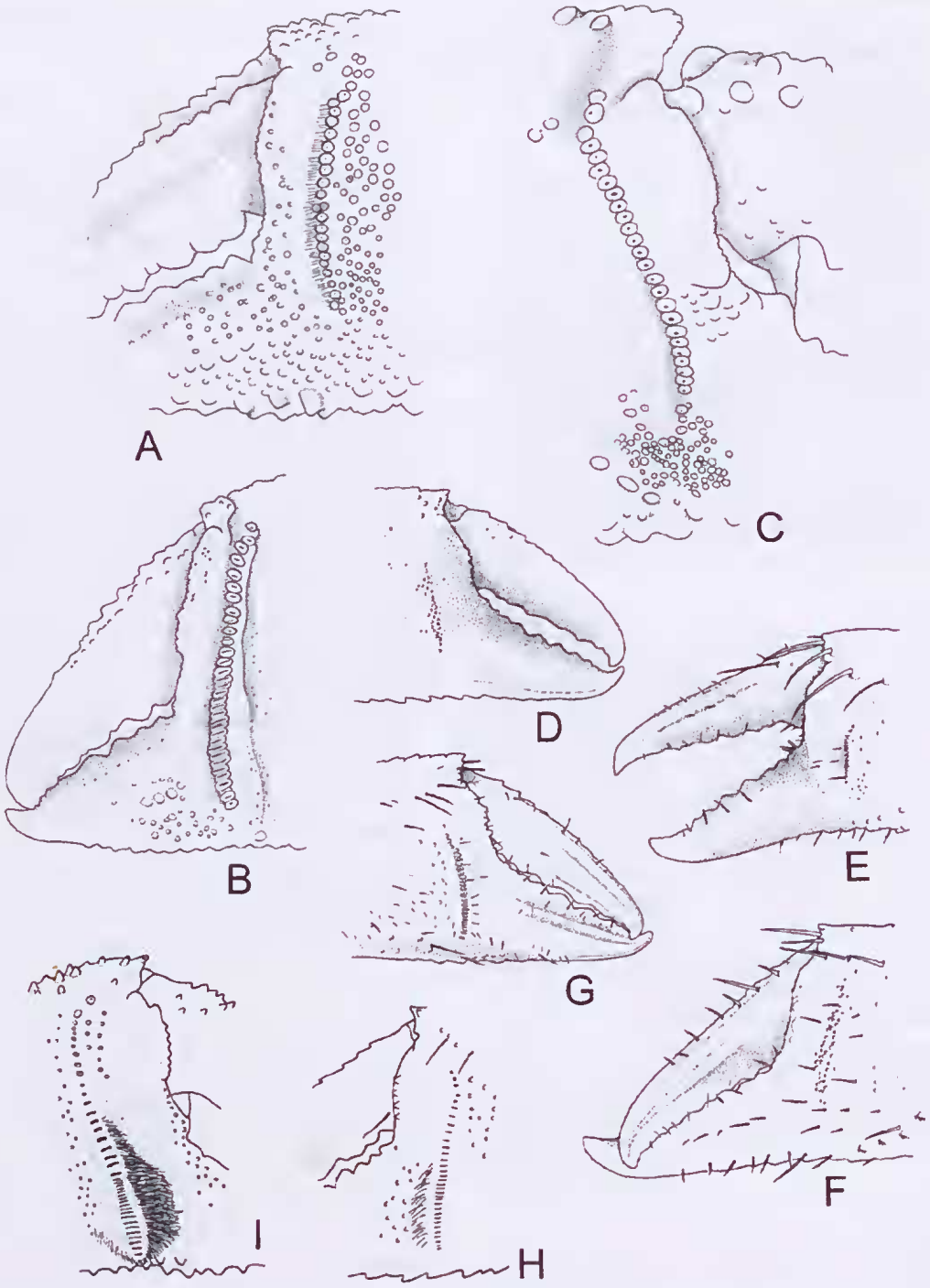

FIG. 1. Stridulating ridges: **A**, *Hoplocypode occidentalis*, SMF-2191; **B**, *Ocypode africana*, SMF-4364; **C**, *Ocypode brevicornis*, SMF-24536; **D**, *Ocypode ceratophthalma*, RMNH 30272, CW 9.5 mm; **E**, same, CW 6.3 mm; **F**, same, 6.2×5.8 mm; **G**, same, CW 13.3 mm; **H**, same, CW 17.5 mm; **I**. same, adult male specimen.

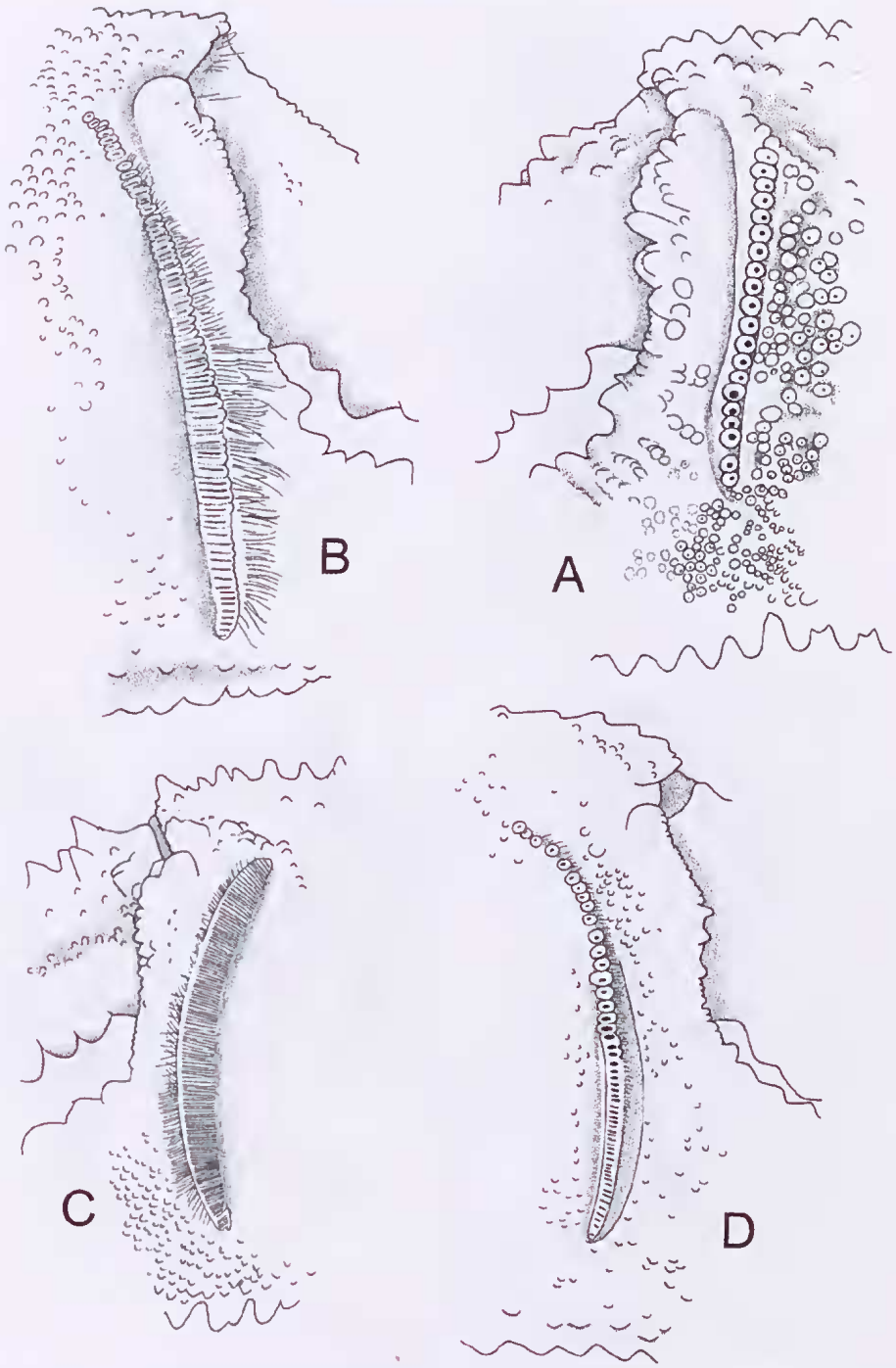

FIG. 2. Stridulating ridges: **A**, *Ocypode convexa*, SMF-7609; **B**, *Ocypode cursor*, SMF-9269; **C**, *Ocypode fabricii*, SMF-7612; **D**, *Ocypode gaudichaudii*, SMF-11443.

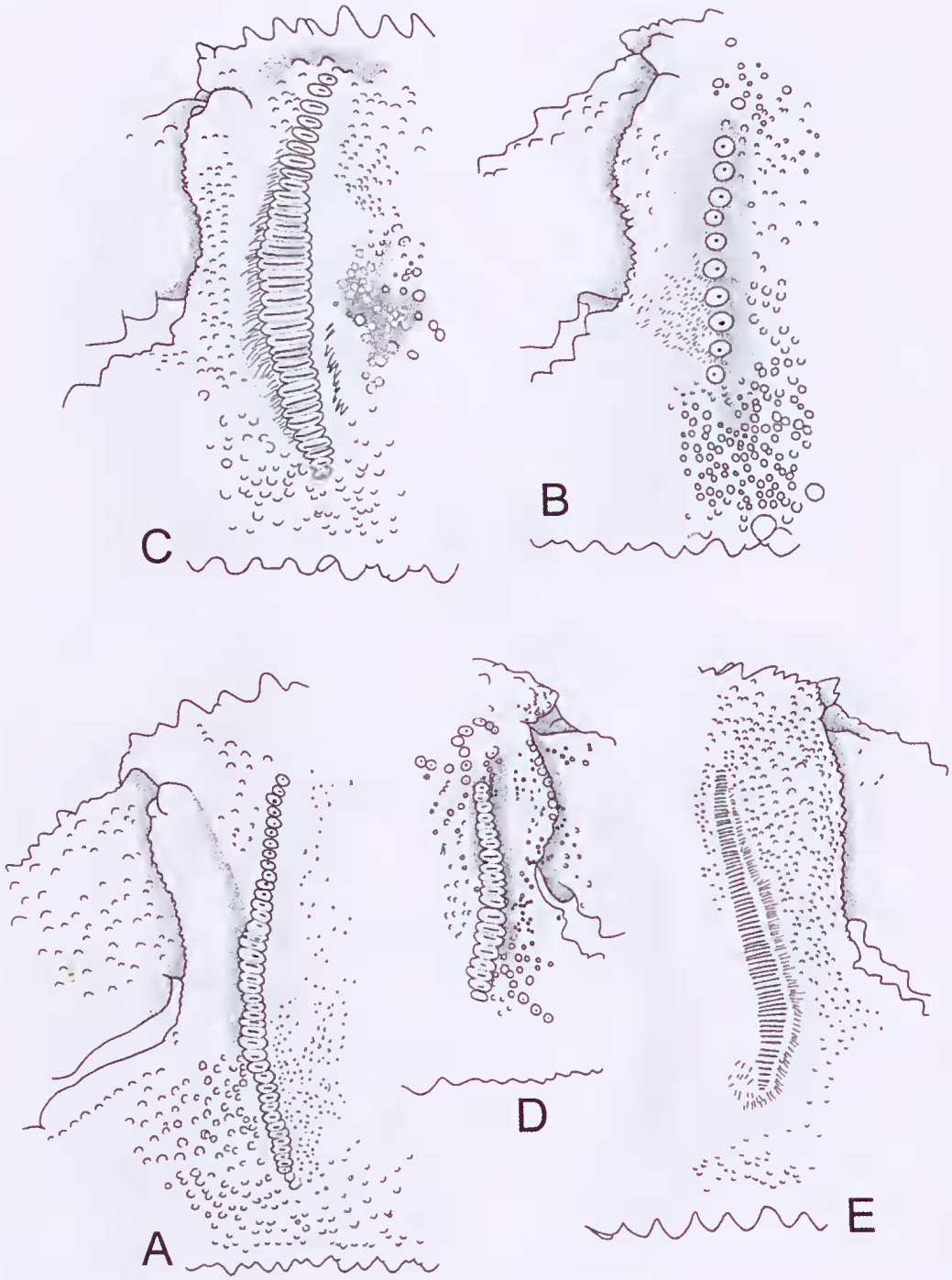

FIG. 3. Stridulating ridges: **A**, *Ocypode jousseaumei*, SMF-24530; **B**, *Ocypode kuhlii*, SMF-23298; **C**, *Ocypode macrocera*, SMF-6772; **D**, *Ocypode madagascariensis*, SMF-7274; **E**, *Ocypode mortoni*, SMF-36912.

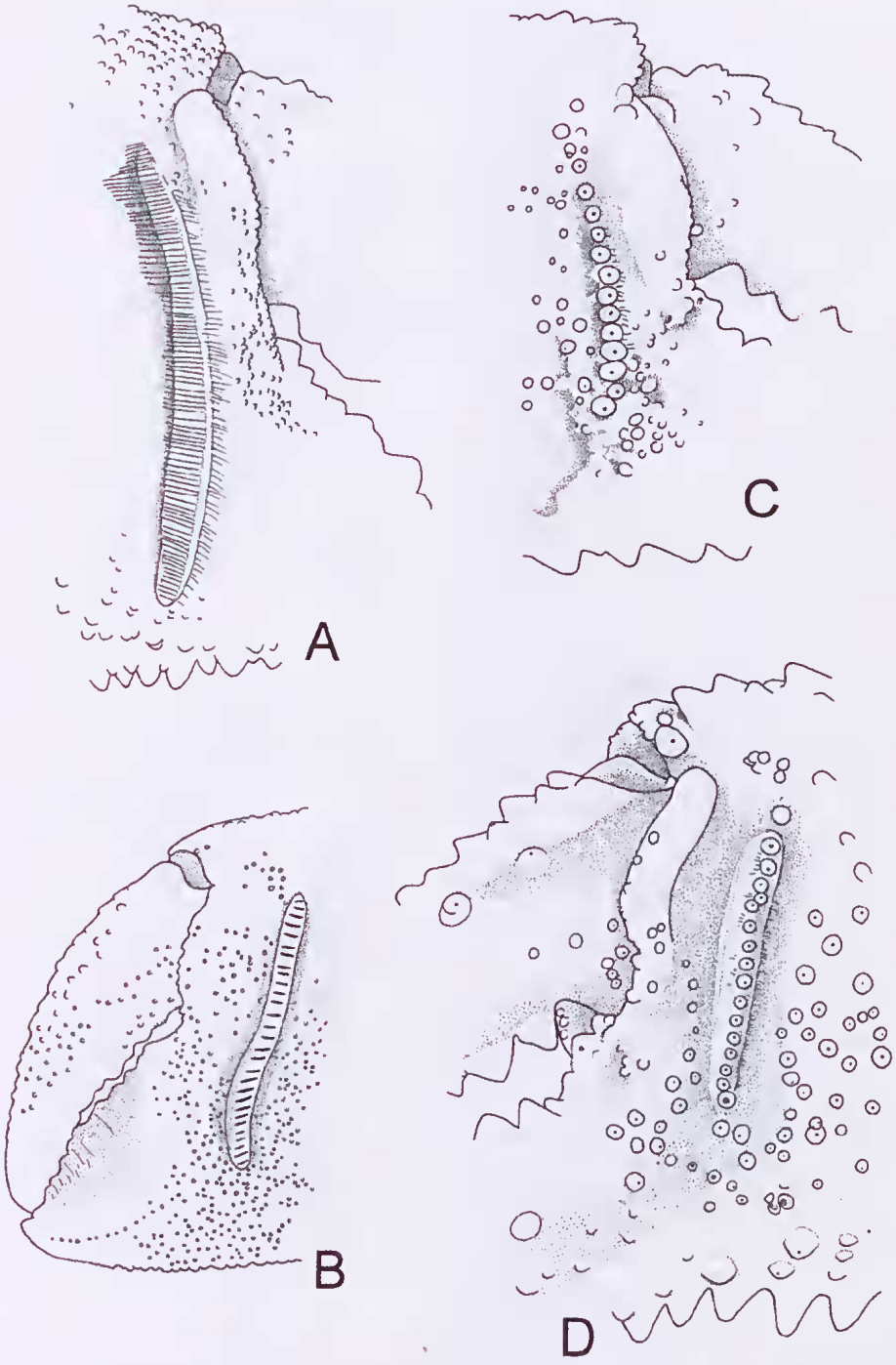

FIG. 4. Stridulating ridges: **A,** *Ocypode nobilii*, SMF-5412; **B,** *Ocypode pallidula*, SMF-10924; **C,** *Ocypode pauliani*, SMF-1958; **D,** *Ocypode quadrata*, SMF-16595.

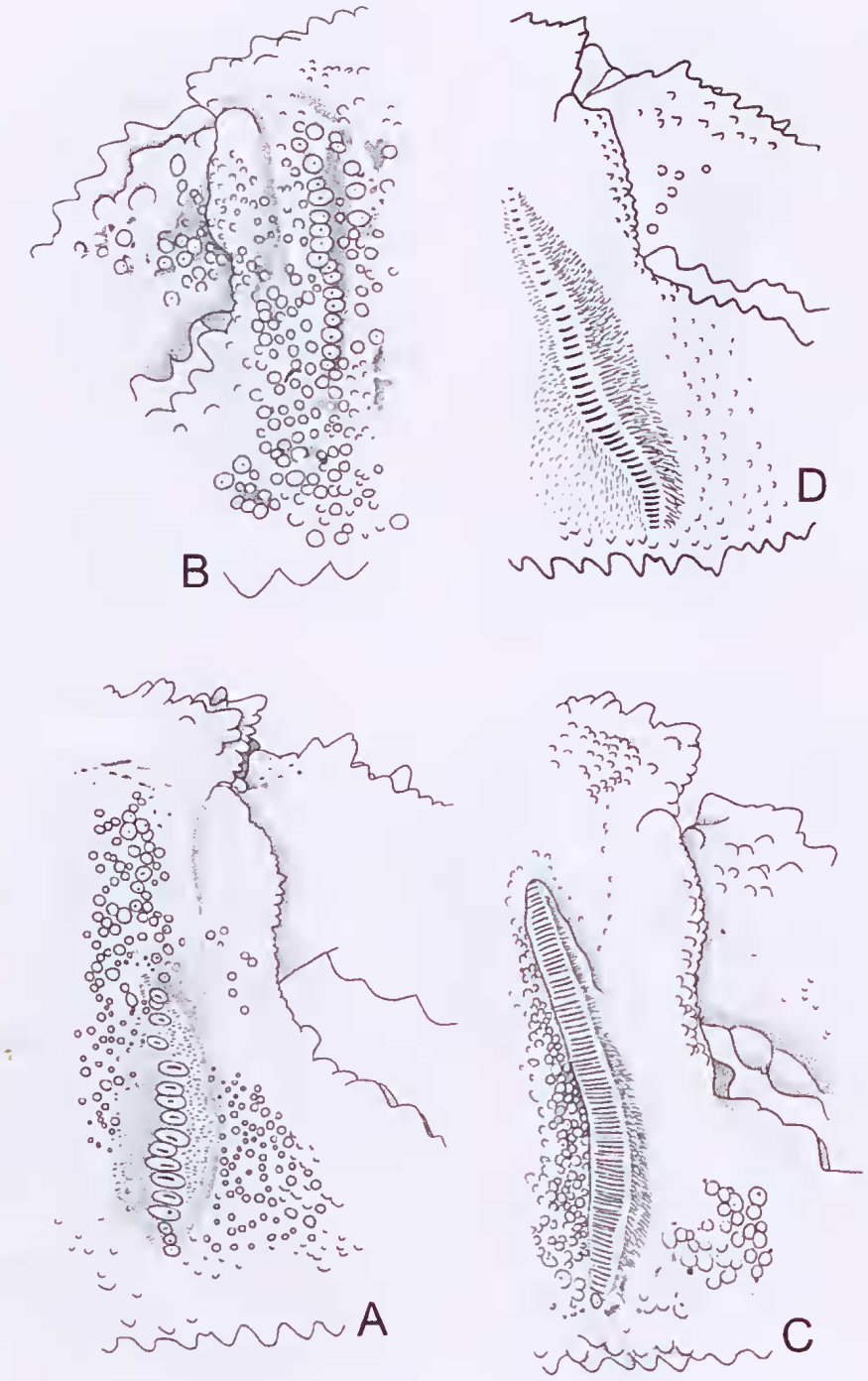

FIG. 5. Stridulating ridges: **A,** *Ocypode rotundata*, SMF-24535; **B,** *Ocypode ryderi*, NHCY-86; **C,** *Ocypode saratan*, SMF-36171; **D,** *Ocypode stimpsoni*.

Table 1. The distribution of the species in the genera *Hoplocypode* and *Ocypode*.

Atlantic Ocean and Mediterranean Sea	
Mediterranean Sea	*Ocypode cursor*
Eastern Atlantic	*O. cursor* *O. africana*
Western Atlantic	*O. quadrata*
Eastern Pacific Ocean	
Eastern Pacific	*Hoplocypode occidentalis* *O. gaudichaudii*
Indo-West Pacific Ocean	
Hawaii, Central and Southern Pacific, and Eastern Australia	*O. ceratophthalma* *O. cordimanus* *O. pallidula*
China and Japan	*O. ceratophthalma* *O. cordimanus* *O. mortoni* *O. pallidula* *O. stimpsoni*
Sarawak, Gulf of Thailand	*O. ceratophthalma* *O. cordimanus* *O. nobilii*
Indonesia	*O. ceratophthalma* *O. cordimanus* *O. kuhlii* *O. pallidula*
Northern and Western Australia	*O. fabricii* *O. ceratophthalma* *O. convexa* *O. cordimanus* *O. pallidula*
India and Indian Ocean	*O. brevicornis* *O. ceratophthalma* *O. cordimanus* *O. macrocera* *O. pallidula* *O. rotundata*
Persian Gulf and Gulf of Oman	*O. rotundata*
Gulf of Aden	*O. jousseaumei* *O. saratan*
Red Sea	*O. cordimanus* *O. saratan*
Madagascar	*O. ceratophthalma* *O. cordimanus* *O. madagascariensis* *O. pallidula* *O. pauliani*
Eastern and Southern Africa	*O. ceratophthalma* *O. cordimanus* *O. madagascariensis* *O. ryderi*

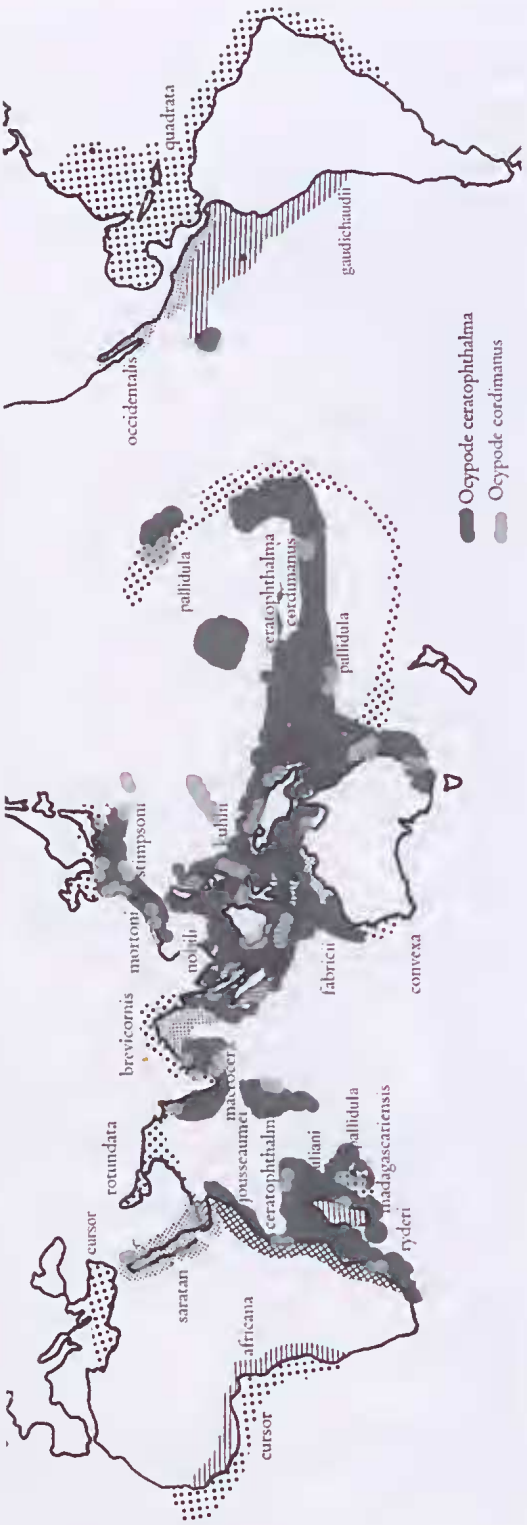

FIG. 6. Distribution map of *Ocypode*.

and armature among species. However, as an agile runner, the ghost crabs have a very particularly broad sternum to provide support for increased leg musculature. The arrangement of setae on the merus and propodus of the walking legs is very characteristic for individual species, but again similarities in pattern are just as likely to be ecotypically convergent, as they are to be synapomorphic.

Gonopod. The significance of gonopod morphology for detecting relationships in brachyuran crabs has been dealt with in several publications (Türkay 1975, Magalhães & Türkay 1996, Brandis *et al.* 1999). The main argument is that evolutionary selection pressure determining the morphology of the copulatory apparatus favors efficient functioning during sperm transfer, and thus is less likely to be impacted by environmental factors. Functionally, the copulatory organ of both sexes must be complementary, and therefore there should be very low variability. This means that a significant change in morphology must occur in both sexes simultaneously, and thus it is highly improbable that closely related species would have very different copulatory structures. Only a gradual change is possible, much slower than in non-sexual characters, and thus these organs are of major significance for determining relationships. Of course, some minor characters, such as slight changes in the length of the palp, can still show some intraspecific variability.

Family OCYPODIDAE Rafinesque, 1815

Ocypodia Rafinesque, 1815: 96.
Ucainae Dana, 1851: 289.
Gelasimiden Nauck, 1880: 8, 17, 23, 64, 66 [unavailable as not in Latin].
Gelasimidae Miers, 1886: viii.
Ocypodidae, Manning & Holthuis, 1981: 192; Davie, 2002: 345; Ng, Guinot & Davie, 2008: 240.

Subfamily OCYPODINAE Rafinesque, 1815

Type genus: *Ocypode* Weber, 1795.

Genera included: *Hoplocypode* gen. nov.; *Ocypode* Weber, 1795.

Remarks. The distribution list shows that many species occur in the Indo-Pacific region, but only three species, *Ocypode ceratophthalma*, *O. cordimanus*, and *O. pallidula* are widely distributed. Interestingly, only *O. ceratophthalma* and

O. cordimanus are sympatric throughout nearly their entire ranges (Fig. 6).

KEY TO THE GENERA OF OCYPODINAE

1. Go1 complex at distal end, hoof-shaped in mesial view. . . . . *Hoplocypode* gen. nov.
– Go1 simple at distal end. . . . . *Ocypode* Weber, 1795

Hoplocypode gen. nov.

Diagnosis. Body deep. Carapace quadrate, regions ill-defined, front deflexed. Eye-stalks large, cornea occupying most of ventral surface of stalk. A1 long; inner antennal-septum broadened. Chelipeds unequal in both sexes, palm of larger chela usually provided with a stridulating ridge of tubercles. P1–4 strong; P5 weaker than others. Most part of male sternite 8 not covered by abdomen. Go1 complex in shape at distal end, hoof-shaped in mesial view.

Type species. *Ocypoda occidentalis* Stimpson, 1860, by present designation and monotypy.

Distribution. Eastern Pacific; Gulf of California to Colombia.

Etymology. *Hoplocypode* is derived from the Greek 'hoplē', meaning a hoof (horseshoe), and refers to the hoof-shaped Go1 of the type species when seen in distal mesial view. Gender is feminine.

Hoplocypode occidentalis (Stimpson, 1860)

(Figs 1A, 7, 29)

Ocypoda occidentalis Stimpson, 1860: 229.

Ocypode occidentalis — Rathbun, 1899: 74; 1918: 372, tab. 129, figs 2–3; 1923: 632; Boone, 1929: 580, text-fig. 16; Glassell, 1934: 302; Crane, 1940: 65, figs 3–8; 1941: 308, figs 3, 4E–F, 5A, C, E, 6A, C; 7A, B, pl. 1 fig. 2, pl. 2 fig. 5; Garth, 1948: 59, pl. 4, fig. 2; Buitendijk, 1950: 279 [in part]; Holthuis, 1954a: 40; 1954b: 162; Bott, 1955: 67; Bright & Hogue, 1972: 9; Ng *et al.*, 2008: 240.

Ocypode gaudichaudii — Lockington, 1877: 145 [not *Ocypode gaudichaudii* H. Milne Edwards & Lucas 1843].

Ocypoda Kuhlii — Miers, 1882: 385 [in part], tab. 17, fig. 8b [not *Ocypode kuhlii* De Haan, 1835].

Material examined. Mexico. No exact locality, male (MHNG); male (ZMH-2798); 3 males, 2 females (ZMH-2941); — Baja California: no exact locality, male, female, 1 juv. female, 6 juvs. (MNHN); female (NHMW); — Estado Baja California Sur: Todos Santos, 2 females (RMNH-7561, Buitendijk, 1950); — La Paz, male (NHMW-1401); 9 males, 6 females (MNHN); — El Mogote near La Paz, female (AMS-P 5495); — Cape St. Lucas, male, female (syntype of Stimpson, 1860, MNHM); female (UZMK); 2 juvs. (UZMK); — Estado Sinaloa: Las Copas, Topolobampo, 1 juv. (RMNH-7611); — Mazatlan (23°16.59′N, 106°28.07′W), 10.i.1974, W. Baumeister; beach at northern end of town, male (SMF-7497), 23.viii.1984, A. Allspach; male, 6 juvs. (SMF-12999); — Estado Guerrero: Acapulco, male (RMNH-7560, Buitendijk, 1950); 4 juvs. (RMNH-7559). **Guatemala**. male (NHMB-564a); 5 males, 4 females (ZMH-2865); 2 males, female (ZMH-2923); male, female (ZMH-2924). **El Salvador**. Depto. Ahuachapán: El Zapote (13°42.7′N, 90°01.9′W), 2 juvs. (SMF-6858), 23.iv.1953, O. Schuster; — Depto. Sonsonate: Metallo (13°37.9′N, 89°53.5′W), 2 juvs. (SMF-5414), O. Schuster; — Acajutla (13°35.3′N, 89° 50.03′W), male, female, 1 juv. (SMF-2210), O. Schuster; — Las Salinas de Cachapa (13°33.5′N, 89°41.5′W), 1 juv. male, 2 juvs. (SMF-2199), O. Schuster; — Las Salinas (13°32.0′N, 89°41.0′W), 11 juvs. (RMNH-9650); Playa de las Piedras (13°31.9′N, 89°40.0′W), 3 juvs. (SMF-6855), 13.ii.1952, O. Schuster; — Depto. La Libertad: Playa Zunzal near La Libertad (13°15.6′N, 89°23.5′W), 2 juvs. (SMF-6857), 27.ii.1953, O. Schuster;— La Libertad (13°29.0′N, 89°19.6′W), 9 males, female (SMF-2191), 2 males (RMNH-9655), O. Schuster;— Playa de las Flores near La Libertad (13°29.1′N, 89°17.7′W), male (SMF-2200), 1 juv. (SMF-16173), O. Schuster; — Toluca (13°27.1′N, 89°13.0′W), 3 juvs. (SMF-6859), 10.xii.1952, O. Schuster; — Depto. La Paz: Playa las Hojas (13°21.48′N, 89°2.65′W), 1 juv. (SMF-16172), 28.xi.1952, O. Schuster; — Amate de Campo (13°21.3′N, 89°02.2′W), male, female, 13 juvs. (SMF-2204), O. Schuster; — Los Blancos (13°20.0′N, 88°58.9′W), 1 juv. (SMF-6853), 17.x.1952, O. Schuster; — Depto. Usulutan: La Pita, mouth of Rio Lempa (13°15.6′N, 88°50.0′W), 2 juvs. (SMF-6856), 19.iii.1953, O. Schuster; — Coral de Mula, Peninsula San Juan del Gozo (13°12.2′N, 88°31.8′W), 2 juvs. (SMF-6854), 17.xii.1952, O. Schuster; — SE tip of Peninsula San Juan del Gozo (13°10.7′N, 88°27.6′W), male, female (SMF-2076), H.M. Peters; —La Chepona, (13°11.0′N, 88°21.0′W), 1 juv. (RMNH-9658); — *ibid.*, male (SMF-2205), O. Schuster; — Estero, 5 juvs. (RMNH-9657). **Panama**. No exact locality. **Incorrect localities.** Mexico: Is. Sacrificio, male (MCM-2340). Honduras. 4 males, 3 females (SMF-4104), H. M. Peters. Venezuela, female (UZMK).

Diagnosis. Middle-sized species. Eyestalks not prolonged distally beyond cornea. Lateral half of orbital margin distinctly concave. Exorbital angles triangular and distinctly protruding anteriorly. Stridulating ridge composed of *c.* 21–22 tubercles. P2–3 propodi setose on dorsal half of anterior surface. Go1 complex in shape at distal end, hoof-shaped. Female genital opening membranous and slightly calcified.

Description. Carapace (Fig. 29) wider than long and covered densely with coarse tubercles. Lateral half of orbital margin distinctly concave. Exorbital angles acutely triangular and directed anteriorly. Lateral margins of carapace directed slightly outward from base of exorbital angle in anterior half of carapace, and then directed mesially in posterior half, and carapace broadest in middle. Pterygostomial region distinctly tuberculate, except around buccal cavern. P1 thoracic sternite (Fig. 7A) sparsely tuberculate medially, bearing tuberculate carinae on anterior and lateral margins. Palm of larger cheliped elongate and distinctly serrated on ventral margin, bearing coarse tubercles on anterior surface. Stridulating ridge (Fig. 1A) composed of *c.* 21–22 tubercles. Smaller cheliped tapering to pointed distal end. Male P2–3 propodi (Fig. 7B–C) with setae on dorsal margin; bearing transverse rows of setae on dorsal half and two median rows (in P2), or one indistinct row of setae (in P3) on anterior surface. P4 propodus with setae only on dorsal margin. P5 propodus naked. In female P4–5 propodi naked on anterior surface. Go1 (Fig. 7D–E) three-sided proximally; hoof-shaped at distal end. Operculum of female genital duct (Fig. 7F) quadrate, membranous, and slightly calcified. Slit of genital opening narrow and mesial with respect to operculum; directed along longitudinal axis of sternum.

Juvenile specimens. In a specimen from El Salvador (4.8×5.8 mm, SMF-2204) carapace distinctly wider than long and covered with fine tubercles on dorsal surface. Exorbital angles located far backward, but already acutely triangular as in adult specimens. Palm of larger cheliped flat on mesial surface. Stridulating ridge composed of short row of tubercles in median third on inner surface of palm. P2–3 propodi setose on dorsal half of anterior surface. In a specimen from El Salvador (6.3×6.4 mm, SMF-6859) stridulating ridge composed of a longer row of irregularly arranged tubercles.

Distribution. Gulf of California to Colombia in the Eastern Pacific Ocean. Type locality: Cape San Lucas, Baja California peninsula, Mexico.

Remarks. *Hoplocypode occidentalis* is very similar to *Ocypode quadrata* from the western Atlantic coast, and has sometimes been regarded as its Pacific Ocean sister species. However, those two species are clearly distinguished from each other by significant differences not only in the structure of the Go1, but also in the arrangement pattern of setae on the anterior surfaces of the P2–3 propodi. Moreover, the difference in distribution between the two species prevents them from being confused; *H. occidentalis* is distributed on the eastern Pacific coast, whereas *O. quadrata* is on the western Atlantic coast. *H. occidentalis* is also similar to the eastern Pacific *O. gaudichaudii* in the pattern of setae on the anterior surfaces of the P2–3 propodi, and they could therefore be confused with each other. However, those two species are easily distinguishable by the differences shown in Table 2. It is very difficult to distinguish juvenile specimens of those two species when they are smaller than CL×CW 5.0×6.0 mm, and this has led to some past confusion in identifications.

Based on the characters given in Table 2, all reports of *Ocypode occidentalis* (= *Hoplocypode occidentalis*) from Peru are incorrect, because they were made, without exception, on the basis of juvenile specimens of *O. gaudichaudii*.

The report of *O. urvillei* from Peru by Doflein (1899), based on a juvenile specimen, has also caused subsequent confusion because his diagnosis was not clear enough for identification, and his only specimen was later lost. Rathbun (1918) considered Doflein's record to refer to *O.*

Table 2. Differences between *H. occidentalis* and *O. gaudichaudii*.

	H. occidentalis	*O. gaudichaudii*
Eyestalks	Not prolonged distally.	Prolonged distally.
Both chelae	Pointed distally.	Truncate distally.
Stridulating ridge	Short, composed of 21–22 tubercles.	Long, composed of 18 tubercles and 38 striae.
P1 palm	Flat on mesial surface.	Distinctly convex on mesial surface.

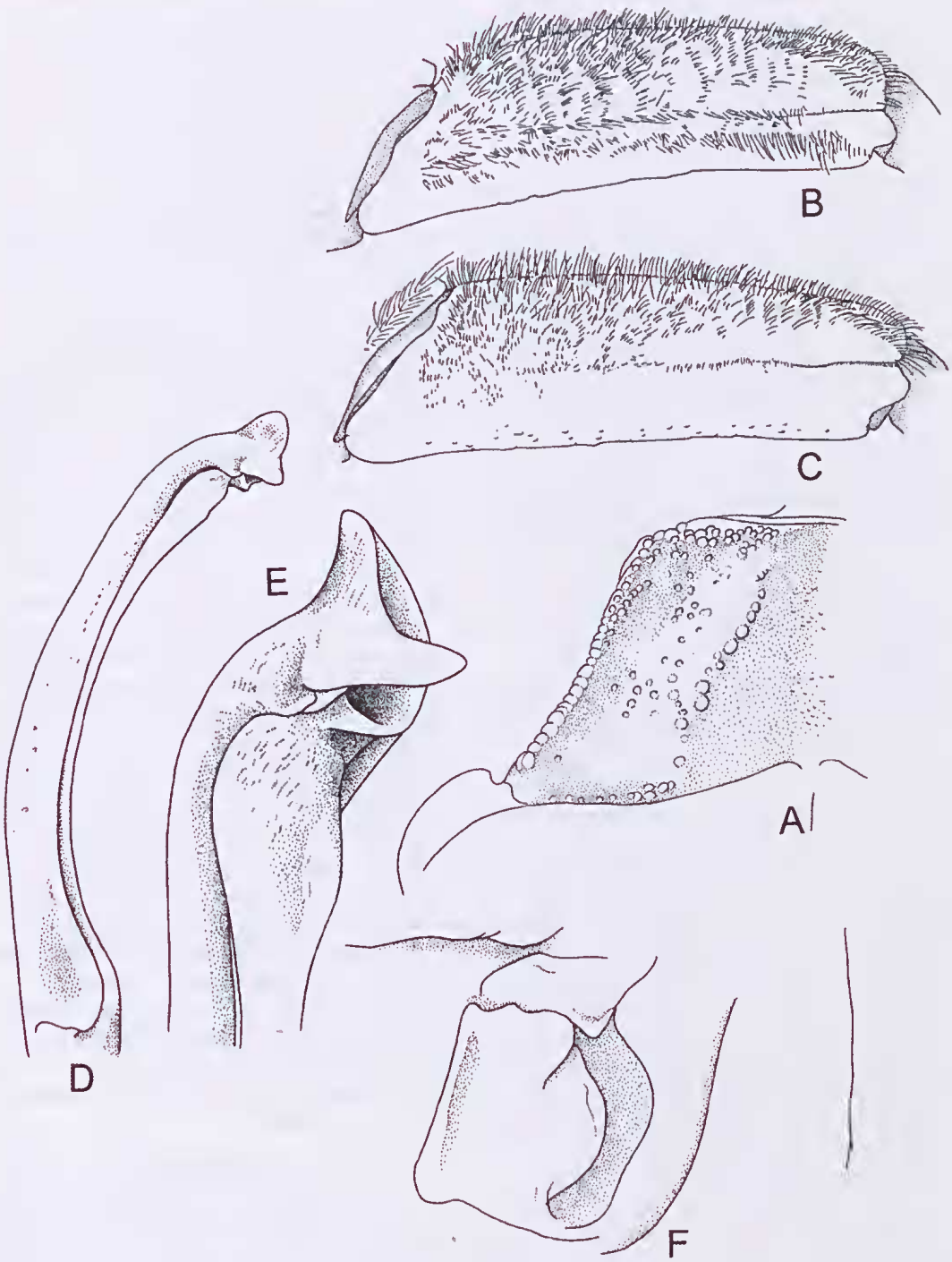

FIG. 7. *Hoplocypode occidentalis*: **A**, P1 thoracic sternite; **B, C**, P2–3 propodi; **D, E**, Go1; **F**, female operculum.

occidentalis (= *H. occidentalis*), but with hesitation. It is logical to assume, however, that Doflein's record must be of the eastern Pacific *O. gaudichaudii*, because *O. urvillei* (= *O. ceratophthalma*) only occurs in the Indo-West Pacific.

Ocypode Weber, 1795

Ocypode Weber, 1795: 92 [type species: *Cancer ceratophthalmus* Pallas, 1772, subsequent designation by Latreille, 1810: 95, 422: gender feminine] [ICZN (1964), Opinion 712; name 1637 on Official List].

Ocypode Fabricius, 1798: 312, 347 [a junior objective homonym of *Ocypode* Weber, 1795; type species: *Cancer ceratophthalmus* Pallas, 1772, by selection by Latreille, 1810: 95, 422; gender feminine] [ICZN Opinion 712; name 1738 on the Official Index of Rejected and Invalid Generic Names in Zoology].

Ocypoda Lamarck, 1801: 149 [an incorrect subsequent spelling for *Ocypode* Weber, 1795] [ICZN (1964), Opinion 712; name 1737 on the Official Index of Rejected and Invalid Generic Names in Zoology].

Monolepis Say, 1817: 155 [type species: *Monolepis inermis* Say, 1817, a subjective junior synonym of *Cancer quadratus* Fabricius, 1787, by selection by Fowler, 1912: 457; gender feminine].

Ceratophthalma MacLeay, 1838: 64 [type species: *Cancer cursor* Linnaeus, 1758, by monotypy; gender feminine].

Parocypoda Neumann, 1878: 26 [junior objective synonym of *Ocypode* Weber, 1795; gender feminine. Type species: *Cancer ceratophthalmus* Pallas, 1772 by monotypy].

Diagnosis. Body deep. Carapace subquadrangular, regions ill-defined, front deflexed. Eye-stalks large, cornea occupying most of ventral surface of stalk which is often produced beyond cornea like a horn. A1 long; inner antennal septum broadened. Chelipeds unequal in both sexes, palm of larger chela usually with a stridulating ridge of tubercles, tubercles with streae, or striae. P1–4 strong; P5 weaker than others; dactylus fluted. A cavity, connecting with branchial chamber, between bases of P3–4, its edges fringed with long setae. Greater part of male thoracic sternite 8 not covered by carapace. Go1 simple distally. (Revised after Barnard, 1950: 83).

Remarks. *Ocypode* Weber, 1795 is most closely related to *Uca* Leach, 1814, but differs in numerous characters. In *Ocypode*, the carapace is subquadrate; the eyestalks are stout; the chelipeds are unequal in both sexes; the palm of the larger chela is usually provided with a stridulating ridge of tubercles, striae, or both; and the male Go1 is incurved distally. In *Uca*, the carapace is wider than long; the eyestalks are slender; the chelipeds are unequal in males, but equal in females; there is no stridulating ridge on the palm of the larger chela; and the male Go1 is slightly incurved.

Species included: *Ocypode africana* De Man, 1881; *O. brevicornis* H. Milne Edwards, 1837; *O. ceratophthalma* (Pallas, 1772); *O. convexa* Quoy & Gaimard, 1824; *O. cordimanus* Latreille, 1818; *O. cursor* Linnaeus, 1758; *O. fabricii* H. Milne Edwards, 1837; *O. gaudichaudii* H. Milne Edwards & Lucas, 1843; *O. jousseaumei* (Nobili, 1905); *O. kuhlii* De Haan, 1835; *O. macrocera* H. Milne Edwards, 1837; *O. madagascariensis* Crosnier, 1965; *O. mortoni* George, 1982; *O. nobilii* De Man, 1902; *O. pallidula* Hombron & Jacquinot, 1846; *O. pauliani* Crosnier, 1965; *O. quadrata* (Fabricius, 1787); *O. rotundata* Miers, 1882; *O. ryderi* Kingsley, 1881; *O. saratan* (Forskål, 1775); *O. stimpsoni* Ortmann, 1897.

There are two other available names, *Ocypode minuta* Fabricius, 1798, and *Ocypode laevis* Fabricius, 1798, however these species have not been reported since the type description, the type specimens appear to have been lost, and the descriptions are so short and ambiguous that they are inadequate for recognising any species. Ng *et al.* (2008: 240) listed them as *incertae sedis*, and we here treat them as a *nomen dubium*. The identity of another Fabricius species, *Ocypode rhombea* Fabricius, 1798, has also been confused in the past, and often treated as a junior subjective synonym of *Ocypode quadratus* (Fabricius, 1787) (see Ng *et al.* 2008: 240). However, in this case, there is a presumed juvenile type specimen in the ZMUC, and based on examination of this, we are confident that *O. rhombea* Fabricius, 1798, is a junior synonym of *O. ceratophthalma* (Pallas, 1772) (see later).

KEY TO SPECIES OF *OCYPODE*

Key works best with adults. In juveniles the eyestalks are not sufficiently developed to be useful; in this case choices should be first restricted according to the region of occurrence (Table 1), and then the stridulating ridges compared to reach a determination.

1. Eyestalks prolonged distally beyond cornea in a stylus, or eyestalks with a setal brush at distal end of cornea. 2
– Eyestalks neither prolonged distally beyond cornea in a stylus, nor bearing setal brush at distal end of cornea. 9
2. Eyestalks with a setal brush at distal end of cornea. Stridulating ridge composed of *c.* 69–96 fine striae [about 23 striae on interspaced tubercles in dorsal half and about 46 closely arranged fine striae in ventral half]. . . . . *O. cursor*
– Eyestalks prolonged distally beyond cornea in a stylus. 3
3. P2–3 propodi naked on anterior surface. Stridulating ridge composed of 23–28 tubercles. . . . . *O. brevicornis*
– P2–3 propodi with setae, or P2 propodus with setae and P3 propodus naked. 4
4. P2 propodus with setae, and P3 propodus naked. 5
– P2–3 propodi with setae. 6
5. Stridulating ridge composed of 10–15 irregularly spaced elongate tubercles with striae. . . . . *O. rotundata*
– Stridulating ridge composed of 67–87 fine striae. P2 propodus with a wide median row of setae on anterior surface.. *O. saratan*
6. Both chelipeds pointed distally. Stridulating ridge composed of 10–11 interspaced tubercles in dorsal third, 8 thick striae in middle third, and 20–30 closely spaced striae in ventral third. . *O. cerathophthalma*
– Both chelipeds truncate distally, or larger cheliped pointed distally but smaller cheliped rounded to truncate distally. . . 7
7. Both chelipeds truncate distally. Stridulating ridge composed of *c.* 18 tubercles in dorsal half and *c.* 38 striae in ventral half. . . . . *O. gaudichaudii*
– Larger cheliped pointed distally but smaller cheliped rounded to truncate distally. 8
8. Stridulating ridge composed of 35–71 striae. not extending ventrally beyond middle of fixed finger. . . . . *O. mortoni*
– Stridulating ridge composed of 36–56 tubercles with striae; 9 slightly interspaced tubercles with striae in dorsal third and 27 closely arranged elongate tubercles with striae in ventral two thirds. . . . . *O. macrocera*
9. Mesial surface of palm of larger cheliped without a stridulating ridge. P2 propodus with setae along dorsal margin and transverse rows of setae on dorsal half, bearing a median row of setae on anterior surface. P3 propodus with thick setae along dorsal margin. . . . . *O. cordimanus*
– Mesial surface of palm of larger cheliped always bearing a stridulating ridge. . . . 10
10. P2–3 propodi with median rows of setae on anterior surface, bearing long setae on and along dorsal and ventral margins. Stridulating ridge composed of 15–18 interspaced tubercles. . . . . *O. quadrata*
– P2–3 propodi with setae on anterior surface, or either P2–3 propodi naked or P2 propodus with setae but P3 propodus naked on anterior surface. 11
11. P2–3 propodi naked, or P2 propodus with setae but P3 propodus naked. 12
– P2–3 propodi with setae on anterior surface. 16
12. P2–3 propodi naked. 13
– P2 propodus with setae, but P3 propodus naked. 15
13. Stridulating ridge composed of *c.*11–13 interspaced stout tubercles with striae in dorsal half and 21–26 closely spaced tubercles with striae in ventral half. . . . . *O. africana*
– Stridulating ridge composed of interspaced tubercles.. 14
14. Stridulating ridge composed of *c.* 10 interspaced tubercles. Greatest width of carapace near midline. . . . . *O. kuhli*
– Stridulating ridge composed of *c.* 15 irregularly arranged tubercles. Greatest width of carapace at anterior 1/3. . . . . *O. ryderi*
15. Stridulating ridge composed of 41–79 elements, which gradually transformed from tubercles into tubercles with striae from above downwards. P2 propodus with a median row of setae on anterior surface. Exorbital tooth directed obliquely forward. Carapace with coarse granulations. . . . . *O. jousseaumei*
– Stridulating ridge composed of 126–133 regularly and closely spaced fine striae. Exorbital tooth directed obliquely forward. P2 propodus with transverse rows of

tubercles on dorsal half of anterior surface, bearing one median row of setae and another one on ventral half. . . . *O. fabricii*

16. Stridulating ridge composed of striae. . 17
– Stridulating ridges composed of tubercles, or tubercles with striae. 19

17. Stridulating ridge composed of 99–120 closely spaced fine striae. P2 propodus setose along dorsal margin, bearing a median row of long setae and another short row of long setae just below on anterior surface. P3 propodus with transverse rows of setae on dorsal half of anterior surface, bearing a median row of setae. . . *O. nobilii*
– Stridulating ridge composed of 17–57 striae. 18

18. Stridulating ridge composed of 30–42 (in male), or 17–29 (in female) rather interspaced thick striae, extending to ventral fourth of palm. Ventral margin of palm of larger chela granulate. P2 propodus sparsely setose on anterior surface, bearing a short median row of scanty setae, and setae along dorsal margin. P3 propodus sparsely setose on dorsal half of anterior surface, bearing setae and spinules on dorsal margin. . . . . *O. pallidula*
– Stridulating ridge composed of 44–57 narrow striae, extending to near ventral margin of palm. Ventral margin of palm of larger chela distinctly serrate. P2 propodus with a median row of thick setae on anterior surface. P3 propodus with transverse rows of setae on dorsal half of anterior surface, bearing a median row of setae. . . . . *O. stimpsoni*

19. Stridulating ridge composed of 20–30 closely arranged tubercles with striae. P2–3 propodi setose on dorsal half of anterior surface. Go1 strongly crooked laterally in distal part. . . . . *O. madagascariensis*
– Stridulating ridge composed of tubercles. 20

20. Stridulating ridge composed of 7–13 tubercles. P2–3 propodi with setae on and along dorsal margin, which are expanding distally onto anterior surface. . . . . *O. pauliani*
– Stridulating ridge composed of 19–24 tubercles. P2 propodus with setae on dorsal margin, and P3 propodus with a row of setae along dorsal margin on anterior surface. Go1 smootly curved in distal part. . . *O. convexa*

Ocypode africana De Man, 1881
(Figs 1B, 8, 30)

Ocypode africana De Man, 1881: 253; Büttikofer, 1890: 465, 487; Ortmann, 1897: 365; Rathbun, 1900: 275; 1921: 462, pl. 53; Bouvier, 1922: 74; Rossignol, 1957: 86; Guinot-Dumortier & Dumortier, 1960: 136, 148, tab. 3; Bott, 1964: 30; Forest & Guinot, 1966: 89; Kensley, 1970b: 180; Penrith & Kensley, 1970: 252, 260; Manning & Holthuis, 1981: 218; Antia, 1989: 264; Ng, Guinot & Davie, 2008: 240.
Ocypode hexagonura Hilgendorf, 1882: 23.
? *Ocypoda africana* — Miers, 1882: 386.
Ocypoda africana — De Man, 1883: 155; Doflein, 1904: 127; Nobili, 1906c: 318; Bouvier, 1906a: 199; 1906b: 187; 1907: 497; Sendler, 1912: 190–191; Balss, 1914: 106; 1922: 80; Odhner, 1923: 23; Monod, 1927: 612; Roux, 1927: 238; Irvine, 1932: 7, fig. 19; 1947: 286, fig. 192; Bruce-Chwatt & Fitz-John, 1951: 117; Capart, 1951: 176, fig. 67; Monod, 1956: 395, figs 555–558; Gauld & Buchanan, 1956: 295, 296, 299; Dubois, 1957: 7; Sourie, 1957: 14, 31 [footnote], 45; Rossignol, 1957:119 [key]; 1962: 119; Longhurst, 1958: 53, 88; Gauld, 1960: 71; Guinot & Ribeiro, 1962: 66; Uschakov, 1970: 447, 455 [listed]; Via Boada, 1980: 59, pl. 1 figs 7, 8, 8a.
Ocypode Edwardsi Osório, 1890: 48, 49; 1895a: 253; 1895b: 57; 1898: 193 [a junior subjectice synonym of *Ocypode africana* De Man, 1881].
Ocypode edwardsii — De Man, 1896: 90.

Material examined. No exact locality. Africa, male (NHMW), iii.1885, 'Helgoland Expedition'; — West-Africa, 4 males, female [det. Balss] (ZMH-2746); — West-Africa, 3 juvs. [det. Th. Monod] (MNHN), 1910, A. Gruvel. **Sierra Leone**. No exact locality, female (NHM-1955.10.7.32); — Freetown, Lumley beach, 1 damaged juv. (NHM-1957.5.26.66); — *ibid.*, male [det. Th. Monod] (MNHN), 1882, Chaper. **Liberia**. Monrovia, 1 juv. (USNM-20577), Cook & Collins; — *ibid.*, Mouth of Mesurado River, male, female, 1 juv. (USNM-20667), Cook; — *ibid.*, Ocean Beach in front of Camp Johnson, 1 specimen (USNM-105883), 1 specimen (USNM-105881), 21.vii.1952, G.C. Miller; — Kap Mesurado near Monrovia, 11 males, female (ZSM), 1908, Scherer; — Paynesville, c. 9 km SE of Monrovia, beach of ELWA-hospital (6°15.55´N, 10°43.04´W), 3 males, 3 females (SMF-9823), 12.iv.1981, J. Voelker; — Mouth of Junk River, from mud under beach roots, 2 males (USNM-125758), 20.vii.1968, T. C. Rutherford. **Cote d'Ivoire**. Abidjan, 4 males, 6 females (MNHN), 1959, Rancurel; — surroundings of Sassandra (4°56.58´N, 6°5.23´W), 1 juv. male (SMF-9391), 19.iii.1976; — Assinie, female [det. Th. Monod] (MNHN), 1896, Alluaud. **Ghana**. No exact locality, male [det. Th. Monod] (MNHN), 1882, Chaper; — Accra, 2 males, 1 juv. female (NHM); — *ibid.*, Christiansborg beach, male, female (MNHN), 1948, R. Bassindale;

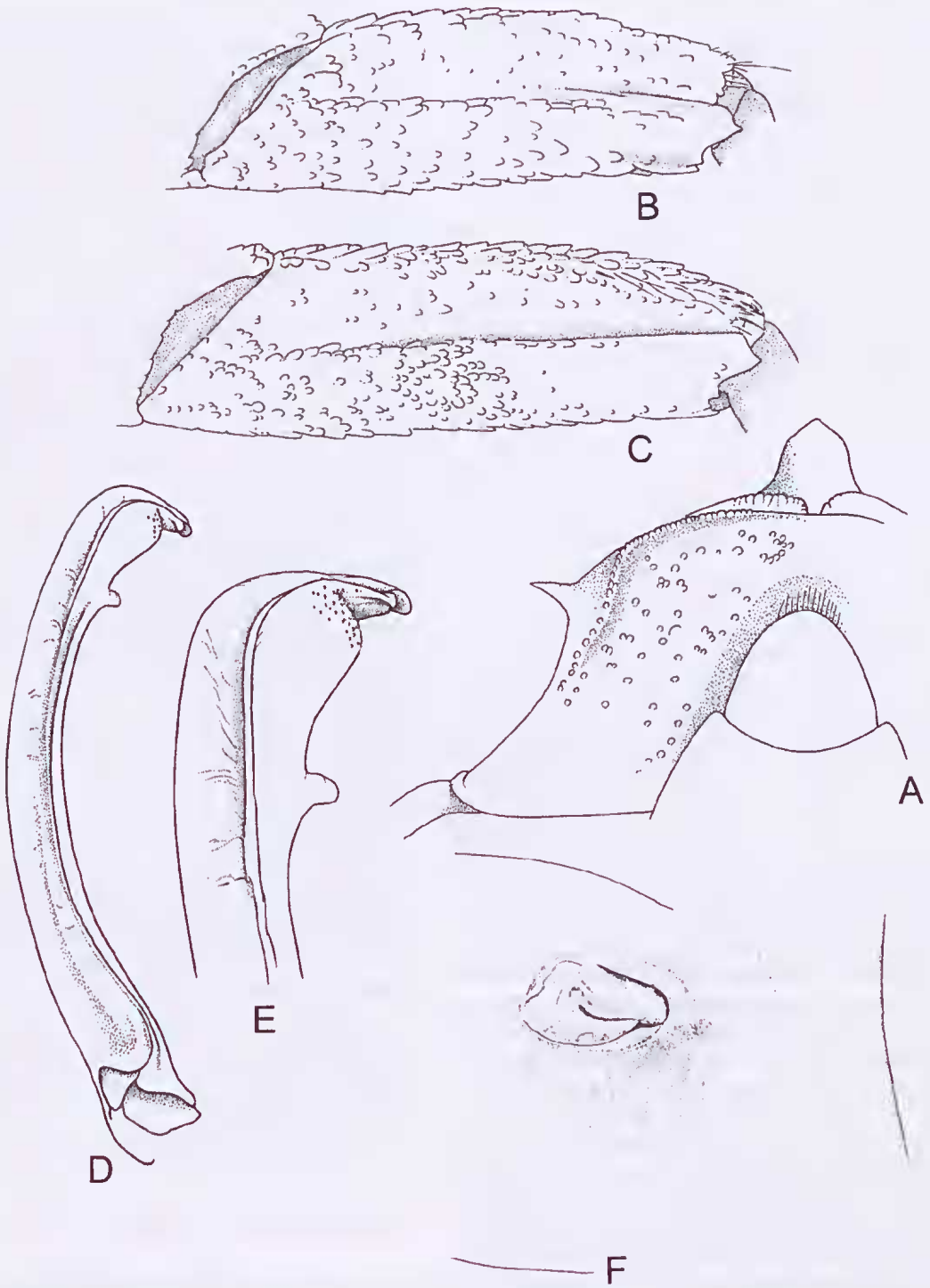

FIG. 8. *Ocypode africana*: **A,** P1 thoracic sternite; **B, C,** P2–3 propodi; **D, E,** Go1; **F,** female operculum.

Prampram, 2 males (NHM-1940.4.9.3). **Togo**. No exact locality, male, female (ZMH-2749); — Aného (= Anecho), male (ZMH-5566); — Lomé, 2 juvs. (ZMH-5567). **Benin**. Cotonou, 1 juv. (ZMH-29771), vi.1967 'Afrika-Expedition'. **Nigeria**. Lagos, female (NHM-1891.4.1.46–47). **Cameroon**. Douala (4°3.06′N, 9°41.34′E), 6 males (SMF-4364), 16.xii.1913, A. Haas; — Souelaba, 2 males, 2 females [det. Th. Monod] (MNHN), 1932–36, Th. Monod; — Rocher du loup (2°36.16′N, 9°50.37′E), S of Kribi, beach, 3 males (SMF-11714), 16.ii.1980, F. Ferrara. **Equatorial Guinea**. Mbini (= Benito) (1°35.48′N, 9°37.07′E), 3 males, female (SMF-6120), H. Eidmann; — Bata, 2 males [det. Th. Monod] (MNHN), 2 males, 2 females [det. Th. Monod] (MNHN), 1892, Pobéguin; — Bioko (= Fernando Poo), male (NHMW), 7.iii.1885, 'Helgoland-Expedition'; — *ibid.*, male, female (NHMW), 13.iii.1885, 'Helgoland-Expedition', Sta. 184; — Annobón, 3 juvs. (NHM-1960.10.3.1–3). **São Tomé and Principe**. São Tomé, 2 males (ZMH-2751); — *ibid.*, 2 juv. males, 1 juv. female, 5 juvs. (MNHN), 1906, A. Gravier. **Gabon**. No exact locality, male, female (NHMW), 5.iii.1886, Herrman; — Cape López, 3 males (ZMH-2747); — *ibid.*, 1 dry female [det. as *Ocypode nitida*] (MNHN-3305S); 1 dry female [det. as *Ocypode nitida*] (MNHN-3306S), 1865, Duparquet; — *ibid.*, 1 dry male [det. as *Ocypode nitida*] (MNHN), Oeuvre de la Ste-Enfance; Cape Lopez, NW of Port Gentil, 1 juv. male, 1 juv. female, 5 juvs. [det. Th. Monod] (MNHN), 1907, Ronbaud & Weiss. **Republic Congo**. No exact locality, 3 males, 5 females [det. Th. Monod] (MNHN), 1892, Dybowsky. **Democratic Republic of Congo**. Banana (5°59.38′S, 12°23.1′E), male, 1 ovig. female (SMF-1960), 12.v.1886, P. Hesse; — *ibid.*, 2 juvs. (USNM-54244); 5 males, 2 females (USNM-54245), viii.1915, H. Lang; — *ibid.*, beach, 1 juv. [det. A. Capart] (IRSNB), 10.viii.1948; — Muanda (= Moanda-Tonda) (5°56.1′S, 12°20.54′E), 2 females, 2 juvs. (SMF-6757), viii.1947, Dartevelle. **Angola**. Cabinda, female (ZMH-2748); — Benguella, 4 juvs. (NHM-1906.2.5.11–14).

Diagnosis. Middle-sized species. Eyestalks neither prolonged distally beyond cornea nor bearing a brush at distal end of cornea. Lateral half of orbital margin concave. P2–3 propodi naked. Stridulating ridge composed of 11–13 interspaced tubercles with striae in dorsal half and 21–26 closely spaced tubercles with striae in ventral half. Go1 strongly crooked laterally at distal end with broad bulge, bearing a thumb-like palp. Operculum of female genital opening protruding mesially, bearing strong lateral rim.

Description. Carapace (Fig. 30) wider than long, and covered with fine tubercles on dorsal surface. Lateral half of orbital margin slightly concave. Exorbital angles broadly triangular, and protruding slightly forward. Lateral margins of carapace directed slightly outward from tip of exorbital angle in anterior third of carapace, and then directed mesially in posterior two-thirds, and carapace broadest at anterior third. Pterygostomial region with sparsely scattered fine tubercles except along each lateral side of buccal cavern. P1 thoracic sternite (Fig. 8A) sparsely tuberculate in anterior half, but smooth in posterior half, bearing triangular protrusion at anterolateral angle, and tuberculate carina on anterior to anterolateral margin. Palm of larger cheliped relatively broad, finely tuberculate on anterior surface, and finely serrated on ventral margin. Smaller cheliped pointed distally. Stridulating ridge (Fig. 1B) composed of 11–13 interspaced tubercles with striae in dorsal half and 21–26 closely spaced tubercles with striae in ventral half. P2–5 propodi (Fig. 8B–C) naked on anterior surface. Go1 (Fig. 8D–E) three-sided proximally, and crooked laterally at distal end with a broad bulge, bearing a thumb-like palp. Operculum of female genital opening (Fig. 8F) protruding mesially, bearing strong lateral rim.

Distribution. West coast of Africa from Mauretania to Namibia. Type locality was reputed to be the Congo, but according to Manning & Holthuis (1981), this is erroneous and the specimen would have come from Musserra, Angola.

Remarks. *Ocypode africana* from the eastern Atlantic is similar to *O. gaudichaudii* from the eastern Pacific in the morphology of the Go1, however differs from the latter, because in *O. africana* both chelipeds are distally pointed, and the P2–3 propodi are naked on the anterior surface. In *O. gaudichaudi* both chelipeds are truncate distally, and the P2–3 propodi are setose on the dorsal half of the anterior surface. *Ocypode cursor* also occurs in the eastern Atlantic, but differs from *O. africana*, because in *O. cursor* the eyestalks bear a brush at the distal end of the cornea, and the Go1 lacks a palp.

Ocypode brevicornis H. Milne Edwards, 1837
(Figs 1C, 9, 31)

Ocypode brevicornis H. Milne Edwards, 1837: 48; Ng *et al.*, 2008: 240.

Ocypode platytarsis H. Milne Edwards, 1852: 141; Guinot-Dumortier & Dumortier, 1960: 135, figs

15a–c; Guinot-Dumortier, 1961: 85, fig. 8; Veerannan, 1974: 36–42, tabs 1–4, figs 1–2; Serène, 1968: 97; Paulraj *et al.*, 1982: 115–128, tabs 1, 3–7. Nadarajalingam & Subramoniam, 1987: 43–53, tabs 1, 3, 4; Ng *et al.*, 2008: 240.

Ocypoda platytarsis — Heller, 1865: 42 [in part]; Kingsley, 1880: 180; Miers, 1882: 383, pl. 17, figs 5, 5a; Henderson, 1893: 380; Alcock & Anderson, 1894: 202; Ortmann, 1897: 359, 363; Alcock, 1900: 345, 348; Laurie, 1906: 426; Kemp, 1915: 218; Gravely, 1941: 105; Pillai, 1951: 27; Raja Bai Naidu, 1954: 89–95, 98–100, figs 1–17; Sarojini, 1962: 189, tab. 1, fig. 1 G; Thampy & John, 1970: 203–210; Ramadevi *et al.*, 1990: 261–265, tab. 1, figs 1–5; Chhapgar, Desai & Patel, 2004: 185.

Ocypode neglecta Ortmann, 1894a: 766, pl. 23, fig. 18.

Ocypode platytarsus — Clayton, 2001: 37–55.

Material examined. Oman. Khawr Al-Milh southern part (20°23′N, 58°17′E), tongue of land Bar Al Hikman, Gulf of Masirah, male (SMF-24536); male (SMF-24537), 31.v.1995, D. Clayton; — Al Ashkirah, S Ras el Hadd (21°48′N, 59°32′E), male (SMF-24538), 1.vi.1995, D. Clayton. **India.** Malankara (= Malabar), 2 males, 2 females, 2 juvs. (NHM-1898.6.17.77–81); male, female (ZSM from ZSI),'Investigator-Expedition; male (MNHN-3308S); 2 males (MNHN-3309S); — Eastern coast, 3 males (ZMK-1536); — Tharangambadi (= Tranquebar), 1 juv. male, female (UZMK); — Puducherry (= Pondychery), male [lectotype of *Ocypode brevicornis*] (MNHN-4028S); male [holotype of *Ocypode platytarsis*] (MNHN); 6 males (MNHN); — Puri, 1 juv. (NHM-1956. 1.14.16); — Krakatau, Kolkata (= Calcutta), 1 juv. (NHMB-561b); — Nicobars, without exact locality, male [from Heller, 1865] (NHMW), 'Novara Expedition'. **Sri Lanka (Ceylon).** Without exact localities, 2 males (NHM-52); female, 1 juv. (NHM-1907.5.22.381–383); 1 juv. male, 1 juv. female (NHM-75.14); — Colombo, male, 1 juv. (ZMH-2968), 1901; — *ibid.*, 2 males [17.0×25.5, 10.6×17.4 mm], ix.1900, G. Duncker; female [32.8×44.2 mm] (ZSM-1442/1), 9.ix.1900, G. Duncker; — Dehiwala-Mount Lavinia (6°49.87′N, 79°51.73′E), 10 juvs. (SMF-6754), 23.iii.1974; — Kuchchaveli (8°49.09′N, 81°6.15′E), 2 juvs. (SMF-5427), 9–10.xi.1962, Brinck, Anderson & Cederholm, Lund Univ. 'Ceylon Expedition'; — Trincomalee, male (NHMB, 561a); 2 females (NHMW); — Trincomalee & Pamban (= 'Paumben'), 2 males, 6 juv. males, 1 juv. female (UZMK). **Missing or uncertain localities.** Without localities: male (ZMH-30357); 1 juv. male (NHM-60.15); 1 juv. (SMF-5425); 2 juvs. (SMF-5426); 3 juvs. (SMF-5428); 3 dry specimens (UZMK). — Tahiti, male [from Heller, 1865] (NHMW-1957), 'Novara Expedition'.

Diagnosis. Large-sized species. Eyestalks prolonged distally beyond cornea in a stylus. Carapace almost trapezoid. Lateral half of orbital margin directed obliquely backward. Exorbital angles rectangular. Stridulating ridge composed of 23–28 tubercles. P2–5 propodi naked on anterior surface. Go1 slender and slightly curved laterally in distal part, bearing broad and flat palp distant from distal end. Female genital opening lengthwise and almost parallel with sternum. Operculum with anterior thick rim directed obliquely backward.

Description. Carapace (Fig. 31) distinctly wider than long and scattered dorsally with coarse tubercles, becoming larger from middle toward lateral sides. Lateral half of orbital margin directed obliquely backward. Exorbital angles rectangular. Lateral margins of carapace directed slightly outwards from base of exorbital angle in anterior third of carapace, and then directed mesially in posterior two-thirds, carapace broadest at anterior third. Pterygostomial region beset with distinct tubercles, becoming smaller and indistinct toward each side of buccal cavern. P1 thoracic sternite (Fig. 9A) with a pair of low humps with fine tubercles anteriorly near base of Mxp3, bearing distinct tuberculate transverse carina at anterior third, which continuous with tuberculate lateral carina, and fine tubercles along mesial and posterior margins. Palm of larger cheliped elongate, scattered with coarse tubercles on anterior surface, distinctly serrated on ventral margin and coarsely tuberculate on dorsal margin. Stridulating ridge (Fig. 1C) composed of 23–28 tubercles. Smaller cheliped narrowing to pointed distal end. P2–5 propodi (Fig. 9B–C) naked, and tuberculate on anterior surface, bearing denticles on dorsal margin. Go1 (Fig. 9D–E) stemlike and three-sided proximally, and slightly curved laterally in distal part, bearing a broad and flat palp distant from distal end. Female genital opening (Fig. 9F) lengthwise and almost parallel with sternum. Operculum also lengthwise, bearing anteriorly a thick and straight rim directed obliquely backward.

Juvenile material. In a small specimen (10.0× 13.0 mm, SMF-6754) carapace distinctly wider than long and covered with coarse tubercles on dorsal surface. Eyestalks not yet prolonged distally beyond cornea, but cornea broadened at distal end. Palm of larger cheliped long. Stridulating ridge already composed of tubercles as in adult specimens. P2–3 propodi with a smaller number of spinules on dorsal margin of

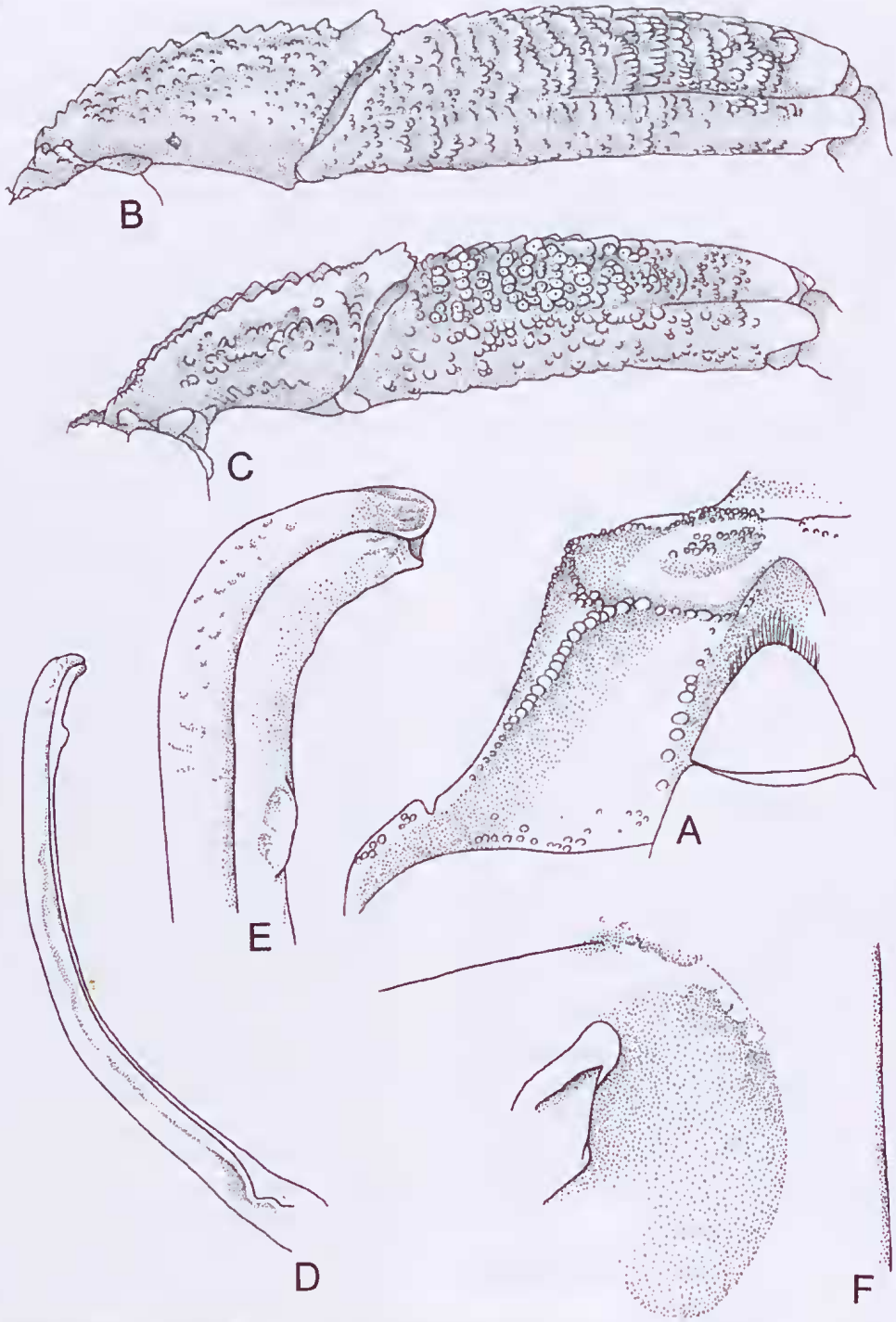

FIG. 9. *Ocypode brevicornis*: **A,** P1 thoracic sternite; **B, C,** P2–3 carpi and propodi; **D, E,** Go1; **F,** female operculum.

anterior surface than in adult specimens. In a slightly larger specimen (11.5×14.6 mm, SMF-6754) eyestalks already bearing a small distal protrusion. Lateral half of orbital margin slightly concave, therefore exorbital angles tooth-shaped and located backward. This small tooth at exorbital angle develops fully in course of growth. Palm of larger cheliped elongate. Stridulating ridge composed of tubercles as in adult specimens. P2–3 propodi with tubercles on anterior surface as in adult specimens.

Distribution. Oman, India; Nicobars; Sri Lanka. Type locality: East coast of India.

Remarks. H. Milne Edwards (1837) originally described *Ocypode brevicornis* based on two juvenile specimens from Pondychery, India, however subsequently the same author also described *O. platytarsis* H. Milne Edwards, 1852, based on adult specimens from the same locality. Kingsley (1880: 180) synonymised *O. brevicornis* with *O. ceratophthalma*, and since then *O. platytarsis* has been considered to be the fourth Indian species besides *O. ceratophthalma*, *O. cordimanus*, and *O. macrocera*. Our careful re-examination of the holotype of *O. platytarsis* in the MNHN, Paris, has shown it to be identical with *O. brevicornis*, and, therefore, *O. platytarsis* is here synonymised with *O. brevicornis*. In order to stabilise the usage, one of the syntypes of *O. brevicornis* (CB 26.0 mm, MNHN-4028S) is selected here as the lectotype.

Ocypode brevicornis is clearly distinguished from all other Indian Ocean *Ocypode* species by the following characters; the P2–3 propodi are naked, the stridulating ridge is composed of 23–28 tubercles, the Go1 bears a broad, flat palp distant from the distal end, and the female genital opening is located longitudinally below the operculum developed lengthwise on the lateral side of the concavity. The record of *O. platytarsis* (= *O. brevicornis*) from Tahiti, in the Pacific, by Heller (1865: 42) is presumed to be a misidentification, because *O. brevicornis* is now considered to be restricted to the Indian Ocean.

Ocypode ceratophthalma (Pallas, 1772)

(Figs 1D–I, 10, 32)

Cancer cursor Linnaeus, 1758: 625 [in part]; 1767a: 1038 [in part]; 1767b: 1038 [in part]; Herbst, 1782: 74, pl. 1, figs 8–9 [in part].

Cancer arenarius Toreen in Osbeck 1765: 479 [a *nomen oblitum*, a subjective synonym of *Ocypode ceratophthalmus* (Pallas, 1772); see Low & Ng 2012: 43–46].

Cancer ceratophthalmus Pallas, 1772: 83; (9): pl. 5, figs 7–8; Fabricius, 1781: 499; 1787: 315; 1793: 439 [*nomen protectum*, see Low & Ng 2012: 46].

Cancer caninus Herbst, 1782: 78.

Ocypode ceratophthalma — Weber, 1795: 92; Fabricius, 1798: 347; Bosc, 1801–1802: 194; Latreille, 1803: 47, pl. 45, figs 1–2; Leach, 1814: 393 [in part]; Latreille, 1818: 252, pl. 274, fig. 1; Latreille, 1818: pl. 274, fig. 1; Bosc, 1830: 247; De Haan, 1835: 58; H. Milne Edwards, 1837: 66, pl. 17; Kraus, 1843: 41; Adams & White, 1848: iii; H. Milne Edwards, 1852: 141; H. Milne Edwards, 1852: 105; Stimpson, 1858: 100; A. Milne-Edwards, 1868: 71; Hilgendorf, 1869: 82; A. Milne-Edwards, 1873: 270; Hoffmann, 1874: 13; Miers, 1877: 135; Hilgendorf, 1879: 802; Miers, 1880: 308; De Man, 1881: 245; Ortmann, 1894a: 762, 767, pl. 23, fig. 20; Ortmann, 1894a: 767; Borradaile, 1900: 595; Lanchester, 1900b: 751; Lanchester, 1900a: 258 [in part; *O. nobili*]; Borradaile, 1901: 67, 96; Rathbun, 1902b: 123; Rathbun, 1906: 833; Borradaile, 1907: 65; Stimpson, 1907: 108, pl. 12, fig. 12; Borradaile, 1910: 408; Rathbun, 1910a: 321 [in part]; Laurie, 1915: 416; Maki & Tsuchiya, 1923: 202, pl. 23, fig. 2; Edmondson, 1923: 8; McNeill, 1926: 316; Urita, 1926a: 421–438, 1 fig; Balss, 1934: 226; Takahashi, 1934a: 8–14; Miyake, 1936: 511; Estampador, 1937: 542; Balss, 1938: 76; Miyake, 1939: 221; Horikawa, 1940: 21–31; Chace, 1942: 202; Barnard, 1950: 86, fig. 17c–d; Suvatti, 1950: 153; Tweedie, 1950: 321; Fourmanoir, 1953: 88; Holthuis, 1953: 28; Altevogt, 1959: 130–133, figs 2, 4; Stephenson, Endean & Bennett, 1958: 269; Guinot-Dumortier & Dumortier, 1960: 135, 146, 148, tab. 3; Edmondson, 1962: 15, figs 6a, 7a; Shen & Liu, 1963: 141; Garth, 1965: 37, figs 23–26; George & Knott, 1965: 17, fig. 1A, B, 2B; McNeill, 1968: 85; Allender, 1969: 63, tabs 1–3; Bright & Hogue, 1972: 11; Sakai, T., 1976: 600, text-fig. 327b, pl. 207; Berry, 1976: 35–37, 1 unnumbered text-fig; Yang, 1986: 153, fig. 2; Dai *et al.*, 1986: 419, text-fig. 231; Poupin, 1996: 73; Yu *et al.*, 1996: 58, fig. 58; Jeng, 1997: 87; Carpenter, 1998: 1152, fig.; Davie *et al.*, 1998: 19; Wang *et al.*, 1998: 69, figs 60–62; Rosenberg & Langer, 2001: 345–353, tab. 2, fig. 2; Davie, 2002: 357; Marumura, M. & Kosaka, A., 2003: 69; Yodo *et al.*, 2006: 2, 4, 5, figs 3, 5; Mano *et al.*, 2008: 2, 5, 6, 7, 8, tabs 1–2, figs 2–7; Seike & Nara, 2008: 594, tab. 2; Ng *et al.*, 2008: 240; Poupin, 2011: 18, fig. 8F.

Ocypode rhombea Weber, 1795: 92 [Nomen nudum].

Ocypode rhombea Fabricius, 1798: 348; Olivier, 1811: 418; Desmarest, 1825: 122; Audouin, 1826: 80, pl. 1, fig. 2 [in part]; Lucas, 1840: 58.

Ocypode cursor — Olivier, 1811: 416 [not *Cancer cursor* Linnaeus 1758].

Ocypode ceratophthalmus — Latreille, 1817: 16; Lamarck, 1818: 252; Desmarest, 1825: 121, pl. 12, fig. 1; H. Milne Edwards, 1838: 463; Stebbing, 1910: 326; Day, Millard & Broekhuysen, 1954: 140, 153; Millard & Harrison, 1954: 166; Taramelli, 1955: 31; 1963: 73; Michel, 1964: 11; Green, 1964: 407–413; Crosnier, 1965: 93, figs 152, 160, 167–168, pl. 8, fig. 1, pl. 10, fig. 3; Serène, 1968: 97; Kensley, 1970a: 104; Horch & Salmon, 1972: 1–2, 6–10, tab. 2, figs 2–6; Jones, 1972: 31–43, tab. 1, figs 3, 4a, 4c, 4e, 4g, 5; Horch, 1975: 193; Dai & Yang, 1991: 458, text-fig. 231, pl. 58 (4); Jackson, Smale & Berry, 1991: 280–286; Huang *et al.*, 1992: 143, fig. 2, pl. 1B, tab. 1; Ng *et al.*, 2001: 35.

Ocypode Urvillei Guérin, 1829: pl. 1, fig. 1; 1838: 9; H. Milne Edwards, 1852: 141 [in part]; A. Milne-Edwards, 1868: 71 [in part].

Ocypodes — Audouin & H. Milne Edwards, 1829: 143, pl. 14, fig. 1.

Ocypoda (*Ocypode*) *ceratophthalma* — Voigt, in Cuvier, 1836: 119.

Ocypoda ceratophthalma — H. Milne Edwards, 1837: 48; Lucas, 1840: 57, pl. 1, fig. 1; Heller, 1865: 42 [in part]; Streets, 1877: 114; Richters, in Moebius, 1880: 155; Kingsley, 1880: 179 [in part]; Lenz & Richters, 1881: 423; Miers, 1882: 379, pl. 17, fig. 1; 1884: 237, 542, 573; 1886: 238 [in part]; Osório, 1888: 238; De Man, 1887–1888c: 107; 1888b: 351; Pfeffer, 1889: 30; Walker, 1890: 110; Thallwitz, 1891: 42; Henderson, 1893: 387; Aurivillius, 1893: 17, pl. 2, figs 1–6; Zehntner, 1894: 178; De Man, 1895: 570; Ortmann, 1897: 362, 364; Alcock & Anderson, 1894: 202; Alcock, 1900: 345; Andrews, 1900: 164; Calman, 1900: 24; Doflein, 1900: 144; Lanchester, 1901: 548; De Man, 1902: 477, pl. 19, fig. 1; Nobili, 1903: 20; Doflein, 1904: 126; Nobili, 1905a: 494; Lenz, 1905: 365; Laurie, 1906: 426; Nobili, 1906b: 310; Calman, 1909: 705; Lenz, in Voeltzkow 1910: 558; Pesta, 1911: 54 [in part]; Bouvier, 1915: 122; Parisi, 1918: 96; Tesch, 1918: 36; Balss, 1922a: 141; Sendler, 1923: 21; Calman, 1925: 166; Nakazawa, 1927: 1123, fig. 2165; Gravely, 1927: 148; Cott, 1929: 755, pl. 1, fig. 1; De Man, 1929: 2; Gordon, 1931: 528; 1934: 9; Takahashi, 1934b: 74; Balss, 1935: 140; Takahashi, 1935: 78; Tweedie, 1937: 141; Chopra & Das, 1937: 418, fig. 17a-a'; Sakai, T., 1939: 614, pl. 104, fig. 5; 1940: 32; Ward, 1942: 103; Tweedie, 1947: 27; Buitendijk, 1947: 280; Sakai, T. & Nakazawa, 1947: 664, fig. 1915; Lin, 1949: 26; Tweedie, 1950: 127; Fourmanoir, 1954: 1, fig. 1; Sakai, T., 1956: 53; Chhapgar, 1957: 44, pl. 13a–c; Sarojini, 1962: 191, tab. 1, fig. 1 H; Sankarankutty, 1961: 125; Hashmi, 1963: 240; Baksi, Ray & De, 1980: 184–187, pl.1 figs 6–7, pl. 2, figs 1–2.

Ceratophthalma cursor — MacLeay, 1838: 64.

Ocypode urvillei — Owen, 1839: 80; Borradaile, 1900: 595; Stebbing, 1917: 11.

Ocypoda urvillei — Lucas, 1840: 57; Kingsley, 1880: 181; Doflein, 1904: 406; Bouvier, 1915: 122.

Ocypode cursor — White, 1847: 35 [in part].

Ocypoda pallidula — Dana, 1852: 324, pl. 20, fig. 1.

Ocypoda Urvillii — Dana, 1852: 328; 1855: pl. 20, fig. 5.

Ocypoda brevicornis var. *longicornuta* Dana, 1852: 327; 1855: pl. 20, fig. 4a, e.

Ocypoda brevicornis — Dana, 1852: 326; 1855: pl. 20, fig. 3.

Ocypode cordimanus — Jacquinot & Lucas, 1853: 64; Heller, 1865: 42; Ooishi, 1970: 94, pl. 16, fig. 2.

Ocypoda Macleayana Hess, 1865: 143, pl. 4, fig. 8; Haswell, 1882: 95.

Ocypode Fabricii — Hilgendorf, 1869: 82.

Ocypode aegyptiaca — Hoffmann, 1874: 13.

Parocypoda ceratophthalma — Neumann, 1878: 26.

Ocypoda cordimanus — Kingsley, 1880: 185 [in part]; Lenz, 1901: 476.

Ocypoda fabricii — Kingsley, 1880: 182.

Ocypoda macleayana — De Man, 1887a: 696.

Ocypoda Kuhlii — Pfeffer, 1889: 30.

? *Ocypoda ceratophthalma* — Matsuura, 1894: 55; Schenkel, 1902: 581.

Ocypoda Urvillei — Nobili, 1907: 407; Bouvier, 1921: 57.

Ocypode sp. — Tu *et al.*, 1923: 819.

Ocypoda sp. — Gordon, 1934: 9 [in part].

Ocypode gaudichaudii — Estampador, 1937: 542.

Cancer francisci Curtiss, 1938: 175; Ng, Eldredge & Evenhuis, 2011: 45, 51.

? *Ocypode longicornuta* — Ng *et al.*, 2008: 240.

Material examined. Unknown locality: — 1 juv. male [syntype of *Ocypode rhombea* Fabricius] (UZMK); 2 juvs. (SMF-6732); 6 males, 2 females, 2 juvs., 2 damaged specimens (SMF-1934. These specimens were labelled as from the Red Sea, coll. Rüppell. Indeed the handwritten 1832 catalogue includes such a sample, but without any numbers of specimens. As the species has never again been found in the Red Sea and the label with the specimens was written around 1912, most of the Rüppel material usually having labels written in 1832, this Red Sea record must be considered doubtful); 4 males (SMF-36204, ex. T. Sakai coll.); 3 females (SMF-36206); 1 juv. male, 2 juvs. (SMF-36207); 2 juvs. (SMF-36208); 1 juv. male (SMF-36238, probably from Japan, but not definitely, as the T. Sakai collection also includes specimens from other regions); male (ZMG-129); male (ZMG-130, possibly from the Philippines, as locality numbers contained in the vials are similar to those written by Semper); — 'South Seas' (= Micronesia, Melanesia), 1 juv. (ZMG-128), purchased Capt. Pöhl; no further data, 1 juv. male, 1 juv. female, 3 juvs, 1 ovig. female [det. Balss as *Ocypode affinis nobilii*] (NHM-85.18), Dr. Millot. **East Africa.** No further data, female (ZMH-2809); 1 juv. [16.9×19.8 mm] (ZMH-2824). **Somalia.** Migiurtina [a former sultanate, now part of the region of Bari], Ras Hafun, female (MCG-144). **Kenya.** No further data, 1 juv.

female [det. Bouvier 1921] (MNHN); — Lamu Island, male (NHM-1983.11.9.3); — Mida Creek S of Watamu, Swatami Mangrove (3°24.05′S, 39°57.95′E), 2 males (SMF-18276);— Kilifi Creek (3°38.27′S, 39°51.58′E) between Malindi and Mombasa, female (SMF-18287), xii.1985, W. Baumeister; — 7 miles North of Mombasa, Bamburi beach, 10 males, female (RMNH-26016); — Mombasa, Kikambala (3°49.65′S, 39°49.71′E), female (SMF-6111); female (SMF-6112), 20.iii.–5.iv.1971, Z. Števčić. **Tanzania**. Zanzibar: No exact locality, 1 juv. female (ZMH-2966); female (USNM-72530); male (MNHN-B 3271S); 1 specimen with many legs of *O. ryderi* [det. A. Milne-Edwards, 1868] (MNHN-B3312S); female, 1 juv. (NHM-1964.7.1.81); 2 males, female (ZMH-2816); male (ZMH-2820); female [det. Pfeffer, 1889] (ZMH-2961); 26 juvs. [det. Pfeffer, 1889] (ZMH-2965); 1 juv. (MNHW); 2 juvs. (NHMW); 1 juv. male, 2 juvs. (NHMW); male (NHMW); — close to Zanzibar town, male (NHMW), St. Paulay, 'Saida Expedition'; — NW-coast, Mkokotoni, 1 juv. female [det. Lenz, 1905] (ZSM); — East coast, 2 males, 4 females, 6 juvs. (NHM-1964.7.1.74–80); — Dar es Salam, 9 males, 9 females, 3 juvs., 1 damaged specimen (NHM-1973.51). **Mozambique**. Beira, 2 males, 3 juv. males, female, 2 juv. females, 1 juv. (ZMH-K–2824), 21.vi.1912, P. Timm; — Inhambane, mud flat, female (ZMH-29789); 2 males (ZMH-29831); — Inhambane, Praia do Tofo, male (ZMH-29810); — Costa do Sol, N of Maputo, female (RMNH-27421); — Maputo (= Lourenço Marques), 4 males, 4 females, 3 juvs. (ZMH-29808); — *ibid*., Polana coast, 1 juv. (RMNH-16279–16281). **South Africa**. Kwa Zulu Natal: Boteler Point (27°1.0′S, 32°51.92′E), 3 males, 2 females (SMF-10930), 2-3.i.1976, S. Alexander; — Durban, 1 molted male (ZMH-2962); Durban Bay, male (NHM-1917.6.19.31); — *ibid*., Salisbury Island, male, 2 juv. males, 3 juv. females, 6 juvs. (RMNH); — — Eastern Cape: Port Alfred, 2 specimens (NHMW); — Port Elisabeth, 1 juv. (ZMH-11845). **Madagascar**. No exact locality, male, larger cheliped (MNHN); 13 juv. males, 6 juv. females, 58 juvs. (SMF-1933); female (SMF-1958); female (SMF-6750); 1 juv. male, 1 juv. female (NHM-88.5); male, 2 females (MNHN); male [det. Crosnier, 1965] (MNHN); 4 males, 4 females, 7 juvs. (MNHN); male (MNHN); male [det. Crosnier, 1965] (MNHN); — Nosy Bé (13°23.78′S, 48°12.33′E), 2 males, 2 females (SMF-1936), 7.vi.1883, A. Stumpf; 5 males, female [det. Hoffmann, 1874] (RMNH-229); — South-West of Morombe, 3 males, 2 females (MNHN); — St. Augustin (= Ianantsony), 8 males, female (MNHN); — East coast, Fenerive (= Fenoarivo), male (MNHN). **Réunion**. No further data, male (MHNG); — St. Paul (21°0.54′S, 55°16.09′E), beach, 2 males (SMF-18274), 1.ii.1989, H. G. Müller; — Beach at Caphomard (21°2.0′S, 55°13.25′E), 1 juv. (SMF-18272), 30.i.1989, H. G. Müller; — N l'Etang-Sale-les-Bains, Pnte. Des Avirons (21°14.21′S, 55°18.39′E), beach, from burrows, male (SMF-18273), 31.i.1989, H. G. Müller. **Mauritius**. No exact locality, male (NHMW); 3 males, female (NHMW); 2 males [det. Pesta, 1911] (NHMW); female [det. Pesta, 1911] (NHMW); 5 males [det. Bouvier, 1915] (MNHN); 3 males (MNHN-B3274S); 2 males (MNHN-B3273S); female (MNHN-B3291S); 2 specimens (MNHN-B3279S); 3 specimens (MNHN-B3289S); 1 specimen (MNHN-B3290S); 2 males (MHNG); — Flic en Flac, female (MI); — Tamarin, male, female (MI); — Fouquets I., 2 males [det. Richters, 1880] (ZMK-1520); male [det. Richters, 1880] (ZMK-1541); male, female [det. Richters, 1880] (ZMK-1543). **Republic of Seychelles**. No exact locality, 2 juvs. (NHM-1974.552); — La Digue, in front of Choppy's Bungalow (4°21.16′S, 55°49.57′E), male, 4 females (SMF-12909), 7.v.1979, M. Ackermann; — *ibid*., male, female, 3 juvs. (SMF-12917), 8.v.1979; male (SMF-12919); — Mahé, male (NHMW); — Wizard I., Cosmoledo Is, male (NHM-1969.11.13); — Ile des Roches, Amirantes, male [det. Miers, 1880] (NHM-82.24); — Amirante Is, Poive-Atoll (5°45.0′S, 53°18.0′E), 4 juvs. (SMF-18271), I. Eibl-Eibesfeldt. **Chagos Archipelago**. No further data, 1 juv. (ZMH-2821); — Diego Garcia (7°15.5′S, 72°22.52′E), male (NHM-1968.803); 1 juv. (NHM-1969. 1172); 1 juv. (SMF-5389); 1 juv. male, 1 juv. female (SMF-1939); female (NHMW). **Maldives**. No further data, male (NHM-1960.12.5.2); male (NHM-1966.2.1. 61–62); — Addu Atoll, Gan Island, male (NHM-1965. 7.20.6–7); — Addu Atoll, Beach of Hithadoo I. (0°36.51′S, 73°5.1′E), 2 males (SMF-6730), 1.i.1958, W. Klausewitz; — Rasdoo-Atoll NW of Ari (= Alifu) Atoll, Kuramathi (4°15.72′N, 72°57.96′E), male (SMF-24953), 15.vii.1999, D. Kovac; 2 females (SMF-24954). **India**. No further data, 2 juvs. (ZMH-2866); — Western coast, without more data, 8 males, 3 females (ZMH-26973); Western coast between Colachel and Goa, 1 juv. male (SMF-36253), 1984, W. Bee; — Maharashtra: Mumbay (= Bombay), male (MNHN-B3270S); 1 juv. male (NHMW-2081); — Alibag, South of Mumbay, many juvs. (ZMH-26906); — Karnataka: Karwar, specimen(s) (ZMH-26991); — Kerala: Malabar, 4 juvs. (NHM-1898.6.17.77–81); — *ibid*., 4 males, female, 2 damaged specimens (ZMH-2803), Capt. Schwinghammer; — Badagara, Azhitala, Murat River (11°33.4′N, 75°35.7′E), female (SMF-36257), 26.vi.1984, W.H. Bee; — Chaliyar River, Beypore, ferry beach to Chaliyam (11°9.91′N, 75°48.33′E), 1 juv. (SMF-36252), 6.v.1984, W. Bee; — Chaliyam, Forest office (11°9.67′N, 75°48.54′E), 1 juv. male (SMF-36254), 21.v.1984, W. Bee; — *ibid*., 1 juv. male (SMF-36251), 20.vi.1984, W. Bee; — Pondicherry: Malabar, Mahé, 4 juv. males, 1 juv. female (MZT-1100); — Tamil Nadu: Southern coast, 1 juv. male, 1 juv. female (NHM); — Pamban, 2 males (NHM-1890.10.20.4–5); — Lakshadweep: Agatti (10°51.51′N, 72°11.45′E), male (SMF-6727), 18.x.1974, Krammig; — Kalputhi (= Kalipatti): S of Agatti (10°48.83′N, 72°10.13′E), 2 males, 2 juv. males, female, 2 juv. females (SMF-6728), 13.x.1974, Krammig; — Bangaram (10°56.35′N, 72°17.38′E), male, female (SMF-6729), 15.x.1974, Krammig. **Nicobar Islands**:

No further data, female [det. Heller 1865] (NHMW), 'Novara Expedition'; 1 juv. male, 1 juv. female [det. Heller, 1865] (NHMW), 'Novara Expedition'. **Sri Lanka**. No further data, 1 juv. (NHM-1907.5.22.380); male (BMN-1974.152). — Colombo (6°55.41´N, 79° 50.67´E), male (ZSM); 1 juv. (SMF-6737); — Mount Lavinia (6°49.87´N, 79°51.73´E), male, 7 females, 18 juvs. (SMF-6731), 29.iii.1974, Z. Ševčić; — Moragalla Beruwela Beach (6°26.85´N, 79°58.98´E), *c.* 50 km S of Colombo, male (SMF-18275), 6-16.v.1989, H.G. Müller; —Weligama, male (NHMW); — Trincomalee, male, female (NHM-1934.1.16.159); male (NHMW-1156). **Myanmar**. Yangon (= Rangoon), 2 juv. males, 1 juv. female (USNM-106702). **Thailand**. No further data, 1 juv. [19.0×22.7 mm] (SMF-19319); male, 4 females (USNM-210884); 3 males, 2 females (USNM-210884); 1 juv. female (USNM-112170); — 'Eastern coast', male (USNM-230087); — Phuket: Pa Tong Bay (7°53.89´N, 98°17.75´E), 4 juv. males, 1 juv. female, 2 juvs. (SMF-11020), 1–4.ii.1983, Z. Ševčić; — West coast, male (USNM-127110); — NW point, 1 juv. male, 1 juv. female (RMNH-24991); — Satun: Koh Terutao, beach (6°37.84´N, 99°36.99´E), male [exchange with UZMK] (SMF-7845), 1.iii.1966, '5th Thai Danish expedition'; — Songhkla: Songhkla city, male (USNM-230087); — Surat Thani: Koh Tao, 2 females (USNM-107725); 1 juv. (USNM-104216); — Chon Buri: Sriracha N of Koh Samet Island, 2 juvs. (RMNH-27750); — Trat: Koh Chang, female (USNM-63656); 2 juvs. (NHM-1898.11.18); — probably around Koh Chang, 3 juv. males, 1 juv. female (RMNH-27118). **Singapore**. Beach (1°17.73´N, 103°53.93´E), male (SMF-1945), E. Marx; 5 males, 2 females, 6 juvs. [det. Lanchester, 1900] (NHM-1900.10.22.183–190); 3 males (NHMW-2079), i.1910, M. Pfister; — no further data; 1 juv. (NHMW). **Vietnam**. Con Son (= Poulo Condore), male (MNHN); female (MNHN). **China**. Exact localitiy unknown, male (MNHN-B3269S); — Hongkong, male, female (NHM-1935.3.19.9); female, 1 juv. female (NHM-1930.12.2.194); male (ZMH-2802); — Amoy (= Xiamen), female (MNHN). **Taiwan**, male, 2 females [det. Balss, 1922] (ZMH); — *ibid.*, female (SMF-8809), J. Dörjes; — Mai Liao (23°47.9´N, 120°10.6´E), 2 males, female (SMF-8807), 27.viii.1977, J. Dörjes; 1 juv. female (SMF-8810); —Tainan-city, Anping district, male [det. Balss, 1922] (ZSM); male, female, 1 juv. female [det. Parisi, 1917] (MCM-1614); — Hainan, Qukou (20°1.07´N, 110°32.85´E), sandy beach, male [36.2×41.7 mm]; female [31.4×34.4 mm] (SMF-36228), 14.iii.1992, H. L. Chen & M. Türkay; — Hainan, Sanya (18°16.65´N, 109°28.09´E), male, female [exchange with Institute of Oceanology, Academia Sinica Qingdao] (SMF-36191), 14.iii.1955. **Japan**. No further data: 2 males [coll. T. Sakai] (SMF-24527); —'unknown, but possibly Okinawa', female [coll. T. Sakai] (SMF-36225). — Shizuoka-Prefecture: Izu-Shirahama, Shimoda, Sagami Bay (34°41.46´N, 138°58.38´E), 2 juv. males, 2 juv. females (SMF-6751), 14.ix.1974, H. Suzuki. — Kochi Prefecture: Ikumi-kaigan (33°31.68´N, 134°17.06´E), Toyo-cho, 25 males [20.6×24.1 – 12.9×15.8 mm]; 15 females [19.4×24.5 – 14.5×17.6 mm] (SMF-36222), 11.ix.1998, I. Mano; — Shirahama, North of Ikumi-kaigan, Toyo-cho, 3 juvs. (SMF-36237), 5.viii.1992, Hirata; — Usa bay off Ryu Village (33°25.92´N, 133°27.19´E), 1 damaged male (SMF-36232), 2.ix.2004, K. Sakai; — Tosa-shi, Usa-Inoshiri, Entrance of Uranouchi Inlet (33°26.0´N, 133°26.19´E), 4 juv. males (SMF-16608), 19.x.1979, M. & H. Türkay, K. Sakai; — Okinohama (32°57.34´N, 132°59.57´E), Ogata-cho, 3 juvs. (SMF-36230), 21.viii.1994, T. Shimeno; — Kagoshima-Prefecture: Manose-gawa B. (31°26.72´N, 130°17.29´E), 2 females [15.3×18.1, 15.0×17.6 mm] (SMF-36234), 26.v.1996, M. Sato; — Ibusuki, northern beach (31°15.99´N, 130°39.7´E), 1.xi.1979, M. & H. Türkay, K. Sakai; — Amami-Ohshima: Akagina (28°27.38´N, 129°40.33´E), 4 females, 1 damaged specimen (SMF-6741), 20-24.vii.1966, K. Sakai; — Yoron I. (27°3.11´N, 128°24.9´E), male (SMF-6734), 18-24.viii.1966, K. Sakai; — *ibid.*, Kori (27°2.17´N, 128°24.47´E), male [19.9×23.9 mm] (SMF-36233), 27.vii.1966, K. Sakai; — Chabana (27°3.11´N, 128°24.9´E), male [17.1×20.0 mm] (SMF-36231), 3.xi.1966, K. Sakai; — Okinawa, female [coll. T. Sakai] [27.2×32.2 mm] (SMF-36225); — Okinawa-honto, 1 juv. [coll. T. Sakai][8.2×10.0 mm] (SMF-36239); — Kushi (26°42.56´N, 127°49.54´E), Nago-City, Okinawa, 2 females [20.8×26.1, 11.9×13.8 mm] (SMF-36220), viii.1987, R. Higa; — Onna Coast (26°27.32´N, 127° 48.47´E), 3 males [34.3×38.0 – 9.1×11.4 mm], 2 females [25.7×30.0, 25.6×26.0 mm] (SMF-36221), 23.viii.1992, W. Shimabukuro; — Nakadomari (26° 16.9´N, 127°49.0´E), upper tidal zone, 2 males [14.6×17.7, 6.2×7.3 mm], 1 juv. (SMF-36235), viii.1983, R. Higa; — Hentona (26°44.89´N, 128°10.78´E), male, 2 females (USNM-171693); — Tokashiki-jima, West of Okinawa-honto, Awaren (26°10.23´N, 127°20.72´E) , 4 females (SMF-6733), 24.ix.1973, K. Sakai; — Ishigaki Island (24°20.0´N, 124°11.33´E), 2 males (MCM) [det. ? Parisi, 1917]; male, female (SMF-6740); female (ZMH-2811); — Taketomi-jima (24°20.13´N, 124°5.63´E), 1 juv. female (SMF-6735) [ded. K. Sakai], 1–8.v.1973, Uchida & Uda; — Ogasawara Is: Chichi-jima, male (MCM-1613). **Philippines**. No exact localities, 3 males, female (USNM-109780); 2 males (MNHN-B3937S); 2 males (MNHN-B3277S); 2 males (MNHN-B3275S); male (RMNH-231); 1 juv. male, 1 juv. (NHM-84.31); — *ibid.*, fish market, 2 males (SMF-12495), [det. A. Schreiber], iii-iv.1983; — Luzon: Manila, female (ZMH-2806); — Laguna, 2 juvs. (ZMG-127), 'Blovar Expedition' [this locality is very improbable, because the Laguna is a freshwater-lake, it might therefore refer to another locality around Manila], 1876, K. Semper; — Mindoro: No exact locality, 1 juv. (USNM-171315); — Panay: Iloilo, male (USNM-73200); — *ibid.*, beach at Jaro river mouth, 1 juv. male (USNM-73203); — Negros: Victorias, Magnanud River, 1 juv. male (USNM-73272); — Samar: E-coast, surroundings of General MacArthur

(11°14.63′N, 125°33.27′E), 2 males, female (SMF-9999), viii.1978, W. Lobin; — Mactan I.: Maribago (10°17.16′N, 124°0.09′E), NW coast of Hilutangan Channell, 2 juvs. (SMF-18683), J.J. Janssen. **Malaysia.** No further data, 1 juv. female, 1 juv. (NHM-1898.11.18); — Pulau Langkawi, Pantai Kok (6°21.62′N, 99°42.03′E), 2 males (SMF-19481), 16-28.iii.1992, H.G. Müller; — Batu Feringgi, Northern coast of Pinang I., 2 males (RMNH-29450); — Pinang, Muka Head (5°27.92′N, 100°14.29′E), beach, 2 juvs. (SMF-36240), 5.iv.1994, B. Hellmund; — Port Dickson, many males & females (RMNH-5323); — Malacca, 1 juv. (NHMW); — Johor, male, female (MHNG);— Pulau Babi Besar, beach (2°25.88′N, 103°58.72′E), male, female (SMF-20287), 9.iv.1981, H. G. Müller; — Sarawak: no further details, male (NHM-1895.10.10.2–3); male (USNM-233139); — Palau Labuan, 1 juv. male (RMNH-15486–15491); male, female (NHMW); 1 juv. male, 2 juv. females, 1 juv. (NHMW); — Baram river, male, female (NHM-1898.10.25.22); — Buntal, Santubong, 2 males (NHM-1900.12.20.21) [det. Lanchester, 1900]. **Indonesia.** No exact locality, male (ZMH-2825); 3 juvs. (ZMH-2972); — Sumatera: No exact locality, female (IRSNB-6729); female (NHM); — Pulau Nias, no exact locality, 3 males, 2 females (RMNH-2061); many males and females (RMNH-15483); — Lahewa (= Luau Vara, Luah Vara), North-West corner of Pulau Nias, male (MCG); — Pulau We, 1 juv. (ZMH-2967) [det. Doflein, 1904]; male (RMNH-15492); 1 juv. male (RMNH-15486–15491); male (RMNH-15507); male (RMNH-15487); male (RMNH-15480); 1 juv. (RMNH-2151); male, 2 females (RMNH-15482); 2 males (RMNH-15483); — Region Pasaman, Batang Tamak, Mangrove North of Airbangis (0°12.92′N, 99°21.94′E), sandy beach, 1 juv. male (SMF-36260), 21.ii.1994, Th. Ziegler; — Padang, female (NHMW-2082); — Bengkulu (= Benkoelen), 1 juv. (USNM-87355); — Jaga Utara I. (= Noordwachter Eiland or Pulo Sebiri) (5°12.0′S, 106°27.0′E), SE of Lampung, Sumatera, 3 males, 6 females (ZMG-124), J. Brock; — Java: No exact locality, 2 males, female, 1 juv. (MHNG); male, female (MHNG); — Java Sea, male, female (RMNH-2002); — North coast of Java, male, 1 juv. male, 1 juv. female (RMNH-2004); — Alkmaar Island in front of Jakarta Bay, 2 juv. males, 1 juv. (RMNH-15486–15491); — Jakarta Bay, 10 juvs. (RMNH-15486–15491); — Jakarta, Tanjung Priok, 3 males (RMNH-15479); 38 juvs. (RMNH-154845); males (RMNH-2367); — Semarang, female (MNHN); — Southern coast, Cilacap (= Tjilatjap), male, 3 females (NHMW); — Irian Jaya (0°21.07′S, 132°10.42′E), 1 juv. (RMNH-D 15499), 3.vii.1952, L. D. Brongersma & W. J. Roosdorp; — Nicobar, 2 juvs. (NHMW) [det. Heller, 1865]; — Lesser Sunda Islands: No exact locality, female (NHRM-St5970); 1 juv. female (NHRM-St5971); — Lombok: Ampenan, 1 juv. female (MCZ-7246) [det. Rathbun, 1910]; — Flores: Ende, 3 males, 8 females (RMNH), 'Snellius Expedition'; — Sumba: Rua, about 14 km South of Waikabubak, 1 juv. (NHMB); — near Timor, 2 juv. females (RMNH-15486–15491); — Timor: Kera Island North-West of Kupang, 5 males, 1 juv. female, 1 juv. (RMNH), Snellius Expedition; female, 3 juvs. (RMNH); — Pulau Kisar, north-east of Timor Island, male, 1 ovig. female (RMNH), 'Snellius Expedition'; — Pulau Leti, E of Timor, male (RMNH-10600);— Sabalana (= Postillon) Islands: Sarasa, male (RMNH), 'Snellius Expedition'; — Sapuka-Beser (= Sapoeka), male, 3 juv. males, 2 females, 1 juv. female (RMNH), Snellius Expedition; — Kepulauan Aru: No exact locality, 1 juv. (NHMW-1886); female, 5 juvs. (NHM-84.31), 'Challenger Expedition'; — Wamar Island, Dobo (5°45.43′S, 134°12.94′E), 4 males, 1 juv. male, 1 juv. (SMF-1941); —Trangan Island, Ngaigoeli coast (6°37.98′S 134° 5.46′E), male (SMF-1938); 1 juv. (SMF-1963); — Kepulauan Kai: no exact locality, male (MCG-135); — Pulau Ut (= Oet), sandy beach (5°35.19′S, 132° 40.77′E), male (SMF-7847) [exchange with Copenhagen Museum], 23.iv.1922, Danish Expedition to Kai Is; — Kalimantan; — Palau Maratua, East of Kalimantan, male, 3 juv. males, 2 females, 1 juv. female (RMNH), 'Snellius Expedition'; — Pulau Karakelong, Maririka (= Meriri) (4°25.88′N, 126°42.87′E), female (SMF-1937); — Talaud-Islands (North of Sulawesi); no exact locality, female (ZMH-14980); male (MNHN-B3272S); female (MNHN-B3285S); male (NHM-80.6); male, 2 females (RMNH-230); — Spermonde Archipelago [off Makassar, SW Sulawesi], all from 'Snellius-Expedition': Samalona, 3 juvs. (RMNH); — Koedingareng Lompo, 1 juv. (RMNH); — Madeang, male, 4 juv. males, 4 juv. females (RMNH); — Lankadea, 8 males, 2 juv. males, 2 females (RMNH); 3 males, 2 females (RMNH); — Gonto Soea, 2 males (RMNH); — Makassar, female (NHM-80.6); 1 juv. female (NHMB-562c) [det. Schenkel, 1902]; — Pulau Butung SE of Sulavesi. Bau-Bau (= Bava Bava) (5°27.38′S, 122°36.03′E), male (SMF-1944), 31.viii.1909, J. Elbert; — Pulau Binongko, South-East of Sulavesi, 1 juv. male, 6 juv. females, 4 juvs. (RMNH) 'Snellius'Expedition; — Sula Archipelago: Pulau Taliabu, 9 males, 5 females (RMNH), 'Snellius' Expedition; female (RMNH); — Moluccas: Ternate (0°45.64′N, 127°21.64′E), 2 males, female, 1 ovig. female, 7 juvs. (SMF-1930), W. Kükenthal; — *ibid.*, 2 males, 3 juv. males, 2 females, 3 juv. females (RMNH), 'Snellius Expedition'; 1 juv. male, female, 38 juvs. (RMNH); 2 juvs. (RMNH); 1 juv. (RMNH); 2 juvs. (RMNH); — Bacan (= Batjan), male (NHM-80.6); — Halmahera (1°8.73′N, 127°52.64′E); — No exact locality, male (SMF-1940), W. Kükenthal; — Kau Bai, Halmahera, 2 males (RMNH), 'Snellius Expedition'; — Kau Bai, Halmahera, 7 juvs. (MCZ-7245) [det. Rathbun, 1910]; — Pulau Obilatu, 9 males, 2 females (RMNH) 'Snellius Expedition'; — Pulau Buru, male, female (MNHN-B3311S) [det. H. Milne Edwards, 1852] ; — Pulau Ambon (= Amboina) (3°37.82′S, 128°15.41′E), 3 males (MCG); 2 males (MNHN); 1

juv. male (SMF-5423); 5 males, 1 juv. (SMF-1932); male (MHNG); male (RMNH-226); 2 males (NHMW); 1 juv. (NHMW) [det. Pesta, 1911]; — *ibid.*, 5 males, 6 juv. males, 2 females, 6 juv. females, 8 juvs. (RMNH), 'Snellius Expedition'; — Haruru (= Harolo), 11 males (RMNH), 'Snellius expedition'; — Irian Jaya: No exact Locality, 'East Coast', 2 males, 2 females (RMNH-25857); — Misool Island, 1 juv. (NHM) [det. Gordon, 1934]; — Kafal Island near Misool Island, male, 2 juv. males, female (RMNH), 'Snellius' Expedition; — Pulau Miossu (formerly Middelburg Eiland) (0°21.07′S, 132°10.42′E), 1 juv. (RMNH); — Mapia Islands, Pegun-Island, male, female (RMNH); 1 juv. male (RMNH-15493–15500); — East of Manokwari, 2 juvs. (RMNH-15493–15500); 1 juv. male, 1 juv. female, 3 juvs. (RMNH-15493–15500); — Mansinam Island off Manokwari, 3 juv. females (IRTSNB-9223) [det. Gordon, 1934]; — Cenderawasih Bay (formerly Geelvink Bay), Numfoor Island, Kameri, 1 juv. male, 1 juv. female (RMNH-16279–16281); — Cenderawasih Bay (formerly Geelvink Bay), Nabire, many males & females (RMNH-15402); — Cenderawasih Bay (formerly Geelvink Bay), Aropen, 1 juv. female (RMNH-15493–15500); — South of Jayapura (formerly Hollandia), 2 juv. males (RMNH-16279–16281); — North of Jayapura (formerly Hollandia), 1 juv. male, 1 juv. female, 3 juvs. (RMNH-15493–15500); — Papua Province, estuary of Kali Bocaja at Holtekang on South-East coast of Humboldt (= Yos Sudarso) Bay, 2 males (RMNH-15502); male, 1 juv. male, female (RMNH-16283); — Teluk Yautefa (= Jautefa Bay) South of Jayapura, 1 juv. male (RMNH-15493–15500); — Mimika river, South coast of Westirian, male (NHM-1911.8.1.24). **Papua New Guinea**. Mainland Papua; — North-East New Guinea, male (NHMW); — Tarawai Is. (= Bertrand. Is.) (03°12.9′S, 143°15.56′E), female (SMF-1943), Hanseatische Südsee-Expedition, E. Wolf; male, female, 1 juv. female (SMF-3610); — Huon Bay, 'Bukauka 6 km West of Lae' [could refer to Bukaua, 14 km East of Lae, inasmuch 'west' from Lae would be inland]; — Close to Katau-River mouth near Kadawa on South-West coast, female (MCG-131); — Papua Bay, Yule Island (about 100 km NW Port Moresby), female (MZT-1103); 3 males (MCG-133); male (MCG-135); male (MCG-143); — Hula SE of Port Moresby, 20 juvs. (MCG-132); — Beagle Bay, male (MCG-129). **Admiralty-Islands**: North coast, female (ZMH-5771); — Bismarck Archipelago; — No exact localities, male (ZMH-5782); female, 11 juvs. (ZMH-5785); — Duke of York Island, 2 males (NHM-77.8); — New Britain, 7 males, 2 females, 1 juv. (ZMH-5820). **Solomon Islands**: No exact locality, female (NHMW); — Buka Island (5°27.26′N, 154°37.47′E), 1 juv. (SMF-6736); 1 juv. [5.5×6.5 mm] (RMNH-15499). **Australia**. No exact locality, male (ZMG-125); — Western Australia: 'West coast', 3 males (ZMH-11617); — 'Northwest coast', female (NHM-1932.11.30.165); — Thevenard Island, female (NHM-1960.10.6.5); — Onslow, town-beach (21°38.16′S, 115°6.84′E), male, female (SMF-10331), 6.x.1975, G. Hartmann & G. Hartmann-Schroeder; — Point Cloates near Coral Bay, male, female (NHM-1960.10.6.3–4); — Northern Territory: North-West of Cape Arnhem, 5 males, 5 females, 2 juvs. (USNM-178294); — Gulf of Carpentaria at North East end, 1 juv. female (USNM-178294); — *ibid.*, Groote Eylandt, East coast, female (USNM-178294); — *ibid.*, Groote Eylandt, Umba Kumba at north end, female (USNM-178294); — Queensland: Torres Strait, 3 males (NHM-1955.4.22.182–186); 2 juvs. (NHM-1954.9.14.121–122); male, female, 1 damaged specimen (NHM-1954.4.22.182–186); — *ibid.*, Thursday Island, male, 3 females (NHM-82.7) [det. Miers, 1882]; — *ibid.*, Friday Island, female (NHM-84.31) [det. Miers, 1882]; — Cape York, Somerset, male, female (MCG); — Great Barrier Reef, 3 males, female (NHM-1937.9.21.261–263); — *ibid.*, Raine Island, male (NHM-84.31), 'Challenger Expedition'; — *ibid.* Bunker Group, male (MNHN); — *ibid.*, Lady Musgrave Island, 1 juv. (NHM); — Yarrabah (16°54.28′S, 145°51.85′E), North East of Cairns, sandy beach, 2 juvs. (SMF-16561), 6.vi.1980, M. Türkay; — Ellis Beach (16°43.9′S, 145°39.42′E), North of Cairns, 10 males, 5 females (SMF-16562), 8.vi.1980, M. Türkay; — *ibid.*, 3 males, 1 juv. (SMF-16563), 4.vi.1980, M. Türkay; — Green Island (16°45.47′S, 145°58.39′E), 1 juv. (SMF-9855), 15.v.1957, H. Felten; — Brampton Island (20°48.6′S, 149°15.86′E), female (SMF-3610) [vend. S. Kellner]; — North Stradbroke Island, Northern part, beach (27°26.64′S, 153°32.23′E), male, damaged [15.9×19.5 mm] (SMF-36229), 29.ix.1999, M. Türkay; — ibid., central part, beach (27°31.33′S, 153°30.13′E), 3 males [17.1×21.2 - 13.0×16.2 mm], 1 juv. (SMF-36226), 30.ix.1999, M. Türkay; — Bribie Island, Woorim Beach (27°4.03′N, 153°12.28′E), female (SMF-16560), 25.v.1980, M. Türkay; — New South Wales: Sydney municipality: Sydney, no further data, juv. female [holotype of *Ocypoda macleayana* Hess, 1865] (ZMG-126); — Collaroy, Long Reef (33°44.31′S, 151°18.43′E), sandy beach, male [23.0×27.4 mm], female [26.2×32.1 mm], 1 juv., damaged (SMF-36227), 24.v.1980, M. Türkay; — Balmoral Beach, Mosman, 1 juv. (RMNH-10600); Maroubra Bay, 2 juvs. (USNM-17035); — Double Bay, 1 juv. (MCG-127); — Pt. Stephens, Nelson Bay, 2 males, 3 females, 4 juvs. (MNHN); — Jervis Bay, 1 juv. (NHM); — Botany Bay, 2 juvs. (NHM-84.31) [det. Miers, 1886], 'Challenger Expedition'; — South Australia: South Australian coast, 2 juvs. (NHM-84.31) [det. Miers, 1886]. **Palau**. No further data, male (NHMW-1623), 'Challenger Expedition'. **Northern Marianas**. Saipan, Garapan, Beach (15°12.51′N, 145°42.94′E), male, 18 juvs. (SMF-19495), x.1990, G. vom Berg; — *ibid.*, 8 juvs. (SMF-19496), 10.viii.1990, A. Allspach. **Guam**. No exact locality, female (USNM-33159), 'Albatross Expedition'; — *ibid.* (appr. 13°28.67′N, 144°45.44′E), male, 20 juvs. (SMF-19494), x.1990, G. vom Berg; — Ritidian Point,

1 juv. (USNM-170990); — Tumon Bay, female (USNM-171477); 1 juv. (USNM-170990); — Piti Bay, female, 2 juvs. (USNM-170990); — Bijia Point, male (USNM-170990); 1 juv. female (USNM-171477); — Cocos Island, male (NHM-1925.2.11.3); male (NHM-1925.2.11.1–2). **Micronesian Federation**. Kapingamarangi Atoll: Hare Island, male (USNM-104979); —Turuaimu Island, male (USNM-104983); — Caroline Islands: No further data, male, female (NHM-1898.11.1.69–71); — Pohnpei (= Ponape) (6°5 0.0′N, 158°19.69′E), male (SMF-22444), 8.vii.1986, K. Sakai; — Woleai Atoll, female (ZSM). **Marshall Islands**. No exact locality, male (USNM-172586); male (USNM-176603); — Enewetak (= Eniwetok) Atoll: No exact locality, male (USNM-172224); — Rigili Island, 7 males, 3 females (USNM-172224); — Araanbiru Island, 1 juv. female (USNM-172586); — Bikini Atoll: Uorikku Island, 3 males, female (USNM-17224) [det. Holthuis, 1953]; — Emon Island, female (USNM-176603); — Rongelap Atoll: Rongelap I., 1 juv. (USNM-101144); — Bikar Atoll: Bikar Island, male (USNM-94272) [det. Holthuis, 1953]; 2 males (USNM-94273) [det. Holthuis, 1953]; male (USNM-94274) [det. Holthuis, 1953]; — Taka Atoll: No exact locality, male (USNM-93601) [det. Holthuis, 1953]; — Ailuk Atoll: Ailuk Island, male (NHM-84.31) [det. Holthuis, 1953]; — Ujae Atoll: Enylamij Island, male (USNM-93602) [det. Holthuis, 1953]; — Kwajalein (= Kwadjelinn) Atoll: No exact locality, female (NHRM-St14267); 1 juv. (NHRMSt 14755). **Vanuatu** (= **New Hebrides**). Ambrym, male, 9 juvs. (MHMG); — Tanna, 1 juv. (NHM-75.69); — Prov. Tafea, Aniwa (= Jmmer) (19°13.84′S, 169°36.8′E), East of Tanna, 2 males (SMF-1929) [det. Sendler, 1923], 'Hanseatische Südsee-Expedition', E. Wolf. **New Caledonia**. No exact locality, female (MNHN-B3287S) [det. A. Milne-Edwards, 1872]; — N-Province, Ponérihouen, beach, (21°3.65′S, 165°24.57′E), 4 juvs. (SMF-36236), 23.iii.1994, T. Ziegler; — South-province, Ile des Pins, southern beach (22°40.49′S, 167°29.02′E), among debris after storm, 2 females [28.5×33.9, 20.3×23.9 mm] (SMF-36223); female [38.6×41.8 mm] (SMF-36224), 28.iii.1994, T. Ziegler. **Loyalty Islands**. Lifou Island, Cap des Pins, 4 males (NHM-1950.12.11.1–2). **Norfolk Islands**. No exact Locality, male (MNHN). **Fiji Islands**. No exact locality, male (USNM-66613); female (NHMW); — *ibid.*, 1 juv. (NHM-84.31) [det. Miers, 1886], 'Challenger Expedition'; — Viti Levu: No exact locality, female (ZMH-2810); male, 1 juv. (ZMH-2957); — Makaluva Island, *c.* 6 km South-East of Suva (18°11.32′S, 178°31.12′E), 1 juv. male, 3 juv. females (USNM-74486); — Kadavu (=Kandavu): No exact locality, 2 males, female, 7 juvs. (NHM-84.31) [det. Miers, 1886]; female (NHM-84.31) [det. Miers, 1886], 'Challenger Expedition'. **Kiribati**. Gilbert Islands: Onotoa Atoll, male (RMNH-9652); 3 males (USNM-93824) [det. Holthuis, 1953]; 2 males (USNM-94227) [det. Holthuis, 1953]; — Aranuka Atoll, 1 juv. (NHRMSt 14756); — Abemama (= Apamama) Atoll, 3 juvs. (NHRMSt 14266); — Phoenix Islands: Kanton Island (= Abariringa), male (USNM-76921); male (USNM-77268); — Line Islands: Kiritimati (= Christmas Island), 4 males (NHM-1957.11.6.9–10); male (NHM-1896.10.31.21); — Tabuaeran (= Fanning Island), female (USNM-2304) [det. Streets, 1877]. **Hawaiian Islands**. No exact Locality, 2 males (MNHN); — *ibid.*, female (SMF-9838), xii.1980, Sudhaus; — Oahu: No exact locality, 2 juvs. (USNM-171520); male, female (ZMH-27719); 2 males, female (ZMH-27720); — Kaneoha Bay, Coconut I., male (USNM-64175); male (USNM-64176); — Kailua, 20 juvs. (NHMW); 3 juv. females, 8 juvs. (NHMW); — Honolulu, Kahala, 1 juv. male, 4 broken pieces (RMNH-15486–4991); — *ibid.*, Waikiki Beach, 1 juv. (USNM-182729). **Samoa**. No further data, female (NHM-76.17); — No exact locality [but probably western Samoa which was a German and later, until 1962, New Zealand colony, purchased Mus. Goddefroy], male (SMF-1942); many males & females (ZMH-2804); — Upolu, female, 1 juv. female (NHMW) [det. Pesta, 1911]; — *ibid.*, Apia, 6 males, 4 females (USNM-43289); male (NHM-1931.5.26.15). **American Samoa**. Tutuila: Pago Pago, 1 juv. female (USNM-43285). **French Polynesia**. Society Islands: Bora Bora, Motu Babu Cay, 1 juv. male, 1 juv. (USNM-213821); — Raiatea Island, male (USNM-123617); — Tahiti, 1 juv. male (ZMH-2955); 1 juv. female (NHM); — Tahiti, Papeete, 2 juvs. (USNM-89871); — Tahiti, Papeete (17°31.45′S, 149°31.14′W), 4 males, 1 ovig. female (SMF-1931), 'Hanseatische Südsee-Expedition'; — Tuamotu Islands: No exact locality, 2 females (USNM-94563) [det. Holthuis, 1953]; 1 juv. female (USNM-33158), 'Albatross Expedition', Fakarava ; — Rangiroa, 2 males, 2 females (UZMK); — Gambier Islands: No exact locality, male (MNHN) [det. Nobili, 1907]; female (MNHN) [det. Nobili, 1907]; — Mangarewa, male (MNHN-B4027S), Zelée Expedition. **Clipperton Island**. — No further data, male, female (USNM-107292); 7 males, 8 females (MNHN).

Diagnosis. Middle- to large-sized species. Eyestalks prolonged distally beyond cornea in a stylus. Exorbital angles broadly triangular and protruding laterally in large specimens. Stridulating ridge composed of 10–11 interspaced tubercles in dorsal third, 8 thick striae in middle third, and 20–30 closely spaced striae in ventral third. Smaller cheliped narrowing to pointed distal end. P2–3 propodi setose on dorsal half of anterior surface, bearing one (in female) or two (in male) median rows of setae. Go1 slender, bearing palp. Sternite sunken around round operculum towards genital opening; no discernible lateral rim.

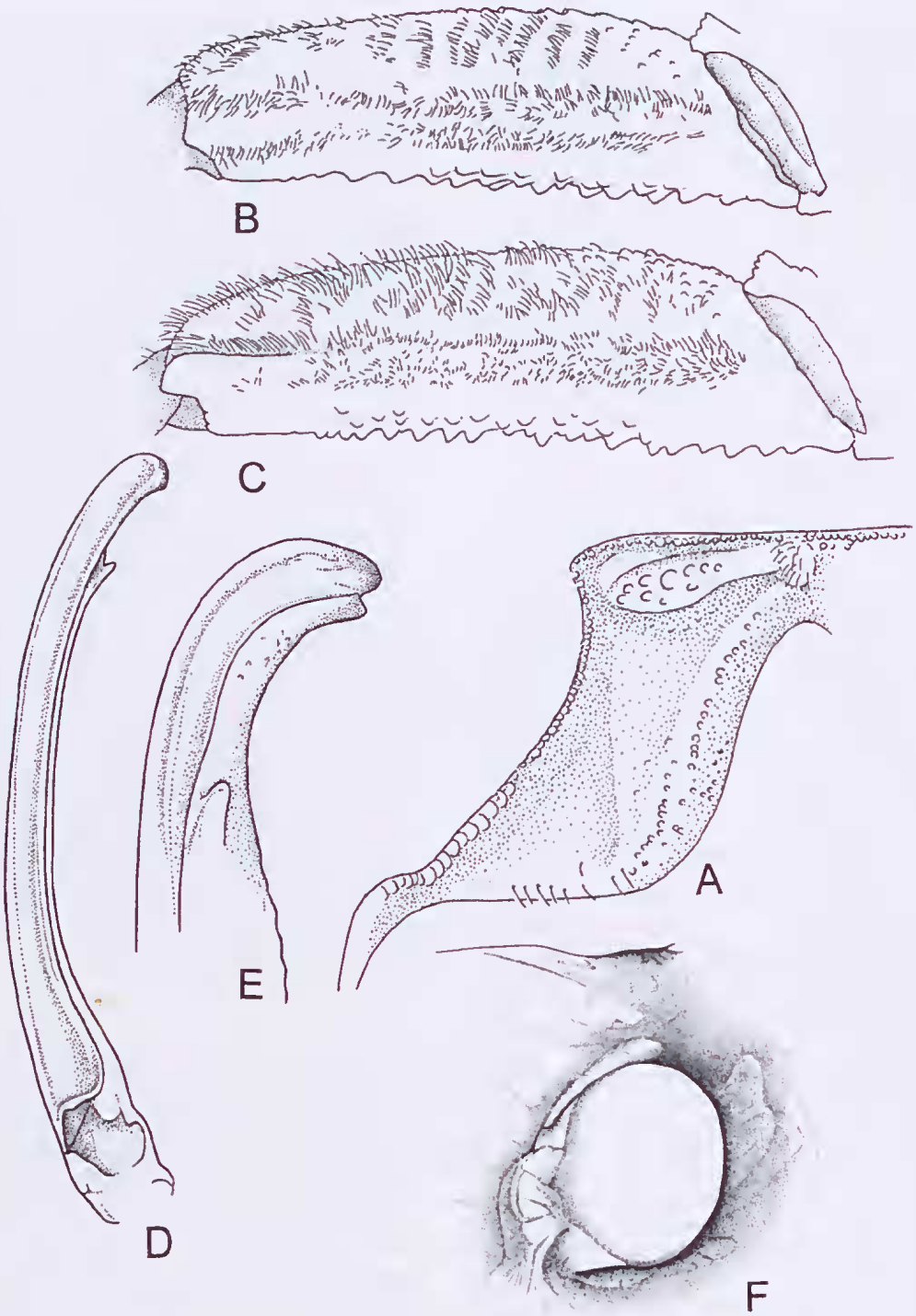

FIG. 10. *Ocypode ceratophthalma*: **A**, P1 thoracic sternite; **B, C**, P2–3 propodi; **D, E**, Go1; **F**, female operculum.

Description. Carapace (Fig. 32) slightly wider than long and covered with densely arranged fine granules on dorsal surface. Eyestalks prolonged distally beyond cornea in a stylus. Lateral half of orbital margin slightly concave, and directed obliquely backward in adult specimens. Exorbital angles broadly triangular and directed laterally. Lateral margins of carapace directed distinctly outward from base of exorbital angle in anterior third of carapace, and then directed inward in posterior two-thirds. Carapace broadest at exorbital angles, or in specimens with smaller exorbital angles, at anterior third. Pterygostomial region entirely tuberculate, but tubercles small along lateral sides of buccal cavity. P1 thoracic sternite (Fig. 10A) smooth and bordered with tubercles, bearing tuberculate humps anteriorly. Palm of larger cheliped broad, covered with coarse tubercles on anterior surface, and distinctly serrated on dorsal and ventral margins. Stridulating ridge (Fig. 1D–I) composed of 10–11 interspaced tubercles in dorsal third, 8 thick striae in middle third, and 20–30 closely spaced striae in ventral third. Smaller cheliped narrowing to pointed distal end. P2–3 propodi (Fig. 10B–C) with oblique rows of setae on dorsal half of anterior surface, bearing one (in female) or two (in male) median rows of setae. Go1 (Fig. 10D–E) slender, three-sided proximally, and slightly curved laterally in distal part, bearing a small protruding palp directed distally and distant from distal end. Sternite sunken around round operculum (Fig. 10F) towards genital opening, no discernible lateral rim.

Juvenile specimens. In a specimen from New Guinea (5.5×6.5 mm, RMNH-15499) eyestalks not prolonged distally beyond cornea. Carapace distinctly wider than long and covered with densely arranged fine granules on dorsal surface. Lateral half of orbital margin straight and directed laterally. Exorbital angles rectangular. Palm of larger cheliped much longer than broad, and more sharply serrated on dorsal and ventral margins than in adult specimens. Stridulating ridge distinct and composed of sparsely and irregularly arranged tubercles. P2–3 propodi bearing a median row of setae on anterior surface and setae on dorsal margin, both of which meet distally. In slightly larger specimens lateral half of orbital margin strongly bent, and exorbital angles directed laterally. In a specimen from eastern Africa (16.9×19.8 mm, ZMH-2824) eyestalks not yet prolonged distally beyond cornea in a stylus, but just as a small projection, while in a specimen from Tahiti (19.0×22.7 mm, SMF-1931) distal prolongation completely lacking.

Distribution. Indo-Pacific from the western Indian Ocean (except Red Sea) to Japan, Micronesia, and eastwards to Polynesia and Clipperton Island. Type locality: Unknown.

Remarks. The present species was reported for the first time by Peter Simon Pallas (1772) under the name of *Cancer ceratophthalmus* with his description and figures. It seems, however, that Pallas' species had already been included in a species described as *Cancer cursor* by Linnaeus (1758) based on specimens from Palestine (what we consider now to be the 'true' *cursor*) and India (presumed to be Pallas' species). So, earlier authors often confused *O. ceratophthalma* with *O. cursor*, and even synomymised the former with the latter. Herbst (1782) described *C. cursor* with reference to a specimen from East-India, but largely following Hasselquist's description (1762) of *Cancer anomalus* (= *O. cursor*) based on a specimen from Palestine. He referred to *C. ceratophthalma* Pallas as a synonym of *C. cursor* Linnaeus. However Herbst's specimen has turned out, on examination, to be clearly different from Haaselquist's; in Herbst's specimen the eyestalks are prolonged distally beyond the cornea in a stylus (*O. ceratophthalma*), whereas in Haaselquist's they are not prolonged distally beyond the cornea, but bear a brush at the distal end of the cornea (*O. cursor*). McLeay (1838) and White (1847) also synonymised *O. ceratophthalma* with *O. cursor*. Later White went as far as to name his specimen from the Red Sea *O. cursor* rather than *O. saratan*. MacLeay (1838: 64) used the name *Ceratophthalma cursor* for the whole taxon. It is evident that the specimens named *O. cursor* based on the specimens from India and the Red Sea were not correctly identified, because they are clearly different from *O. cursor* from Palestine and Syria.

It is quite difficult to identify juvenile specimens, which were at times even treated as good species. *Ocypode rhombea* described from

the Indo-West Pacific by Fabricius (1798) has turned out to be conspecific with *O. ceratophthalma* as shown by a thorough examination of the type specimen. On the other hand *O. rhombea* reported from the western Atlantic by H. Milne Edwards (1837) and White (1847) has turned out to be conspecific with *O. quadrata*. *O. brevicornis* (Dana, 1852: 326) and *O. brevicornis* var. *longicornuta* (Dana, 1852: 327) were synonymised with *O. ceratophthalma* by Kingsley (1880), however, it has turned out that *Ocypode brevicornis* H. Milne Edwards (1837) is not synonymous with *O. ceratophthalma*, but a valid species distributed in Oman, India and Sri Lanka. *Ocypode macleayana* Hess, 1865 from Sydney was synonymised with *O. ceratophthalma* by De Man (1888c: 351), who had in fact examined Hess' type specimen, and could thus confirm his earlier suggestion (De Man 1887: 696). The reasons for making *Ocypode urvillei* Guerin a junior synonym of *O. ceratophthalma* were explained in detail by Sakai, K. & Türkay (1976: 86). All this shows that access to type specimens is absolutely necessary for sound decisions in *Ocypode*, because juveniles differ so much from adults.

O. ceratophthalma is distributed widely in the Indo-Pacific and although it is easily recognisable by the morphology of the stridulating ridge, the male Go1, and the pointed smaller cheliped, it has nevertheless at sometime been confused with almost all other species of *Ocypode*. This has probably been caused by the uncritical use of growth dependent characters. Tu *et al.* (1923: 819) described *Ocypode* sp., calling it Sandkrabbe (= Sunagani) and indicating its characters as follows; the anterolateral angles of the carapace are sharply pointed; the eyestalks are prolonged, so that the species is most probably determined as *O. ceratophthalma*. Its reference is shown as Zoological Nomenclature (A complete Dictionary of Zoological Terms), however it should be shown as Doubutsugaku-Daijiten [= Zoological Encyclopedia].

Ng *et al.* (2008: 240) questionably included *Ocypode longicornuta* Dana, 1852, from Tonga and Singapore, (originally described as *Ocypode brevicornis* var. *longicornuta* Dana, 1852), as a possible valid species, however *O. brevicornis* var. *longicornuta* had already been synonymised with *O. ceratophthalma* by Kingsley (1880), and after having examined the figure by Dana, we fully agree with this conclusion. Thus, we treat *Ocypode brevicornis var. longicornuta* as a junior synonym of *O. ceratophthalma*.

Ocypode convexa Quoy & Gaimard, 1824

(Figs 2A, 11, 33)

Ocypode convexa Quoy & Gaimard, 1824: 525, pl. 77, fig. 2.
Ocypode bombée — H. Milne Edwards, 1837: 49.
Ocypoda convexus — Kingsley, 1880: 185.
Ocypoda Kuhlii — Miers, 1882: 348, pl. 17, fig. 8-8a [in part].
Ocypoda kuhlii — Miers, 1884: 237 [in part].
Ocypode pygoides Ortmann, 1894a: 766, pl. 23, fig. 19; Montgomery, 1931: 451, pl. 25, fig. 1, pl. 27, fig. 5; Serène, 1968: 97.
Ocypoda pygoides — Ortmann, 1897: 364; Balss, 1935: 140.
Ocypode convexa — George & Knott, 1965: 19, fig. 2D; Allender, 1969: 61, tabs 1–3; Davie, 2002: 357; Ng, Guinot & Davie, 2008: 240.
? *Ocypode convexus* — Serène, 1968: 97.

Material examined. Australia. Western Australia: No exact locality, female (NHM-1931.7.24.131); — *ibid.*, male (ZSM), Hamburger Südwest Australien Expedition; — Wooded I., Houtman Rock, male, 2 females (NHM-1931.7.24.128–9); — Dongara, male (ZMH-11519), 17.vii.1905, W. Michaelsen, Hamburger Südwest-Australien-Expedition; — Barrow Island, 2 males [35.8×43.9, 33.4×40.8 mm], female [33.7×42.0 mm] (ZMH-11339) [det. Balss, 1935 as *O. pygoides*], 1905; — Exmouth Gulf, Carnarvon, exterior part of the Gulf, southern and near low tidal line, male (AMS-P19421), 1972, N. Coleman; — 16 km of North Ningaloo (22°34.63′S, 113°39.66′E), near point Cloates, 3 males (SMF-7609 [ex. WAM]); — Bernier Island, female (AMS-P14964), 25.vii.1959, A. Douglas; — Dorre Island, Quoin Bluff, male (AMS-P14963), 19.vii.1959, N. McLaughlin; — Dorre Island, Shark Bay, female (NHM-1960.10.6.1–2) [det. George & Knott, 1965: 19 as *C. convexa*]; — Harrocks (28°22.77′S, 114°25.72′E), North of Geraldton, beach, male (SMF-10332), 17.x.1975, G. Hartmann & G. Hartmann-Schröder; — Geraldton, male (AMS-P14965), x.1929, A. A. Livingstone; — Cottesloe Beach, female (AMS-P4036); — Cottesloe (= Gotteslow) Beach, male (NHM-1931.7. 24.130).

Diagnosis. Large-sized species. Eyestalks not prolonged distally beyond cornea. Exorbital angles triangular and directed anteriorly. Palm of larger cheliped broadened and covered with coarse tubercles on anterior surface, bearing irregularly arranged spiniform tubercles on dorsal margin and regularly arranged distinct

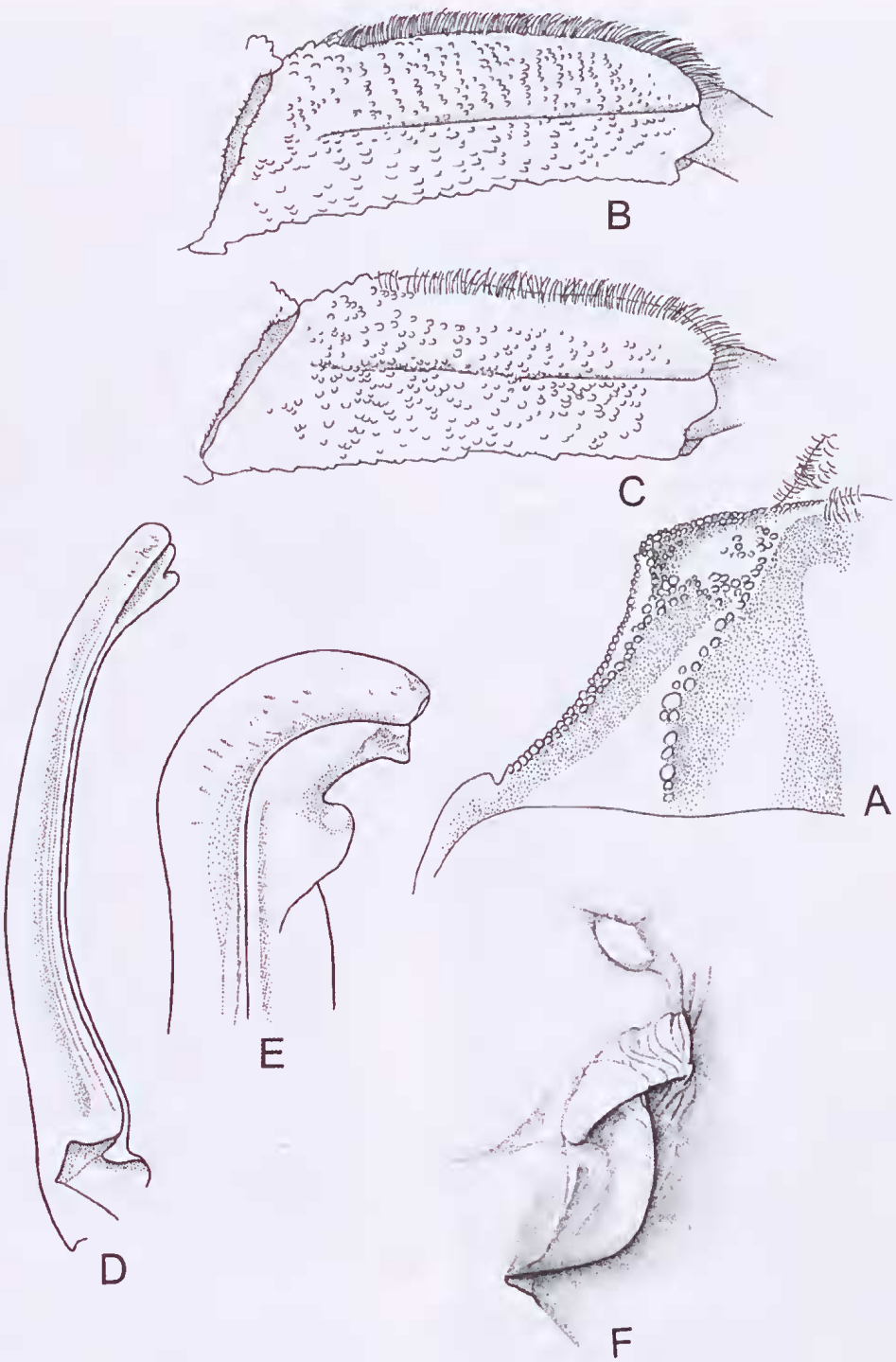

FIG. 11. *Ocypode convexa*: **A**, P1 thoracic sternite; **B, C**, P2–3 propodi; **D, E**, Go1; **F**, female operculum.

spiniform tubercles on ventral margin. Smaller cheliped tapering to pointed distal end. Stridulating ridge composed of 19–24 tubercles. P2–3 propodi setose on or along dorsal margin on anterior surface. Go1 narrowing distally, and slightly curved laterally at distal end, bearing distinct palp. Lateral rim of female genital opening located anterior to operculum.

Description. Carapace (Fig. 33) slightly wider than long, and covered dorsally with densely arranged tubercles, becoming larger and sparsely distributed towards anterolateral sides. Lateral half of orbital margin regularly concave. Exorbital angle triangular and protruding anteriorly. Lateral margins of carapace convex from tip of exorbital angle in anterior third of carapace, and then directed inward in posterior two-thirds, carapace broadest at anterior third. Pterygostomial region tuberculate all over its surface. P1 thoracic sternite (Fig. 11A) hemmed with distinct tuberculate carinae except on posterior margin, bearing tuberculate humps anteriorly, and transverse carina with tubercles in anterior third. Palm of larger cheliped slightly longer than broad, and coarsely tuberculate on outer surface, bearing irregularly arranged spiniform tubercles on dorsal margin and regularly arranged distinct spiniform tubercles on ventral margin. Both chelipeds covered with irregulary arranged tubercles of various sizes on anterior surface. Stridulating ridge (Fig. 2A) composed of 19–24 tubercles. P2 propodus (Fig. 11B) with setae on dorsal margin, and P3 propodus (Fig. 11C) with a row of setae along dorsal margin on anterior surface, but P4–5 propodi naked. Go1 (Fig. 12D–E) three-sided proximally, narrowing distally, and curved laterally in distal part, bearing a distinctly bulging palp protruding distolaterally near distal end. Lateral rim of genital opening horn-shaped and located anterior to operculum. Operculum of female genital opening (Fig. 11F) slightly convex mesially and evenly rounded, and terminated at distal end with a strong fold over distolateral rim.

Distribution. Entire coast of Western Australia, from about Broome in the north to south of Perth. Type locality: Dirk Hartog Island, Shark Bay, Western Australia.

Remarks. The present species was generally known as *Ocypode pygoides* Ortmann, 1894, instead of *Ocypode convexa* Quoy & Gaimard, 1824, because H. Milne Edwards (1837: 49) suppressed *O. convexa* due to uncertainty of the original description and figures. Miers (1882) referred to *O. convexa* as *incertae sedis* and named his material from Shark Bay, Western Australia, Thursday Island, Torres Strait, and Indonesia as *O. kuhlii*. Later Ortmann (1894: 766) introduced *O. pygoides* without paying any attention to Quoy & Gaimard's earlier work, but shortly after his description, Ortmann (1897: 361) suggested that *O. pygoides* might be identical with *O. convexa*. Much later George & Knott (1965) finally showed that *O. pygoides* is identical with *O. convexa* and therefore a synonym of this last species. Since then this usage has been stabilised (Davie 2002). After having re-examined and compared all the species of *Ocypode*, we confirm the synonymies and the current usage. This species is, as can be seen from the figures, delimited from all others by the pattern of setae on the anterior surface of the P2–3 propodi, the shapes of the carapace and the chela of the larger cheliped, as well as the morphologies of the stridulating ridge, the Go1, and the female genital opening.

Ocypode cordimanus Latreille, 1818

(Figs 12, 34)

Ocypode cordimana Latreille, 1818: 198, figs 1–3, 11; Desmarest, 1825: 121; Lucas, 1840: 58; Stimpson, 1858: 100; Hilgendorf, 1869: 82; A. Milne-Edwards, 1873: 271 [in part]; Hoffmann, 1874: 13; Kossmann,1877: 55; Hilgendorf, 1879: 803; Neumann, 1878: 26; Miers, 1879: 489 [in part]; Miers, 1880: 308; Richters, 1880: 155; De Man, 1881: 248; Lenz & Richters, 1881: 423; Haswell, 1882: 95; Miers, 1882: 387, pl. 17, fig. 9; Miers, 1884: 542, 573; De Man, 1887c: 108; 1888b: 352; Ozório, 1888: 243; Pfeffer, 1889: 30 [in part]; Henderson, 1893: 387; Matsuura, 1894: 55; Alcock & Anderson, 1894: 202; Ortmann, 1894a: 761, 764, pl. 23, fig. 16; Zehntner, 1894: 178; De Man, 1895: 572; Ortmann, 1897: 359, 362; Alcock, 1900: 349; Lanchester, 1900b: 752; Lanchester, 1901: 548; Borradaile, 1901: 67, 96; De Man, 1902: 438; Nobili, 1905a: 494; Nobili, 1906b: 310; Stimpson, 1907: 110, pl. 15, fig. 2; Borradaile, 1907: 65; Borradaile, 1910: 408; Lenz, in Voeltzkow, 1910: 558; Stebbing, 1910: 326; Lenz, 1912: 6; Urita, 1917: 72, fig.; Parisi, 1918: 96; Tesch, 1918: 35; Balss, 1922: 142; Maki & Tsuchiya, 1923: 204; Gravely, 1927: 148; Gordon, 1934: 9; Sakai, T., 1934: 319; Takahashi, 1932: 329; 1934: 74; 1935: 78; Estampador, 1937:

542; Tweedie, 1937: 141; Chopra & Das, 1937: 420, fig. 18; Shen, 1937b: 184; Miyake, 1939: 221; Sakai, T., 1939: 613, pl. 104, fig. 1; Sakai, T., 1940: 32; Shen, 1940: 91; Ward, 1942: 103; Sakai, T. & Nakazawa, 1947: 664, fig. 1916; Lin, 1949: 26; Barnard, 1950: 84, fig. 17a–b; Tweedie, 1950a: 126; 1950b: 323; Pillai, 1951: 27; Holthuis, 1953: 28; Raja Bai Naidu, 1954: 95–100, figs 18–30; Sakai, T., 1955: 111; Sakai, T., 1956: 53; Chhapgar, 1957: 45, pl. 13d–f; Stephenson *et al.*, 1958: 269; Guinot-Dumortier & Dumortier, 1960: 136; Sarojini, 1962: 191, tab. 1, fig. 1 l; Sankarankutty, 1961: 125; Shen & Liu,1963: 141; Hashmi, 1963: 240; Inaba, 1963: 170; 1988: 102; Miyake, 1963: 69; George & Knott, 1965: 16, fig. 2A; Sakai, T., 1965: 188, pl. 90, fig. 2; McNeill, 1968: 85; Chakrabati, 1972: 129; Horch, 1975: 193; Sakai, T.,1976: 599, text-fig. 327a, pl. 206, fig. 3; Paulraj, Mullainadhan & Ravindranath, 1982: 115–128, tabs 2–7; Yang, 1986: 153; George, 1982: 187, pl. 1; Dai & Yang, 1991: 455, text-fig. 230, pl. 58 (3); Gamo & Kosakai, 1991: 27, 30, fig. 1; Huang *et al.*, 1992: 142, fig. 1, pl. 1A, tab. 1; Poupin, 1996: 73; Yu *et al.*, 1996: 58, fig. 58; Jeng, M.-S., 1997: 88, fig.; Ng *et al.*, 2001: 36; Bruyn, 2002: 29–30, figs 1, 3, 5, 7; Marumura, & Kosaka, 2003: 69; Ng *et. al.*, 2008: 240.

Ocypoda cordimana — Sakai, T. & Nakazawa, 1947: 664, fig. 1916.

Ocypode cordimanus — Michel, 1964: 11; Crosnier, 1965: 96, figs 154, 162, 171–172, pl. 8, fig. 3; Pretzmann, 1968: 5; Serène, 1968: 97; Sakai, K. & Türkay, 1977a: 178; Sakai, K. & Türkay, 1977b: 97; Dai *et al.*, 1986: 418, pl. 58, fig. 3, text-fig. 230–4; Wang & Liu, 1993: 63, figs 51, 52; Türkay, Sakai & Apel, 1996: 102, figs 1–3; Davie et al., 1998: 19, fig.; Davie, 2002: 357; Poupin *et al.*, 2011: 18.

? *Ocypode cordimana* MacLeay, 1838: 64; Kraus, 1843: 41; White, 1847: 34; Herklots, 1851: 23; Laurie, 1915: 416.

Ocypoda ceratophthalma — Pesta, 1911: 55.

Ocypode albicans — Estampador, 1937: 542.

Ocypoda laevis — Sendler, 1923: 22.

Ocypode aegyptiaca — Balss, 1924: 14 [in part].

Cancer roberti Curtiss, 1938: 175; Ng, Eldredge & Evenhuis, 2011: 45, 52.

Ocypode sinensis Dai *et al.*, 1985: 372, 377, figs 8–14 [in Chinese]; Dai *et al.*, 1986: 418; Dai & Yang, 1991: 456, fig. 230A; Huang *et al.*, 1998: 943, tab. 1; Wang *et al.*, 1998: 64, figs 51, 52; Ng *et al.*, 2001: 36; Yodo *et al.*, 2006: 2, 4, 5, figs 2, 3, 6; Mano *et al.*, 2008: 2, 5, 6, 7, 8, tabs 1–2, figs 2–8; Seike & Nara, 2008: 593, tabs 1–2.

Material examined. Locality unknown. male [30.2× 3.7 mm], female [27.9×32.8 mm] (SMF-1957); 4 males [12.9×15.1– 15.3×17.3 mm] (SMF-36200), T. Sakai; male [25.4×28.9 mm] (SMF-36202); male [17.7×19.7 mm], 2 females [19.0×22.7, 19.6×23.4 mm] (SMF-36203); male [12.8×15.2 mm](SMF-36218). **China.** Fujian Province: Xiamen (= Amoy), male (MNHN), 1925, C.F. Wang; 15 males, 16 females (RMNH-221) [described by De Man, 1881]. **Taiwan** (= Formosa): no further data, female (ZMH-2801); — Lan yu (= Koto-syo) Island, 1 juv. male (USNM-73263) [det. as *O. africana*], 1933, T. Kano; — South-coast, Pingdong County, Kenting National Park, male [21.5×26.3 mm], 2 females [20.9×26.0, 19.5×23.6 mm] (SMF-24955) [det. as *O. sinensis*], 31.v.1997, P.K.L. Ng.; — Hainan Province: Hainan Island, male [32.5×35.8 mm] (SMF-36192); male [18.8×23.5 mm] (SMF-36194); male [18.8×23.5 mm] (BNHM-58–0024) [det. Chen as *O. sinensis*]. — Xisha Is, male [31.8×35.0 mm] (SMF-13233), 13.vi.1975; male [20.5×25.0 mm] (SMF-36193). **Japan.** Kanagawa Prefecture: Yokohama, male (MZT1112); — Kochi Prefecture: Tosa, female [17.7×21.7 mm] (SMF-36201), coll. T. Sakai. — Kagoshima Prefecture: Beach north of Tarumizu at river mouth of Honjou-gawa in the northern part of port (31°29.85´N, 130°41.98´E), female [9.8×11.3 mm] (SMF-16607), 2.xi.1979, H. & M. Türkay; — Ryukyu Islands: Yoron Island, north of Okinawa, 3 males (ZMH-2832); 2 males [7.8×9.6, 15.1×17.6 mm]; female [15.0×18.6 mm] (SMF-6745); — *ibid.*, male [8.4×10.1 mm] (SMF-36219), 3.xi.1966, K. Sakai;— Okinawa, Onna Coast, male [15.9×18.3 mm] (SMF-36213), 23.viii.1992, W. Shimabukuro; — Okinawa, 2 juvs. (USNM-171693); — Ishigaki I., female [11.1×13.2 mm] (SMF-7729), T. Sakai; — Ogasawara-Gunto (= Bonin Is.): Chichi-jima, male [20.1×24.7 mm] (SMF-6742), 25.vii.1971, H. Suzuki; — *ibid.*, male [16.5×19.5 mm] (SMF-6743). **Caroline Islands.** Ruck (= Chuuk) Island, 3 males, 2 females (MCM-1610) [described by Parisi, 1917]. **W-Carolines.** Fais, Hanseatische Südsee-Expedition, male [21.4 ×24.4 mm] (SMF-1954) [det. Sendler, 1923 as *O. laevis*], 22–29.ix.1909, E. Wolf. **Palau Islands.** female [22.0×28.7 mm] (ZMG-120) [Capt. Pöhl vend. 1889]. **Philippines.** No further data, male [28.2× 30.7 mm] (SMF-13556); — Mariveles near Manila or Guindulman, Luzon, 2 males [17.8×21.6, 21.5×25.1 mm] (ZMG-119), 1876, C. Semper; — General MacArthur (11°15´N, 125°32.5´E), E-Samar, female [19.1×23.9 mm] (SMF-9998), viii. 1978, W. Lobin; — Cebu, E Mactan, Maribago, NW-coast of Hilutangan channels (10°17´N, 124°00´E), female [27.9×31.0 mm] (SMF-19744), A. Schreiber. **Mariana Islands.** Wing Beach, Saipan, N-Mariana, female [6.1×7.3 mm] (SMF-19497), 11.viii.1990, A. Allspach. **Vanuatu.** Prov. Tafea, Aniwa (= Jmmer) (19°13.84´S, 169°36.8´E), East of Tanna, male [30.2×32.5 mm] (SMF-1949) [det. Sendler, 1923 as *O. laevis*], Hanseatische Südsee Expedition, E. Wolf. **New Caledonia.** Sandy beach, female [18.9×22.4 mm] (SMF-36215). **Solomon Is.** Sikaiana (= Stewart Island), male [27.2×30.6 mm] (SMF-1953) [det. Sendler, 1923 as *O. laevis*], Hanseatische Südsee-Expedition, E. Wolf. **Papua New Guinea.** Tarawai Is. (= Bertrand. Is.) (03°12.9´S, 143°15.56´E), male [Neotype of *Ocypode cordimanus*, designated by K. Sakai & M. Türkay, 1977] [33.9×37.2 mm] (SMF-1948) [det. Sendler, 1923 as *O. laevis*], Hanseatische Südsee Expedition, E. Wolf. **Australia.** Queensland: Ellice

Beach, north of Cairns, male [12.0×13.8 mm] (SMF-16564), 4.vi.1980, M. Türkay; — Rainbow Beach (25°54.28´S, 153°5.74´E), male [13.5×16.2 mm], 5 juvs. [7.0×7.9, 7.7×9.3, 6.5×7.4, 7.1×8.7, 7.0×8.6 mm] (SMF-9897), A. Türkay; 4 males [17.5×20.7–12.5×15.8 mm]; 4 juvs. (SMF-36214); — North Stradbroke I., N coast (27° 25.56´S, 153° 31.58´E), sand flat and sandy beach, 4 males [17.5×20.7–12.5×15.8 mm], 4 juvs. (SMF-36214), 30.ix.1999, M. Türkay; — *ibid.*, northern part, eastern beach (27°26.64´S, 153°32.23´E), 2 males [24.0×27.9, 10.9×12.8 mm], female [17.6×22.0 mm], 5 juvs. (SMF-36217), 29.ix.1999, M. Türkay; — *ibid.*, east coast, central part of island, sandy beach (27°31.33´S, 153°30.13´E), male [13.7×16.6 mm], 2 females [15.0×19.3, 9.0×11.3 mm] (SMF-36216), 30.ix.1999, M. Türkay; — Gold Coast, Southport, ocean beach, sand dunes, 2 males [21.7×24.1, 19.1×23.0 mm], 3 females [20.2×24.3, 17.9×21.0, 14.8×18.2 mm] (SMF-16565), 30.v.1980, M. Türkay; — New South Wales: Sydney, Port Jackson, male [16.9×19.6 mm], female [17.6×21.6 mm] (SMF-3607), May 1951, S. Kellner; — Sydney, Long Reef (33°44´S, 151°19´E), male, female, 1 juv. (SMF-38306), 24.v.1980, M. Türkay. **Malaysia.** Penang, Muka Head Beach (05°28.3´N, 100°11.2´E), male [22.7×27.0 mm] (ZRCNUS-1987-919) [det. as *O. sinensis*], 13.vi.1987, P.K.L. Ng & S. Harminto. **Indonesia**, Riau Archipelago, Pulau Bintan, Tanjung Tondang (01°10.8´N, 104°18.9´E), male [18.0×20.3 mm] (ZRCNUS-1999-0291) [det. as *O. sinensis*], vii.1995, P. K. L. Ng *et al.* — Sumatera: West Sumatera, Sasak, Sandy Beach, male [19.5×23.9 mm] (SMF-36259), 9.ii.1994, T. Ziegler; — Jaga Utara Is. (= Noordwachter Eiland or Pulo Sebiri) (5°12.0´S, 106°27.0´E), South-East of Lampung, Sumatera, male [30.9×33.2 mm] (ZMG-118), J. Brock; — Lesser Sunda Isles: Bali, Sanus, beach, male [16.0×18.5 mm] (SMF-17298), 29.vii.1979, R. König; — Moluccas: Ternate, 2 females [18.3×24.4, 24.7×29.5 mm] (SMF-1956), Kükenthal; — Halmahera, Tobelo, female [27.8×31.2 mm] (SMF-1952), Kükenthal; — Aru Islands, Trangan (= Terangan), Ngaigoeli (= Ngaigulu) coast (6°37.37´S, 134°5.51´E), male [26.5×29.7 mm] (SMF-1951), 6.ii.1908, H. Merton. **Sri Lanka.** Bentota River, 2 males [8.8×7.8, 13.3×10.9 mm] (SMF-5429), 16.i.1914, J. Mastbaum; — Colombo, beach, female [7.0×9.1 mm] (SMF-6738), 12.i.1914, J. Mastbaut; — Lavinia (6°49.87´N, 79°51.73´E), 5 males [16.1×19.0, 14.9×17.8, 15.1×17.9, 15.8×17.7, 12.9×15.4 mm], 2 juvs. [8.8×8.0, 7.5×9.0 mm], male, damaged [15.3×18.6 mm] (SMF-6744), 29.iii.1974, Z. Števčić; — Kuchchaveli (8°49.09´N, 81°6.15´E), 20 km North-west of Trincomalee, 4 males [14.2×17.4, 15.7×17.9, 18.7×21.8, 19.9×23.7 mm]; 3 females [20.2× 23.1, 21.1×26.0, 21.5×26.8 mm] (SMF-5421), 9-10.xi.1962, Brinck, Anderson & Cederholm, Lund Univ. Ceylon Expededition; — Moragalla, *c.* 50 km South of Colombo, beach of Wormels Reef Hotel, female [18.6×22.6 mm] (SMF-18265), 5-13.v.1989, H.G. Müller. **India.** Kerala Province: Badagara, Azhitala, Murat River (11°33.4´N, 75°35.7´E), female [21.0×25.1 mm] (SMF-36255), 25.vii.1984, W. H. Bee; — *ibid.*, female [13.9×15.8 mm] (SMF-36256), 26.vi.1984, W. H. Bee. **Chagos Archipelago.** Diego Garcia, male [32.7×34.7 mm], female [31.6×35.2 mm] (SMF-1955), 24.ii.1899. **Maldives.** Kuramathi, Rasdhoo Atoll, Alifu (Ari) Atoll, at night, farther away from water line, burrowing in sand, male [39.0×42.8 mm] (SMF-24952), 15.vii.1999, D. Kovac. **Seychelles.** Aldabra Atoll, male [38.0×41.6 mm] (SMF-9983), iii. 1979, M. Vannini; — La Digue (4°20´S, 55°50´E), Choppy's bungalow, beach, male [16.0×18.5 mm] (SMF-12910), 7.v.1979, M. Ackermann; — La Digue (4°20´S, 55°50´E), forest with ground vegetation, 2 males [23.3×25.7, 34.7×37.5 mm](SMF-12911), 8.v.1979, M. Ackermann; female [21.3×24.6 mm]; — La Digue (4°20´S, 55°50´E), open meadow with trees, 2 females [36.7×40.6, 39.5×43.6 mm] (SMF-12946), 16.v.1979, M. Ackermann. **Mauritius.** Round Island (19°52.84´S, 57°39.98´E) female (SMF-38305), 9.iii.1979, Blaich. **Réunion.** La Saline-les-Bains, beach, from burrows, 2 males [26.8×29.9, 28.8×31.2 mm], female [30.2×34.6 mm] (SMF-18266), 28–30.i.1989, H.G. Müller; — Beach at Caphomard (21°2.0´S, 55°13.25´E), male [21.5×23.1 mm], 3 females [29.3×34.1, 22.5×26.1, 21.5×25.3 mm] (SMF-18267), 30.i.1989, H.G. Müller; — N l'Etang Sale-les-Bains, Pnte. Des Avirons (21°14.21´S, 55°18.39´E), beach, from burrows, 3 males [19.5×22.4–23.2×25.7 mm], 4 females [21.2×25.7–29.7×33.5 mm], 2 specimens broken on the lateral margin (SMF-18268), 31.i.1989, H.G. Müller; — Beach at St. Paul, male [28.6×31.4 mm], female [29.7×33.2 mm] (SMF-18269), 1.ii.1989, H.G. Müller; — Harbour of St Gilles les Bains, beach, 4 males [24.0×27.4, 11.3×12.5, 8.1×10.0 mm], female [15.9×18.7 mm] (SMF-18270), 3.ii.1989, H.G. Müller. **Madagascar.** No further data, 3 males [10.5×12.1, 24.9×27.5, 26.3×28.4 mm] (SMF-1950), Ebenau. **Oman.** Khawr Al-Milh, peninsula Barr Al-Hikman, Gulf of Masirah (20°23.0´N, 58°17.0´E), male [20.1× 24.1 mm] (SMF-24528), 31.v.1995, D. Clayton; — Maskat, Quam W. Kaskat (23°37.00´N, 58°30.00´E), female [19.7×16.7 mm] (SMF-24529), 31.v.1995, D. Clayton. **Kenya.** Kilifi Creek, between Mombasa & Malindi, female [19.5×23.6 mm] (SMF-18263), W. Baumeister. **Rep. Djibouti.** Djibouti, Plage du Triton, 1 juv. male [8.3×9.6 mm] (SMF-16566), 18.iii.1987, Allspach, Fischer & Türkay. **Yemen.** Aden, male (MCSNM 2158); — Mukalla, female (NHML-1894.10. 31.13). **Somalia.** Sar Uanle, 20 km South of Kismayu (= Chisimaio), male [18.7×22.5 mm], female [24.0× 27.7 mm] (SMF-9982), vii.1973, M. Vannini. **Eritrea.** Massaua, 2 juvs. (SMF-6749), xii.1965, K.E. Linsenmair; — *ibid.*, female (MZUT-1102), 1903, P. Clivio. **Saudi Arabia**. Naman Island, male (NHMW), 8.x.1896, S.M.S. 'Pola'; male (NHMW), 30.x.1896. **Egypt.** Gulf of Aqaba, Dhahab, 2 males (RMNH-29238), 28.iii.1973, L.B. Holthuis & C. Lewinsohn.

Diagnosis. Middle-sized species. Eyestalks not prolonged distally beyond cornea. Exorbital angles broadly triangular and distinctly protruding anteriorly. Palm of larger cheliped

lacking stridulating ridge. Smaller cheliped narrowing to pointed distal end. P2 propodus setose on dorsal half of anterior surface, bearing a median row of setae. P3 propodus with setae along dorsal margin. Go1 curved laterally over distal part, bearing a distinct protruding palp directed distally. Operculum of female genital opening rounded distally, and protruding mesially. Lateral rim usually distinct distally and then extended mesially.

Description. Carapace (Fig. 34) slightly wider than long, and covered densely with fine tubercles, becoming larger toward lateral sides. Lateral half of orbital margin distinctly concave. Exorbital angles broadly triangular and distinctly protruding anteriorly. Lateral margins of carapace convex from tip of exorbital angle in anterior third of carapace, and then directed inwards in posterior two-thirds, carapace broadest at anterior third. Pterygostomial region distinctly tuberculate except along lateral sides of buccal cavern. P1 thoracic sternite (Fig. 12A) hemmed anteriorly with tuberculate carina and laterally with carina, bearing distinct tuberculate humps anteriorly. Palm of larger cheliped broad, covered densely with fine and coarse tubercles on anterior surface, and distinctly denticulate on ventral margin. Stridulating ridge absent. Smaller cheliped narrowing to pointed distal end. P2 propodus (Fig. 12B) with setae along dorsal margin and transverse rows of setae on dorsal half of anterior surface, bearing a median row of setae. P3 propodus (Fig. 12C) with thick setae along dorsal margin. P4–5 propodi naked. Go1 (Fig. 12D–E) three-sided proximally, narrowing distally, curved laterally in distal part, bearing distinct protruding palp directed distally near distal end. Operculum of female genital opening (Fig. 12F) elongate; rounded distal portion protruding mesially like a bean. Lateral rim usually distinct distally and then extended mesially.

Juvenile specimens: In a small specimen from Okinawa (6.5×7.5 mm, USNM-171693) exorbital angles acutely triangular and distinctly protruding anteriorly. Lateral margins of carapace directed straight downwards from base of exorbital angle in anterior third of carapace; then directed mesially in posterior two-thirds. Palm of larger cheliped broad, finely tuberculate on anterior surface; distinctly and regularly serrated on ventral margin. P2 propodus with setae on dorsal margin, bearing median row of longer setae. P3 propodus with setae only present on dorsal margin.

Distribution. From the Western Indian Ocean including the Red Sea and the east coast of Africa throughout the Indo-West Pacific to French Polynesia. Original type locality: 'Indes orientales'; locality of neotype: Tarawai I. (= Bertrand I.) (03°12.9′S, 143°15.56′E) [Papua New Guinea].

Remarks. The exact identity of this widely distributed and common species, remained uncertain for many years, because its original description was based upon more than one species. However, the selection of a neotype by Sakai, K. & Türkay (1977) made it possible to fix its identity. This species is widely distributed in the Indo-Pacific Ocean, although it has only been collected sporadically in the Red Sea.

Urita (1917) reported the present species from Kagoshima under the Japanese name of 'Mizugani', which is now called 'Minami-sunagani', at the same time stating that the larger cheliped bears no stridulating ridge.

Dai *et al.* (1985) established *Ocypode sinensis* based on specimens from Xisha Island, Jinyin-dao, southern China, whose distribution has later been extended to India, Malaysia Peninsula, the Philippines, Taiwan, and Japan, and distinguished the species *O. sinensis* from *O. cordimanus* which co-occurs in almost the same region, using various external characters as well as the structure of the gastric mill. Later Huang *et al.* (1998: 949, 951, Table 1) listed 11 morphological differences between *O. sinensis* and *O. cordimanus*. These points of difference are evaluated and discussed in the following.

O. sinensis is smaller, stated to reach a smaller maximum size of *c.* 20.0 mm carapace width in an adult male, while *O. cordimanus* is relatively larger, and an adult male reaches *c.* 30.0 mm carapace width. However, such a difference in size of the carapace cannot be used on its own as a major character for delimiting species, and even if it were to be true, it is useless for identifying any specimens less than 20 mm carapace width. Also juvenile and smaller specimens tend to take somewhat different morphology

from adults, and this could explain the differences observed by others.

In *O. sinensis* the carapace is said to be weakly arched dorsally, while in *O. cordimanus* the carapace is strongly arched dorsally. However, the small specimens determined as *O. sinensis* from Hainan Island, China, a male (18.0×20.3 mm, ZRCNUS-1999-0291) and a male (18.8×23.5 mm, BNHM-58-0024), have their carapaces arched just as strongly as larger specimens of *O. cordimanus*, so it is apparent this character is not consistent.

Huang *et al.* (1998: 949) described 'the median part of the suborbital margin is entire, gently convex, without any trance of a cleft (vs. interrupted with a distinct cleft in *O. cordimanus*).' However, *O. cordimanus* is not always characterised as 'interrupted with a distinct cleft, because a male specimen (15.3×18.6 mm, SMF-6744) determined as *O. cordimanus*, has the median part of the suborbital margin lacking a distinct cleft. In two male specimens (12.6×15.2 mm, ZRC-1999-0291, 15.8×17.7 mm, SMF-6744) from Indonesia determined as *O. cordimanus*, the median part of the suborbital margin is entire and regularly denticulate as in *O. sinensis*, while in a male specimen (22.7×27.0 mm, ZRC-1987.919) from Malaysia and another male specimen (18.8×23.5 mm, BNHM-58-0024) from Hainan which were both determined as *O. sinensis* by H. Chen, the median part of the suborbital margin is not entire, but shallowly concave as in *O. cordimanus*, which suggests that these two males might better be determined as *O. cordimanus*, considering their comparatively larger carapace width, so this character is also clearly difficult to use to discriminate between the two species. The same applies to the gap between the supra- and suborbital margins.

In *O. sinensis*, the urocardiac ossicle has the lateral margins of the peduncle weakly convex, tooth plate relatively smaller, zygocardiac ossicle relatively shorter, and premolar longer and more distinctly produced, with about 16 comb-like teeth. This compares with *O. cordimanus* that has the urocardiac ossicle with the lateral margins of the peduncle distinctly convex, tooth plate relatively larger, zygocardiac ossicle relatively longer, premolar shorter and less distinctly produced, and with about 17 comb-like teeth. We consider, however, those characters to be sufficiently variable that they are not useful for separating the species.

The differences that have been listed between the two species in the morphology of the third maxillipeds, their colour, the immovable finger of the male chela, the movable finger of the minor chela, the anterior thoracic sternum, and the male abdomen, are all variable in our opinion, and cannot be used to reliably distinguish the two species.

In our material some of the characters mentioned by Huang *et al.* (1998) appear to be randomly distributed among the size classes. Also because the differences in the Go1 observed between them are not sufficient to separate one species from the other, and they stated themselves 'the differences observed in the Go1 are difficult to use (for differentiation of two species).' They also remarked that 'Specimens of "*O. Cordimana*" reported and figured by T. Sakai (1976) from Japan are probably *O. sinensis* as well. The figure provided (T. Sakai, 1976, pl. 206, fig. 4) agrees very well with what is defined here as *O. sinensis*. In addition, T. Sakai (1976: 599) noted that the specimens of "*O. cordimana*" from Japan measure only up to 25.5 mm carapace width. This small adult size also strongly suggests that the Japanese specimens are *O. sinensis*.' As already discussed however, it is difficult to separate one species from the other based on their size. Smaller specimens often differ in some external characters from larger specimens of the same species (for example, different size-classes of *O. pallidula* have in the past been regarded as two different species). We consider smaller-sized specimens of *O. cordimanus* from Japan are not distinguishable from larger-sized *O. cordimanus* from the continent, though some external differences are observed between the two groups. We here conclude that *O. sinensis* is merely a smaller sized but conspecific form of *O. cordimanus* that cannot be separated at species level by morphological evidence.

The present species has been extensively dealt with in the literature under the name *Ocypode cordimana*. However, as 'manus' is a feminine Latin word, and the generic name

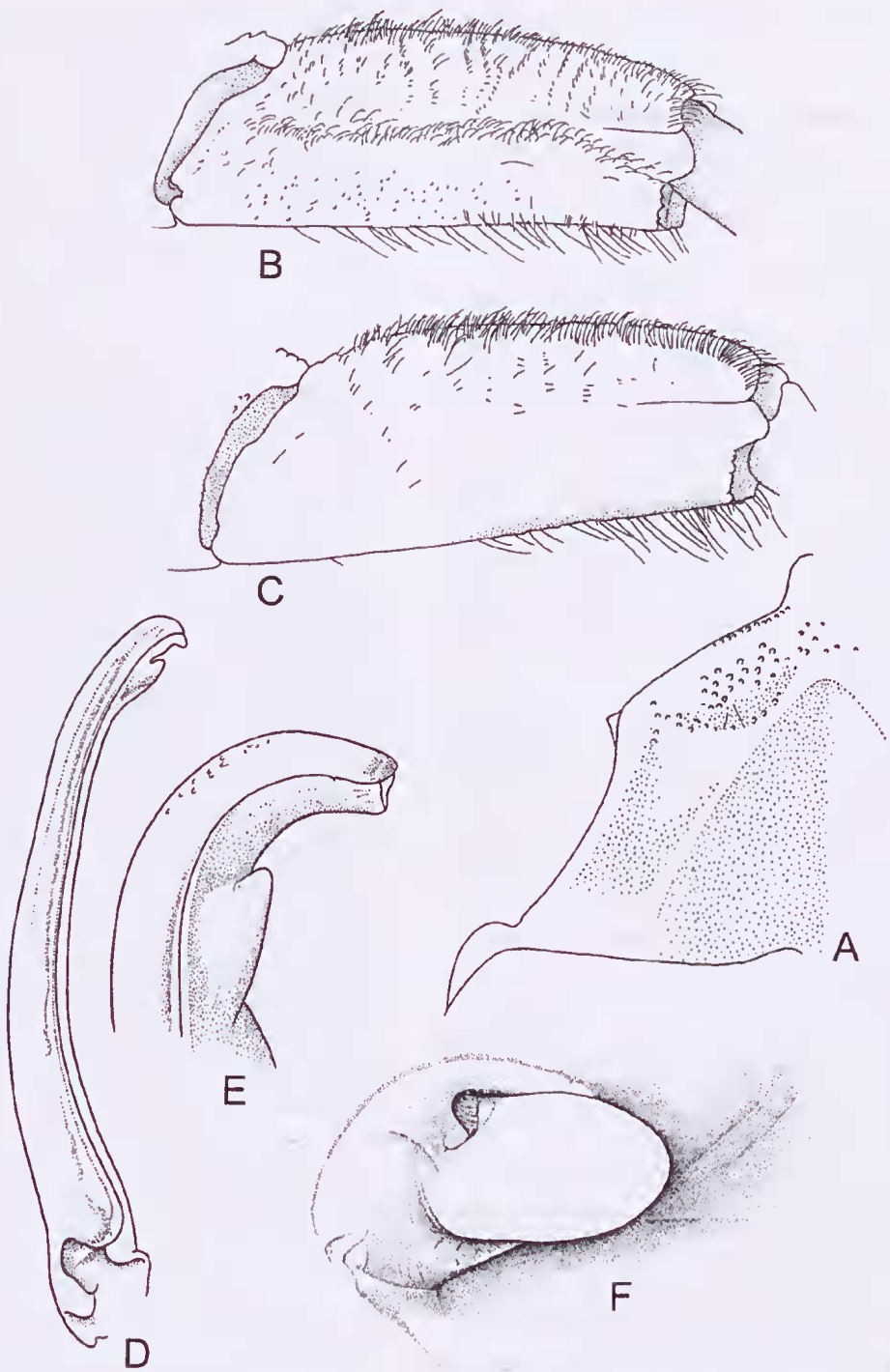

FIG. 12. *Ocypode cordimanus*: **A**, P1 thoracic sternite; **B**, **C**, P2–3 propodi; **D**, **E**, Go1; **F**, female operculum.

Ocypode is also feminine, it should rather be named *Ocypode cordimanus* than *O. cordimana*.

Ocypode cursor Linnaeus, 1758

(Figs 2B, 13, 35)

Cancer cursor Linnaeus, 1758: 625 [in part] [*sensu stricto*]; Müller, 1775: 1098 [in part]; Herbst, 1782: 74 [in part].

Cancer eques Aubert de la Chesnaye des Bois, 1759: 416, 417.

Cancer Cursor – Linnaeus, 1767: 1038 [in part].

Cancer anomalus Hasselquist, 1762: 474.

Ocypoda ippeus Olivier, 1804a: 235, footnote; 1804b: 52, footnote; Ozório (miss-spelling), 1887: 222; Osório, 1889: 133; 1890: 46; 1895a: 249; 1906: 150; Bouvier, 1907: 497; Olivier, 1804: 2: 234, 235, footnote, Pl. 30, fig. 1; 1804c: 52, footnote; Savigny, 1817, Atlas: pl. 1, fig. 1; Lamarck, 1818: 252; Latreille, 1817: 197; Audouin, 1826: 80; Desmarest, 1825: 121; Guérin-Méneville, 1832: 50; H. Milne Edwards, 1835: 47; H. Milne Edwards, 1838: 463; Lucas, 1840: 57; De Man, 1900: 42; Rathbun, 1900: 275; Rathbun, 1921: 461, pl. 52; Monod, 1933: 548.

Cancer hippeus Olivier, 1804b, pl. 30, fig. 1 [an alternative original spelling and considered a *lapsus* of *Ocypode ippeus*, see Low & Ng 2012: 50].

Ocypode Ippeus – Olivier, 1811: 416.

Ocypode chevalier – Latreille, 1817: 16; Latreille, 1829: 46; H. Milne Edwards, 1837: 66.

Ocypode rhombea – Audouin, 1826: 80 [in part, Locality Syria = *O. cursor*].

Ocypode (*Ocypode*) *cursor* – De Haan, 1835: 29.

Ocypoda (*Ocypoda*) *cursor* – Voigt 1835. In: Cuvier, 1836, 4: 119.

Ocypoda cursor – Herklots, 1851: 22; Heller, 1861a: 17; Heller, 1863: 99 [in part]; Kingsley, 1880: 182; Studer, 1883: 13; Miers, 1886: 240; Osório, 1889: 129, 139; Benedict, 1893: 538; Osório, 1898: 193; A. Milne-Edwards & Bouvier, 1900: 107; Doflein, 1904: 127; Odhner, 1923: 23; Bouvier, 1940: 285, text-fig. 178; Capart, 1951: 178, text-fig. 68; Gottlieb, 1953: 441; Monod, 1956: 391, text-figs 552–554; Dubois, 1957: 7, fig. 22; Sourie, 1957: 14, 31, 43, 45; Longhurst, 1958: 53, 88; Gauld, 1960: 71; Nicou, 1960: 140; Guinot & Ribeiro, 1962: 66; Rossignol, 1962: 119; Ribeiro, 1964: 14; Via Boada, 1966: 22–24, 2 figs; Antia, 1989: 264.

Ocypode cursor – H. Milne Edwards, 1852: 142; Stimpson, 1858: 100; Hilgendorf, 1869: 80, 81; Hilgendorf, 1879: 802; 1882: 23; De Man, 1881: 248; Miers, 1882: 380; Büttikofer, 1890: 465, 487; Ortmann, 1894a: 763; Johnston, 1906: 862; Stimpson, 1907: 108; Stebbing, 1910: 326; Vilela, 1949: 65, fig. 14; Barnard, 1950: 88; Sourie, 1955: 52, figs 15–17; Carmin, 1955: 2; 1957: 4; Rossignol, 1957 in Collignon, Rossignol & Roux, Mollusques, Crustacés Poissons A.E.F.: 86, pl. 2, fig. 1; Holthuis & Gottlieb,1958: 99; Altevogt, 1959: 129, fig. 1; Guinot-Dumortier & Dumortier, 1960: 135, figs 16a–b; Holthuis, 1961: 58; Guinot-Dumortier, 1961: 85, fig. 9; Bott, 1964: 31; Forest & Guinot, 1966: 89; Voss, 1966: 30; Kunze, 1967: 466–478, figs 1–13; 1968: 568–569, figs 1–4; Desportes, 1968: 201; Kensley, 1970b: 180; Penrith & Kensley, 1970: 252, 261; Kinzelbach, 1970: 318, text-fig. 1; Pretzmann, 1971: 481; Hartmann-Schroeder & Hartmann, 1974: 5–94: 13, 23; Sakai, K. & Türkay, 1977a: 178; Shuchmann & Warburg, 1978: 255–263; Shiber & Izzidin, 1978: 113–127, figs 1–10; Warburg & Schuchmann, 1979: 147–156, tabs 1–4, figs 1–5; Manning & Holthuis, 1981: 219; Ziese, 1985: 123–125, map 1; Türkay, 1989: 186, figs 5–6; Glaubrecht, 1992: 563–567, fig. 1; Erk'akan, 1993: 2; Ewa-Oboho, 1993: 119–127, tab. 2, figs 1–5; Strachan, Smith, Hamilton, Taylor & Atkinson, 1999: 51–60, tabs 1–5, figs 1–4; Rosenberg & Langer, 2001: 345–353; Voultsiadou & Vafidis, 2007: 108; Ng, Guinot & Davie, 2008: 240.

Oxypoda [sic] *ippeus* – Moseley, 1879: 48, 1 fig.

Occipoda [sic !] *cursor* – Vireira, 1886: 238.

Ocypoda hippeus – Ortmann, 1897: 368, pl. 17, fig. 11; Nobili, 1906c: 317; Bouvier, 1906a: 187; 1906b: 199; Sendler, 1912: 190; Balss, 1914: 79; Gravier, 1922: 120, 1 fig.; Roux, 1927: 238; Monod, 1927: 609; Balss, 1936: 42; Gauld & Buchanan, 1956: 295, 296, 298, 301; Gauld & Buchanan, 1959: 127.

Ocypode ceratophthalma – Pesta, 1911: 88: 54 [in part, material from Fernandes].

Ocypoda cerathophthalma – Balss, 1922b [In: Michaelsen, W.: *Beitr. Kennt. Meeres-fauna W. Afrika* 3: 80].

Ocypode hippeus – Balss, 1914: 106.

Ocypoda aegypticae – Monod, 1937: 18 [in part, material from Suez-Canal].

Ocypoda aegyptiaca – Monod, 1938: 148 [in part, material from Suez-Canal].

Ocypoda cordimana – Bodenheimer, 1937: 281.

Ocypode hypeus [sic!] – Sourie, 1954: 22.

Material examined. No exact locality. Probably NW Africa, female (SMF-22927); – Senegambia, 1 dry female (MHNG) [det. as *O. ippeus*]; – *ibid.*, 2 males (NHMW), 1869, F. Steindachner. **West Africa.** No further locality, 2 males (ZMH-2862); 5 juvs. (ZMH-5570); 3 males, 4 females, 6 juvs. (ZMH-26603) [det. as *O. kuhlii*]; – *ibid.*, 2 males (NHMW-1860), 1885, R. Lippe, 'Helgoland-Expedition'. **Mauritania.** Nuakchott, female (MNHN) [det. Bouvier, 1906 as *O. africana*], 1905, A. Gruvel. **Cape Verde Islands.** No further data, 2 males (MNHN); – *ibid.*, 2 juvs. (SMF-4363), Lindberg; – São Vicente, female (MNHN-3278S); female, 4 juvs. (NHRS-5625); – *ibid.*, male, 2 females, 2 juvs. (MNHN) [det. A. Milne-Edwards & Bouvier,

1900], 1883, RV 'Talisman Expedition'; — *ibid.*, male, 6 juv. males, 3 juv. females, 13 juvs. (NHM-84.31) [det. Moseley, 1879, Miers, 1882, Miers, 1886], 'Challenger Expedition'; — Sal: Santa Maria (16°35.64´N, 22°54.87´W), male (SMF-11058), 3.xi.1981, M. Geisthardt; — *ibid.*, beach in town, 5 juvs. (SMF-19312), 3-7.v.1990, R. Kinzelbach; — Boavista: NE-coast, Punta Rodrigo, beach (16°12.75´N, 22°45.46´ W), male, 2 females [1 heavily damaged] (SMF-8954), 26.xii.1978, R. Von Cosel; — São Tiago: male (NHM-84.31) [det. Miers, 1886] 'Challenger Expedition'; — Tarrafal (15°16.84´N, 23°45.18´W), 1 juv. male, 1 juv. (SMF-9636), 18-21.x.1979, K. Groh & W. Lobin; — E-coast, Praia Baixo (15°3.8´N, 23°28.47´W), beach, 18 males, 2 females (SMF-34546), 2-3.iv.2005, M. Türkay, I. Kröncke, K. Pietratus & W. Rosenboom; — Fogo, male, female (MCG-147) [det. as *Ocypode* sp.]; — Porto do Vale de Cavaleiros (14°55.22´N, 24°30.14´ W), North of San Felipe, 1 juv. male (SMF-9639), 31.x.1979, K. Groh. **Senegal.** Cape Verde, 3 juv. males, 3 juv. females (NHM-1934.8.17.6-7); — Malika NE of Dakar, male, 3 females (MNHN) [det. Monod, 1956], Monod; — Dakar, 7 juvs (NHMW-9832), 1885, 'Helgoland Expedition', R. Lippe; — Dakar, Tratta, female (MNHW 9834) [det. as *O. ceratophthalma*], 1885, 'Helgoland Expedition', Nr. 73, R. Lippe; — Gorée, 1 juv. male, 1 juv. female (NHMW-9829), 1881, K. Höfler. **Sierra Leone.** No further data, female (NHM-1905.1.31.9); — Freetown, 2 males (NHM); —Tagrin coast, female (NHM-1957.5.26.67). **Liberia.** No exact locality, 6 juvs. (MNHN) [det. Monod, 1956], 1882, Chaper; — Grand Cape Mount, 2 males, 2 females (RMNH-2768), 1882, J. Büttikofer; — Cape Mesurado, female (ZSM) [det. Balss, 1922 as *O. africana*], 1908, Scherer. **Côte d'Ivoire.** Abidjan, 2 males, 2 females (MNHN), 1956, Rancurel; — *c.* 10 km W of Sassandra (4°54.26´N, 6°10.0´W), male (SMF-25977), 2.xii.1998, J. Reimer. **Ghana.** No further data, 2 males (RMNH-220) [det. De Man, 1881]: — *ibid.*, female (MNHN) [det. Monod, 1956], Chaper; — Akka, female (NHM-1966.2.18.20). **Nigeria.** Lagos, 8 males, 3 females (NHM-1891.4.38.45); — near Lagos, male (RMNH-23407), 28.v.1965, RV 'Pillsbury' Sta. 316; — Nigerdelta between Brass and Port Harcourt, male, female (RMNH-15517), v-viii, 1960, H. J. G. Beets. **Cameroon.** No further data, female (ZMH-2872) [det. Balss, 1922]; — *ibid.*, 20 juvs. (RMNH-21179), 9.iii.1964, B. de Wilde-Duyfjes; — *ibid.*, 6 males, 3 females (RMNH-21146), 8.iii.1964; — Bibundi, 3 males, 3 juv. males, female (ZMH-2873) [det. Balss, 1922]; 2 males, 4 females (NHRS-t5978); — Limbe (= Victoria), female (ZMH-5568); — Bimbia river, male, 2 juv. males, female (MNHN) [det. Monod, 1927], 1925; — Kribi-beach, male (MNHN) [det. Forest & Guinot, 1966], 29.v.1956, RV 'Calypso', Sta. 33 (3°42´N, 9°15´E). **Equatorial Guinea.** 2 males (MNHN) [det. Monod], Pobequin; — Mbini (= Benito) (1°35.48´N, 9°37.07´E), 1 juv. (SMF-6120), Eidmann; — Cogo (= Kokobusch), 20 km upstream Rio Muni from Elobey Island, female (ZMH-5558) [det. Balss, 1922]; — Bioko (= Fernando Poo): no further data, male (NHM-1905.7.19.13); — sandy beach, male (NHMW-9795) [det. as *O. ceratophthalma*], 1885, R. Lippe, 'Helgoland Expedition'; — beach, 2 males (NHMW-9802) [det. as *O. ceratophthalma*], 1885, R. Lippe, 'Helgoland Expedition'; — muddy ground, about 100-150 m off the water, male (NHMW-9784) [det. as *O. ceratophthalma*], 1885, R. Lippe, 'Helgoland Expedition'; female (NHMW-9783) [det. as *O. ceratophthalma*], 1885, R. Lippe, 'Helgoland Expedition'; — beach, male, female (NHMW-9814) [det. as *O. ceratophthalma*], 1885, R. Lippe, 'Helgoland Expedition'; — Annobón: no exact locality, 4 juvs. (RMNH-23788), 20.v.1965, RV 'Pillsbury', Sta. 281; — *ibid.*, 1 juv. (ZMH-5375) [det. Balss, 1914], 1811, Schultze; male (ZSM) [det. Balss, 1914]; — *ibid.*, 2 males, 2 females (MCG-147), iv.1902, L. Fed. **São Tomé and Principe.** Principe: Pta. Da Mina, sandy beach with rocks, interdidal, 2 males, 1 ovig. female, 2 females (MNHN) [det. Forest & Guinot, 1966], RV 'Calypso', Sta. 112 . **São Tomé**: no exact locality, male, female (ZMH-5377) [det. Balss, 1922]; — *ibid.*, male (MNHN) [det. E. L. Bouvier, 1906], A. Gravier; female (MNHN) [det. E. L. Bouvier, 1906]. **Gabon.** No exact locality, 2 males (ZMH-2871) [det. Balss, 1922]; — *ibid.*, male (MNHN-3294S) [det. Monod, 1956] 1863, Duparquet. **Cape Lopez**, North of Port Gentil, male (ZMH-2864) [det. Balss, 1922]. **Congo.** No further locality data, female (MCG-147) [det. as *Ocypode* sp.], ii.1986; — *ibid.*, 3 males, 6 juvs. (RMNH-219.3), 1878, P. Kamerman; — *ibid.*, female (MNHN) [det. Monod, 1956], 1894, Dybowsky; — Pointe-Noire, 4 juvs. (MNHN); — *ibid.*, 3 males (MNHN), 1959, Rossignol; 4 males, female (MNHN); — *ibid.*, estuary of Noumbi river, female (ZSM), 27.v.1964, A. Strauch. **Congo, Democratic Republic.** No exact locality, 2 males, female (NHMW-1659) [det. as *O. ceratophthalma*], 1885, R. Lippe, 'Helgoland Expedition'; male (NHMW-9763) [det. as *O. ceratophthalma*]; 2 juvs. (NHMW-9828) [det. as *O. cordimana*]; — Banana (5°59.38´S, 12°23.1´E), male, 3 juvs. (SMF-1959), 12.v.1886, P. Hesse; — *ibid.*, 2 juvs. (SMF-6756), 1940, Vleeschouwers; — *ibid.*, 2 males (ZSM), 29.vi.1890; — *ibid.*, male, 1 juv. male, female, 4 juvs. (MCM-1974) [det. as *O. ippeus*], 1915; — Muanda (= Moandağ Tonda) (5°56.1´S, 12°20.54´E), male (SMF-6755); 1 juv. (SMF-4108), Dartevelle. **Angola.** No further data, male (MCM-2111) [det. Catumoelle as *O. ippeus*]; female (ZMH-2860); male (ZMH-5443); — *ibid.*, male (ZMNH) [det. De Man, 1900 as *O. lppeus*], 3.vi.1900; — Cabinda: Landana, male (MNHN) [det. Monod, 1956], 1898, Petit; — Zaire: near Musserra, 2 females (RMNH-1571), 1882, P. Kamerman; — Luanda: male, 2 females (ZMH, 29825); — *ibid.*, beach at St. Paul de Luanda, 8 juvs. (NHMW-9831), 23.vi.1894, J. Klimesch; — Cuanza Sul: Novo Redondo near Sumbe, 1 juv. male, 1 juv. female (ZMH-29817); — Benguela: Lobito (12°21.45´S,

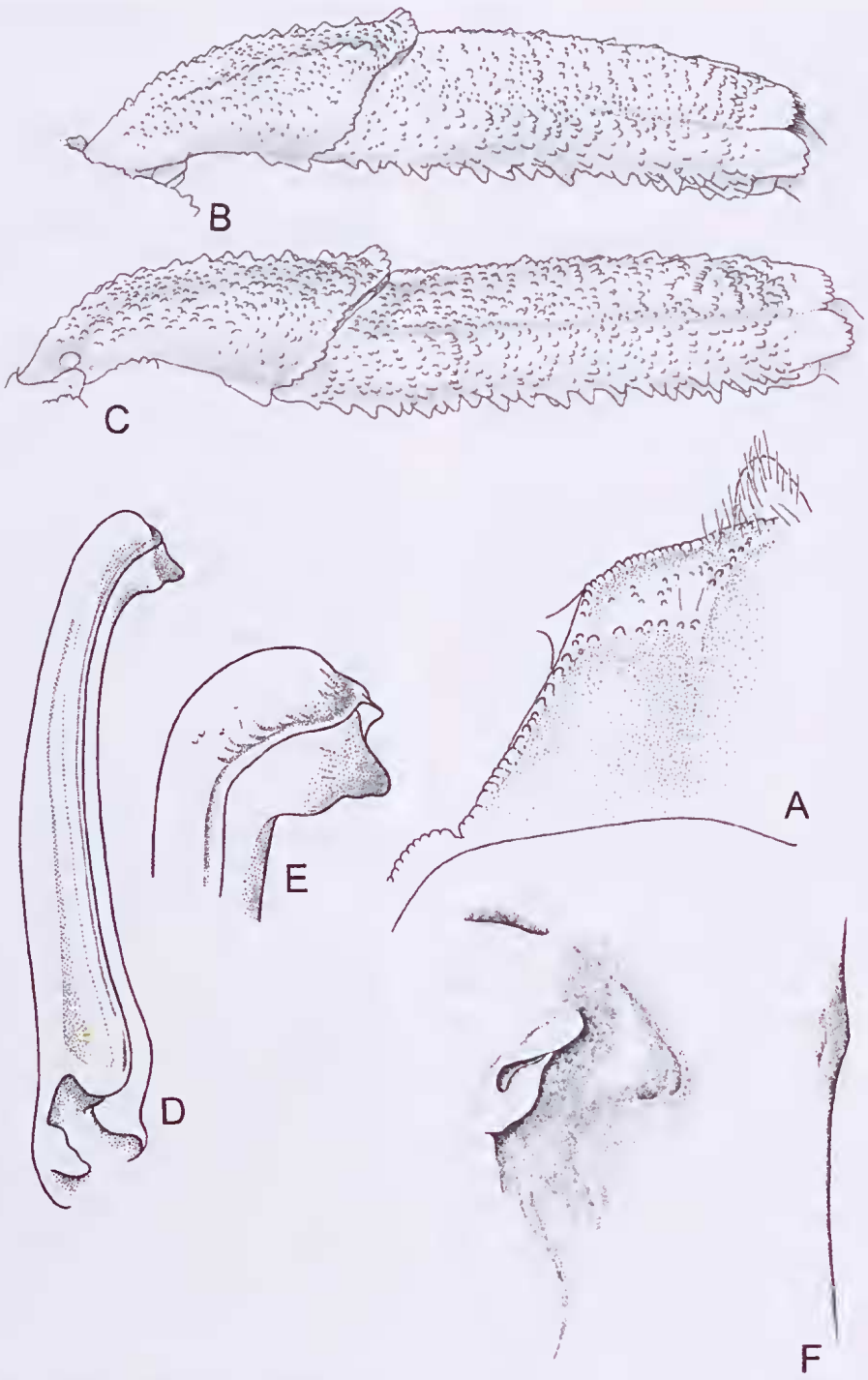

FIG. 13. *Ocypode cursor*: **A**, P1 thoracic sternite; **B**, **C**, P2–3 carpi and propodi; **D**, **E**, Go1; **F**, female operculum.

13°31.77′E), 3 juvs. (SMF-2671); — *ibid.*, Harbour, male (RMNH-1253) [det. De Man, 1900], Kamerman; — Benguela, male (NHM-1906.2.5.9); 4 juvs. (ZMH-29783); — Namibe: Tombua (= Port Alexander), male (RMNH-27226), 9.vi.1967, G. Hartmann; male (ZMH-29806). **Greece**. Karpathos, Pigadia-Bay (35°30.98′N, 27°12.01′E), several body parts (SMF-5104), spring, 1966, N. Polemikos & R. Kinzelbach. **Turkey**. Muğla Province: İztuzu beach (36°47.44′N, 28°37.7′E), SW of Köyceğiz, 2 juvs. (SMF-19311), 17.iv.1989, R. Kinzelbach; — Antalya-Province: Manavgat (36°45.84′N, 31°24.07′E), female, heavily damaged (SMF-2687), Dobal; — İncekum Beach (36°38.33′N, 31°43.58′E) between Alanya and Manavgat, male, female (SMF-4900), 25.v.1966, H. Felten; — Hatay-Province: İskenderun, sandy beach (36°37.24′N, 36°11.87′E), 5 juvs. (SMF-8679), 29.viii.1978, R. Kinzelbach; — Antakya, mouth of Orontes (= Asi nehri) (36°2.91′N, 35°57.73′E) and surroundings, 1 juv. (SMF-23244), 19.ix.1982, R. Kinzelbach; — Samandağ, sandy beach N of Orontes (= Asi nehri) mouth (36°2.79′N, 35° 57.78′E), 2 females (SMF-12165), 19.ix.1982; — beach between Samandağ and Orontes mouth (36°3.77′N, 35°57.31′E), male, female, 4 juvs. (SMF-18282); 1 juv. (SMF- 20443), 9-10.viii.1988, R. Kinzelbach. **Syria**. Nahr al Kabir S of Lataqia, river mouth (35°30.04′N, 35°48.6′E), male (SMF-9296), 5.iii.1979, R. Kinzelbach. **Lebanon**. Khaldé (33°47.27′N, 35°28.55′E), 12 km S of Beirut, sandy beach, male (SMF-9221), 1.v.1973, Lechner; — S of Tyros, sandy beach (33°15.47′N, 35°12.65′E), male, female (SMF-31128), 16.vi.2006, M. Bariche & M. Türkay.

Diagnosis. Large-sized species. Eyestalks not prolonged distally beyond cornea, but bearing a brush at distal end of cornea. Lateral half of orbital margin almost straight. Exorbital angles triangular and protruding outward. Propodi of P2–3 naked on anterior surface. Stridulating ridge composed of 69–96 tubercles with striae. Go1 curved laterally at distal end, lacking a palp. Female genital opening with lateral rim continuous lengthwise to elongate operculum, which is directed anteromesially under median rim.

Description. Eyestalks with a brush at distal end of cornea. Carapace (Fig. 35) wider than long, and covered with densely arranged fine tubercles on dorsal surface. Exorbital angles triangular and protruding outward. Lateral margins of carapace directed slightly outwards from base of exorbital angle in anterior third of carapace, and then directed inwards in posterior two-thirds. Carapace broadest at its anterior third. Pterygostomial region with regularly arranged tubercles. P1 thoracic sternite (Fig. 13A) with tuberculate carina on anterior to lateral margin, and a distinct transverse tuberculate carina at anterior third. Palm of larger cheliped slightly longer than broad, naked, and covered with coarse and fine tubercles on anterior surface. Stridulating ridge (Fig. 2B) curved in dorsal third, and composed of 69–96 tubercles with striae; *c.* 23 tubercles with striae in dorsal third, and *c.* 46 closely pressed tubercles with striae in ventral two-thirds (SMF-9296). Smaller cheliped narrowing to pointed distal end. P2–3 propodi (Fig. 13B–C) naked, bearing distinct spiniform tubercles on anterior surface and ventral margin. Go1 (Fig. 13D–E) three-sided proximally, curved laterally at distal end, lacking palp (SMF-9296). Female genital opening (Fig. 13F) sunken; operculum protruding anteromesially, slipped down under median rim.

Juvenile specimens. Carapace much wider than long. Lateral half of orbital margin slightly concave, so that exorbital angles triangular and directed somewhat anteriorly, tip located posterior to median convexity of orbital margin. Stridulating ridge composed of fine striae, and narrowed and distinctly curved in dorsal third. In a specimen (7.9×9.0 mm, SMF-6756) stridulating ridge less developed in dorsal third, only as an indistinct line. In smaller specimens, stridulating ridge not yet developed in dorsal third, but distinctly developed in ventral two-thirds. In a larger specimen (12.5×15.5 mm, SMF-6756) eyestalks already provided with a brush at distal end of cornea, but in a slightly smaller specimen (10.0×13.0 mm, MNHN-14096) eyestalks not yet provided with a brush. P2 propodus with scanty yellowish spines on dorsal margin. P3 propodus with row of long setae along distal 1/2–2/3 of dorsal margin.

Distribution. Mauritania to Namibia, eastern Mediterranean (from Egypt across the Levant to Turkey and southern Greece). Type locality: 'Mari Mediterranei, Indico'.

Remarks. This species was first described under the name *Cancer cursor* Linnaeus, 1758. Later Hasselquist (1762) described *Cancer anomalus*, and Olivier (1811) listed it under *Ocypode Ippeus*, attributing *O. cursor* to *O. ceratophthalma*. However, all of these species are synonyms of *O. cursor*, because they have the following characters in common: eyestalks bear a brush at

the distal end of the cornea, the stridulating ridge is composed of 69-96 closely pressed tubercles with striae and curved in its dorsal third, and the P2–3 propodi are naked and provided with spiniform tubercles, both on the anterior surface and on the ventral margin.

Ocypode fabricii H. Milne Edwards, 1837
(Figs 2C, 14, 36)

Ocypoda fabricii H. Milne Edwards, 1837: 47; Lucas, 1840: 57; Nobili, 1905b: 230, fig. 1–1a.
Ocypode Fabricii — Gibbes, 1850: 180; H. Milne Edwards, 1852: 142.
Ocypode fabricii — Ortmann, 1897: 361; George & Knott, 1965: 18, fig. 2C; Crosnier, 1965: 98, figs 155, 175, pl. 10, figs 1, 4; Serène, 1968: 97; Allender, 1969: 63; Davie, 2002: 358; Ng *et al.*, 2008: 240.
Ocypoda aegyptiaca — Balss, 1935: 140.

Material examined. Exact localities unknown. No data, male, female (MNHN); male (NHMW); female (SMF-6753 [ex. WAM]) [det. George & Knott, 1965]; — 'Oceanie', male [holotype] (MNHN). **Australia.** Northern Territory. West of Darwin, male, female (USNM-178294), 31.iii.1948, D. H. Johnston; — Western Australia, Broome in Mangrove, male (AMS-P14996); — Crab Creek near Broome, 2 males, female, 1 damaged (ZMH-K32304); — Pretty Pool, Port Hedland (20°18.514′S, 118°38.42′E), 3 males, 3 females (ZMH-K32299), 28.ix.1975, G. Hartmann & G. Hartmann-Schröder; male, female (SMF-10328); — Hersines Cove, 7 km East of Dampier (20°38.384′S, 116°44.662′E), 4 males, 2 females (ZMH-K32281); 2 males (SMF-10329), 2.x.1975, G. Hartmann & G. Hartmann-Schröder; — Nickol Bay, South-East of Dampier, 1 juv. female (NHM-69.38); — Pelican Point, Carnarvon (24°53.908′S, 113°24.533′E), 3 males, female (ZMH-K32294); male (SMF-10330), 13.x.1975, G. Hartmann & G. Hartmann-Schröder; — Shark Bay, male (ZMH-K11338) [det. Balss, 1935 as *Ocypoda aegyptica*]; — Small lagoon North of Denham (25°54.089′S, 113°31.933′E), Shark Bay, male, female (SMF-7612 [ex. WAM]) [det. George & Knott, 1965], 12.iii.1964, D.G. Bathgate; — Monkey Mia Beach (25°47.437′S, 113°41.851′E) near Denham, Shark Bay, male (SMF-23858 [ex. WAM]), 15-16.ix.1974, B. Shaw.

Diagnosis. Middle-sized species. Eyestalks not prolonged distally beyond cornea. Exorbital angles acutely triangular and protruding outward. Stridulating ridge composed of 126–133 fine striae. Smaller cheliped tapering to pointed distal end. P2 propodus with median row of setae (in female) or median row plus another in ventral half (in male). P3–5 propodi naked. Go1 curved laterally and tri-lobed at distal end, bearing an indistinct palp. Operculum of female genital opening rounded distally and protruding mesially; vaginal slit directed obliquely at about 45 degrees to sternal median line.

Description. Carapace (Fig. 36) almost quadrate and covered with coarse tubercles, becoming finer towards middle of dorsal surface. Lateral half of orbital margin slightly concave. Exorbital angles acutely triangular and directed outward. Lateral margins of carapace directed slightly outward from base of exorbital angles in anterior third of carapace, and then directed inwards in posterior two-thirds, forming an epibranchial corner, where carapace broadest. Pterygostomial region distinctly tuberculate except along lateral sides of buccal cavern. P1 thoracic sternite (Fig. 14A) concave at its mesial surface, bearing strongly tuberculate carinae on anterior and lateral margins. Palm of larger cheliped broad and covered densely with fine and coarse tubercles on anterior surface, among which coarser tubercles scattered, bearing distinct denticles on dorsal and ventral margins. Stridulating ridge (Fig. 2C) composed of 126–133 regularly and closely spaced fine striae. Small cheliped narrowing to pointed distal end. P2 propodus (Fig. 14B) with transverse rows of tubercles on dorsal half of anterior surface, bearing one median row of setae and another one on ventral half (in male) or one median row of setae (in female). P3 propodus (Fig. 14C) naked. Go1 (Fig. 14D–E) curved laterally and tri-lobed at distal end, bearing a low flat elevation as palp (SMF-7612). Operculum of female genital opening (Fig. 14F) rounded distally, protruding mesially in shape of button; vaginal slit directed obliquely at about 45 degrees to sternal median line.

Juvenile specimens. In a juvenile (11.5×13.5 mm) carapace slightly wider than long and less quadrate than in adult specimens, and rather similar to those of large specimens of other species. Carapace covered with tubercles, becoming finer from lateral sides towards middle of dorsal surface, as in adult specimens. Exorbital angles directed less outwards than in adult specimens. Stridulating ridge composed of 55 striae, much fewer than those in adult ones, but regularly and closely spaced as in adult ones. P2–5 propodi naked except on anterior surface of P2 propodus, which bears a median row of setae.

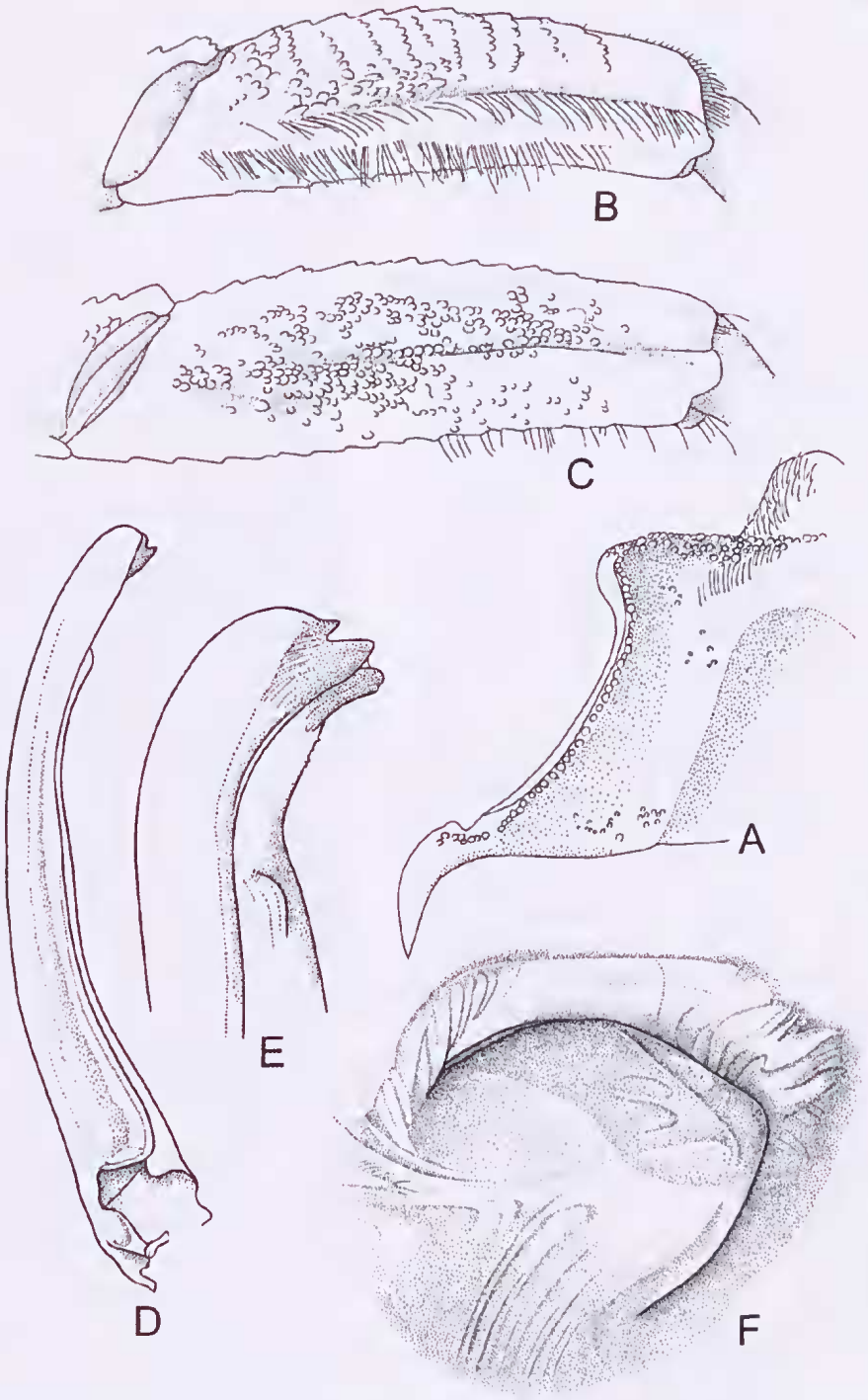

FIG. 14. *Ocypode fabricii*: **A**, P1 thoracic sternite; **B**, **C**, P2–3 propodi; **D**, **E**, Go1; **F**, female operculum.

Distribution. Northern and Western Australia (Darwin to Shark Bay). Type locality: 'Oceanie'.

Remarks. H. Milne Edwards (1837) gave the type locality of *Ocypode fabricii* simply as 'Oceanie' (= Pacific Ocean). Later, Ortmann (1897: 31) remarked that H. Milne Edwards' species is 'unidentificierbar' [sic] (= unidentifiable) because of the imprecise type locality. The identity of a specimen listed by Gibbes (1850) without specific reference to its locality, has also remained unclear, because it was later destroyed by the Philadelphia fire of 1866 (H.S. Feinberg, *in litt.*). Nobili (1905) finally clarified the identity of *O. fabricii* by publishing a thorough redescription of the type specimen, together with a figure of the carapace. He also restricted the type locality to Australia after comparing *O. fabricii* with other species of *Ocypode* collected from the Pacific. The type specimen has also been re-examined by Crosnier (1965), George & Knott (1965), and the present authors, and we all concur that specimens from Northern and Western Australia are *Ocypode fabricii* as described by H. Milne Edwards (1837).

Ocypode fabricii is very similar in morphology to *O. jousseaumei*, but the characters that separate them are discussed under that species account. Juvenile specimens of *O. fabricii* are liable to be confused with those of the sympatric species *O. ceratophthalma*, however, even in the smallest specimen of *O. fabricii* available (carapace width of 13.5 mm) the P2 propodus bears a median row of setae on the anterior surface, but the P3 propodus is naked. In *O. ceratophthalma* the P2–3 propodi are both provided with setae on the dorsal margin, and possess a median row of setae on the anterior surface. Those two species are also different from each other in the morphology of the stridulating ridge; in our juvenile specimen of *O. fabricii* there are 55 regularly and closely spaced striae, whereas *O. ceratophthalma* of the same size has only sparsely and irregularly arranged striae.

Ocypode gaudichaudii H. Milne Edwards & Lucas, 1843

(Figs 2D, 15, 37)

Ocypode Gaudichaudii H. Milne Edwards & Lucas, 1843: Atlas, 9, pl. 11, fig. 4; Lucas 1843: 26; Stimpson, 1860: 61.

Ocypode Gaudichaudi — H. Milne Edwards, 1852: 142.

Ocypoda Gaudichaudii — Nicolet, In Gay, 1852: 163; Dana, 1852: 329; Streets, 1871: 240; Miers, 1882: 383, pl. 17, figs 5, 5a; Cano, 1889: 91, 99, 100, 230; Aurivillius, 1893: 23, pl. 2, figs 7–13.

Ocypoda gaudichaudi — Kingsley, 1880: 181; Ortmann, 1897: 360, 365; Lenz, 1902: 767; Pesta, 1931: 180.

Ocypode gaudichaudi — Ortmann, 1894a: 762, 770, pl. 23, fig. 22; Porter, 1940: 312; Garth, 1957: 105.

Ocypode gaudichaudii — Rathbun, 1898: 603; 1902a: 275; 1906: 834 [no new material, only discussion of record]; 1910b: 550, pl. 43, fig. 2; 1918: 373, pl. 129, fig. 1, pl. 130, fig. 1; Schmitt, 1921: 278, fig. 163, pl. 38, figs 5–6; Boone, 1929: 580, fig. 15; Sivertsen, 1933: 19; Crane, 1940: 65, figs 1, 4, 6–8, and fig. of sternite; 1941: 299, figs 2, 4A–D, 5B, D, F, H, 6B, D, 7E, F; pl. 1, fig. 1; pl. 2, figs 3–4; Garth, 1948: 59, pl. 5, fig. 1; Koepcke, 1953: 1, figs 1–14; Holthuis, 1954a: 40; 1954b: 162; Bott, 1955: 67; Guinot-Dumortier & Dumortier, 1960: 136, 148, tab. 3; Edmondson, 1962: 1, fig. 5a–c; Bright & Hogue, 1972: 9; Horch & Salmon, 1972: 1–2, 4, 10, tab. 1, fig. 1; Full & Herreid, 1983: R530–R536, figs 1–5; Pretzmann, 1983: 315; Robinson, in: Robinson & del Pino, 1985: 182, 183; Trott, 1987a: 213–215, tab. 1; 1987b: 295–303, tab. 1, figs 1–3; 1988: 217–219, fig. 1; 1998: 47–56, tab. 1, figs 1–3; Schober & Christy, 1993: 53–60, tabs 1–3, figs 1–5; Arndt, 1999: 111–114; Quijon, Jaramillo & Contreras, 2001: 91–103, tabs 1–4; Villamar & Cruz, 2007: 142–143, tab. 1; Ng, Guinot & Davie, 2008: 240.

Ocypoda gaudichaudii — Doflein, 1899: 189; 1900: 144 [wrong locality]; Rathbun, 1924: 155, pl. 7; Boone, 1927: 267, fig. 96A [not fig. 96B megalopa, *fide* Crane 1940; Garth 1946 & 1948]; Crane, 1939: 19, 5 figs (no numbering); Garth, 1946: 514, pl. 87, fig. 7; Guinot & Cleva, 2002: 512, fig. 7.

Ocypoda urvillei — Doflein, 1899: 189.

Ocypoda Gaudichauni [sic] — Nobili, 1901b: 53.

Ocypode occidentalis — Garth, 1957: 104 [material = *O. gaudichaudii*; text = *O. occidentalis*].

Material examined. Guatemala. No further locality data, 5 males (ZMH-2931), Paessler; — Puerto San José de Guatemala, female (ZMH-2842). **El Salvador.** Depto Sonsonate: Acajutla, male [18.6×22.7 mm] (SMF-2077), 21.x.1951, H. M. Peters; — Depto. Usulutan: Mouth of Rio Lempa (13°15.6′N, 88°50.0′W), male [18.6×22.7 mm], 2 females [18.0×23.0 mm] (SMF-2202), O. Schuster; — *ibid.*, female (RMNH-9653), 19.iii.1953, M. Boeseman; — La Chapona (13°11.0′N, 88°21.0′W), male (SMF-2201), 11.iv.1953, O. Schuster; — Depto. San Miguel: El Cuco (13°10.35′N, 88°6.6′W), 1 juv. (RNHM-9654), 19.iv.1953, M. Boeseman; — Depto. San Salvador: San Salvador (wrong locality because San Salvador is far inland), 2 males (ZMH-2846). **Nicaragua.** No exact locality, 3 males, 3 females (ZMH-2840), Paessler. **Costa Rica.** No further data, 2 males, 2 females (NHM-1892.6.7.18-20); — Osa Peninsula, Golfo Dulce, male (NHMW) [det.

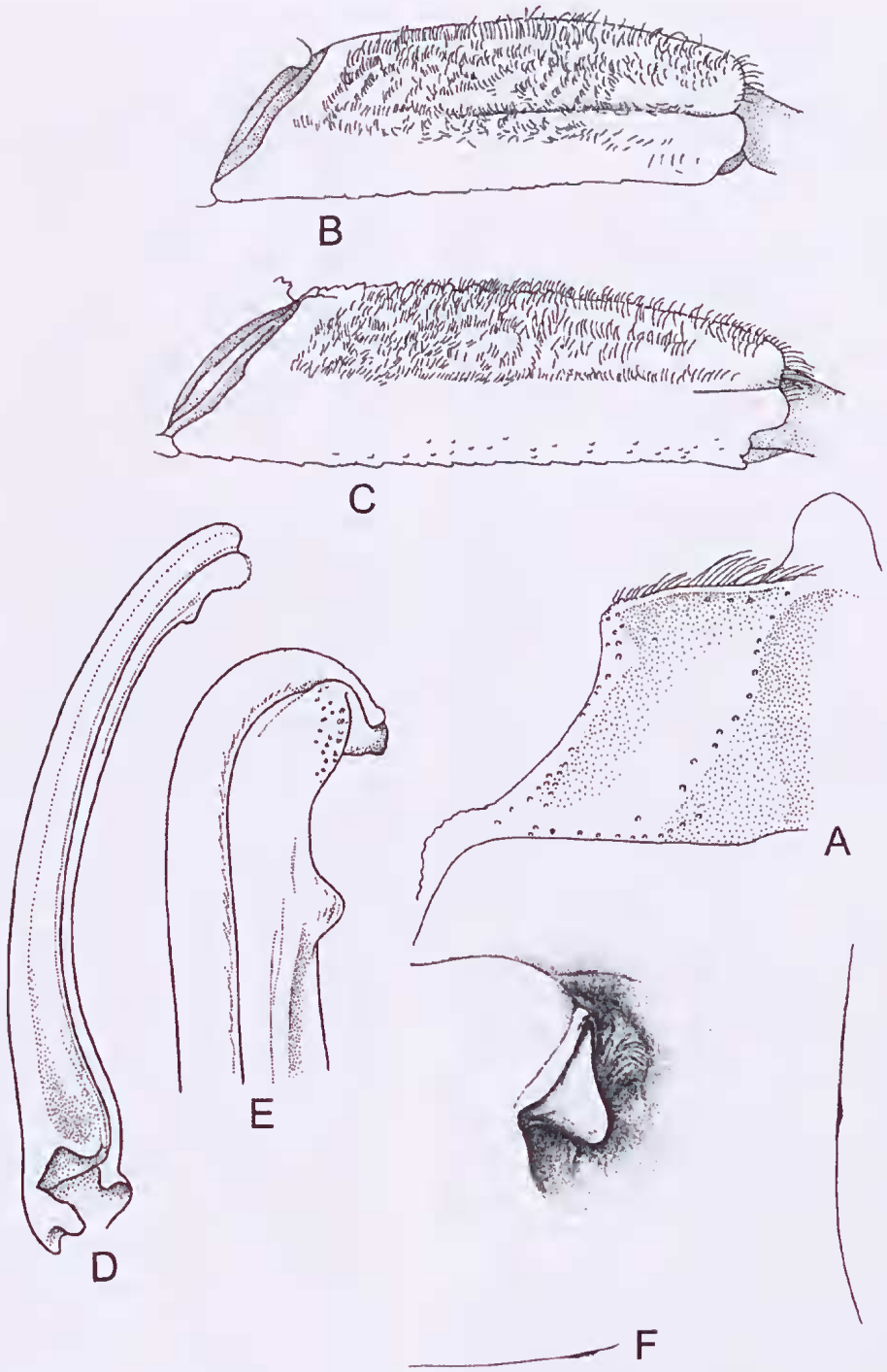

FIG. 15. *Ocypode gaudichaudii*: **A**, P1 thoracic sternite; **B, C**, P2–3 propodi; **D, E**, Go1; **F**, female operculum.

Pesta, 1931], Costa Rica Expedition, 1930. **Panama.** No exact locality, 2 males, female (USNM-168826), J.P.E. Morrisson; — Beach at Venado, 2 juvs. (UZMK), 14.xii.1915; — Isla Taboquilla, 13 males, 4 females (UZMK), 8.xii.1915; — Pearl Islands, Isla del Rey (8°27.12′N, 78°56.59′W), 1 juv. female (SMF-2400); — *ibid.*, SE-coast, Bahia San Telmo (8°18.01′N, 78°53.36′W), male (SMF-22178), 16.ii.1954, RV 'Xarifa'. **Colombia.** Depto. Valle del Cauca: Playa de Choncho in the delta of Rio San Juan (4°5.36′N, 77°29.33′W), male [19.6×24.3 mm] (SMF-9445), 15.ix.1979, H. von Prahl; — Depto. Nariño: Mulatos (2°39.27′N, 78°16.97′W), 2 juvs. (SMF-9444), 21.ix.1979, H. Von Prahl; — Tumaco (1°48.53′N, 78°22.37′W), male [13.2×16.5 mm], female [18.1×23.5 mm] (SMF-7848 [from UZMK]), 21.vii.1948, E. M. Poulsen; — *ibid.*, 2 males [28.3×34.4, 25.9×33.0 mm], 1 damaged male [CL 24.5 mm], 2 females [23.2×28.9, 21.5×27.6 mm] (SMF-6844), viii.1970, F. Klassen; — *ibid.*, beach of El Morro, male, female (SMF-7844 [from UZMK]), 28.viii.1948, E. M. Poulsen; — Depto. Cauca: Isla Gorgona, Arena (2°56.64′N, 78°11.36′W), 4 males [17.8×33.4 – 24.3×29.5 mm] (SMF-18684), 26.i.1979, E. Wedler; — *ibid.*, 4 males, female [21.9×29.2 mm], 13 juvs. [12.6×15.2 – 6.1×6.7 mm] (SMF-18685), 24.v.1979, E. Wedler; — Isla Gorgonilla (2°56.1′N, 78°13.0′W), male [28.8×32.6 mm] (SMF-18686), 27.i.1979, E. Wedler. **Ecuador.** District Esmeraldas, Muisne, beach (36°17.25′N, 80°01.57′W), 2 females [24.6×31.4, 22.8×28.9 mm] (SMF-36244), 29.viii.1985, R. Hutterer; — Galápagos, Rábida (= Jervis) (0°23.98′S, 90°42.41′W), male [27.0×32.4 mm] (SMF-2521), 30.vii.1957, Eibl. **Peru.** Tumbes Province: Surroundings of Puerto Pizarro, Mangrove (3°29.7′S, 80°29.29′W), male (SMF-13157), 15.v.1984, M. Clüsener-Godt; — Surroundings of Bocapán, beach without mangrove (3°43.52′S, 80°44.3′W), 2 females (SMF-13149), 31.vii.1984, M. Clüsener-Godt; — Lima Province: Ventannila, NW of Lima (11°52.31′S, 77°9.43′W), sandy beach, 2 juvs. (SMF-6852), 17.iii.1951, H.W. Koepcke; — Surroundings of Lima, 2 males (SMF-11443), 20.ix.1983, Riede; — Chilca (12°32.15′S, 76°45.22′E), *c.* 70 km South of Lima, sandy beach, male (SMF-2326), 4.ix.1951, H.W. Koepcke; — Coast near Asia (12°46.37′S, 76°36.26′W), 103 km South from Lima, male [16.7×2 1.0 mm], female [27.5×34.3 mm], 2 juvs. [6.5×7.5, 7.0×8.9 mm] (SMF-13148), 4.iii.1984, M. Clüsener-Godt; — Arequipa Province: Surroundings of Camaná (16°39.1′S, 72°42.6′W), pebble beach, 1 juv. (SMF-2311), 15.vi.1951, H.W. Koepcke. **Chile.** Arica (18°26.65′S, 90°42.41′W), male [29.3×36.8 mm] (ZMG-121), 1906, Bürger; — Antofagasta, Isla Santa Maria, beach (23°26.29′S, 70°36.16′W), male (SMF-19210), 15.iii.1989, M. Heisig. **No locality.** 2 males, 3 females (ZMG-122).

Diagnosis. Middle- to large-sized species. Eyestalks prolonged distally beyond cornea in a slender stylus. Larger and smaller chelipeds truncate at distal end. Exorbital angles protruding outward. P2–3 propodi setose. Stridulating ridge composed of 18 tubercles in dorsal half and *c.* 38 striae in ventral half. Go1 curved laterally in distal part and truncate at distal end, bearing conical palp. Operculum of female genital opening protruding mesioposteriorly.

Description. Eyestalks prolonged distally beyond cornea in a slender stylus. Carapace (Fig. 37) distinctly wider than long and covered densely with fine tubercles on dorsal surface. Lateral half of orbital margin directed obliquely backward. Exorbital angles protruding outward. Lateral margins of carapace directed slightly outward from base of exorbital angle in anterior third of carapace, and then directed inwards in posterior two-thirds. Carapace broadest at exorbital angles. Pterygostomial region tuberculate except around buccal cavern. P1 thoracic sternite (Fig. 15A) shallowly and broadly concave medially; hemmed anteriorly with tuberculate carina with setae; and laterally with tuberculate carina. Palm of larger cheliped comparatively longer than in other species of *Ocypode*, and covered densely with fine tubercles on anterior surface, among which are a small number of coarser ones. Ventral margin of palm provided with remarkably stout interspaced denticles. Stridulating ridge (Fig. 2D) composed of *c.* 18 tubercles in dorsal half and 36–38 striae in ventral half. Larger and smaller chelipeds both truncate at distal end of chela. P2–3 propodi (Fig. 15B–C) setose on dorsal half of anterior surface; in a juvenile specimen (CW 21.0 mm, SMF-13148) P2 propodus with a median row of setae on anterior surface and scanty yellowish spinules along dorsal margin and median line, and P3 propodus setose on dorsal half of anterior surface, bearing scanty yellowish spinules along dorsal margin and median line; in another juvenile one (CW 8.9 mm, SMF-13148) P2 propodus almost naked, bearing scanty yellowish spinules along dorsal and ventral margins, and a median line on anterior surface. P3 propodus also naked on anterior surface, bearing scanty yellowish spinules along dorsal and ventral margins. Go1 (Fig. 15D–E) three-sided proximally, and curved laterally in bulging distal part; truncate at distal end, bearing conical palp. Operculum of female

genital opening (Fig. 15F) protruding mesioposteriorly, and narrow anterior part of operculum surrounded by distinct thick rim.

Juvenile specimens. In our smallest specimen (5.1×5.6 mm, SMF-6852) carapace slightly wider than long. Front broad. Exorbital angles located far backward. Palm of larger cheliped distinctly swollen on inner surface. Chelae of larger and smaller chelipeds both tapering to pointed distal end. Stridulating ridge already distinctly raised and composed of fine granules. P2–3 propodi naked on anterior surface. In a slightly larger specimen (6.1×7.5 mm, SMF-2311) eyestalks not yet prolonged distally beyond cornea. Carapace distinctly wider than long, and smooth on dorsal surface. Front strongly reduced in breadth. Lateral half of orbital margin distinctly concave. Exorbital angles broadly triangular, protruding anteriorly, and located far backward. Stridulating ridge distinctly developed, and composed of sparsely arranged striae in dorsal half, and densely and irregularly arranged striae in ventral half. Larger cheliped already truncate at distal end of chela, while smaller cheliped still pointed at distal end of chela.

In a still larger specimen (13.7×17.7 mm, UMK) eyestalks prolonged distally beyond cornea in a small stylus. Lateral half of orbital margin not concave, but rather straight and directed obliquely backward. Exorbital angles protruding slightly outward as in adult specimens. Larger cheliped truncate at distal end of chela, and smaller cheliped rounded distally. Stridulating ridge distinctly developed; composed of tubercles in dorsal half and striae in ventral half. In a much larger specimen (18.5×24.5 mm) both larger and smaller chelipeds truncate at distal end of chela.

Distribution. Pacific coast of the Americas, from Guatemala to Chile (Valparaiso is the southern-most known locality). Type locality: 'Côtes de Chili'.

Remarks. The present species was introduced through a figure by H. Milne Edwards & Lucas (1843), though its formal description was not published until a year later, in 1844, by Lucas (1844: 17) alone. For practical purposes it is very important to distinguish this species from *H. occidentalis*, because those two species are both distributed in the eastern Pacific from Central to South America. Adult specimens of *O. gaudichaudii* are distinctly different from those of *H. occidentalis* particularly in the structure of the male G01 and female genital opening. *O. gaudichaudii* is also differentiated by both chelipeds with truncated chelae, and this is also true of juveniles over a certain size. Although Crane (1941: 302) reported this for specimens with a carapace width as little as 10.0 mm, our examination of a series of specimens suggests that this feature is only reliable for specimens greater than 24.5 mm carapace width. Smaller specimens are best determined by the structure of the stridulating ridge. Other useful characters for adults include the laterally protruding exorbital angles, and the styli extending beyond the cornea, but these are not useful for identifying juveniles. Past confusion in reliably identifying juveniles of *O. gaudichaudii* and *H. occidentalis*, has led mis-identifications and mistakes in distribution records.

Cano (1889) reported *O. gaudichaudii* from Honolulu, Hawaiian Islands, but Rathbun (1906: 834) remarked that his report needed verification. Edmondson (1962: 15) also stated: '.... there is no confirmation of its occurrence in the Hawaii Islands or anywhere else in the Central Pacific area.' It is certain that Cano's report of *O. gaudichaudii* from the Hawaiian Islands is incorrect. Rathbun's reports (1910, 1918) of *O. gaudichaudii* from San Pablo, Lower-California are also doubtful, and as Schmitt (1921: 278) commented that 'it is very probable that the label on this lot is either incorrect or the result of an exchange.' The reports of *O. gaudichaudii* by Boone (1927, 1929) are based on Rathbun's reports without mentioning Schmitt's comments. We re-examined Rathbun's specimens and did confirm that her identification was correct, but agree that they were probably mis-labelled as this species has never since been reported from either Hawaii or California. *O. gaudichaudii* was also reported from the Galápagos Islands by Rathbun (1899, 1902, 1918), Boone (1927), Sivertsen (1933), and Garth (1946), but not from Clipperton Island (Garth, 1965: 37). There is, however, an adult male specimen of the present species from Clipperton Island, which was found included in a collection preserved at the Museum National

d'Histoire Naturelle (MNHN) in Paris. The problem is that this adult male is the only specimen from Clipperton Island. So further investigation will be required in order to confirm this locality is correct. Doflein (1900) reported *O. gaudichaudii* from the Atlantic coast of Panama, about which he himself remarked that 'the specimens are from the Atlantic Ocean as described clearly on the label, though this species has been reported only from the Pacific Ocean.' [translation of German text]. The examination of his specimens (male & female, ZSM) shows that they were correctly identified as *O. gaudichaudii*, which suggests that this species may have reached the Atlantic coast of Panama through the Panama Canal. Again, this record needs confirmation before the Atlantic Panama can be safely included in the distribution of the present species. Therefore, the present species has to be regarded as a Pacific American element, with a distribution area ranging from Guatemala to Chile including the Galápagos Islands.

Ocypode jousseaumei (Nobili, 1905)
(Figs 3A, 16, 38)

Ocypoda Jousseaumei Nobili, 1905b: 233, fig. 2; 1906b: 310.

Ocypode jousseaumei — Laurie, 1915: 416; Crosnier, 1965: 99, figs 156, 163, 173–174, pl. 10, figs 2, 6; Serène, 1968: 97; Türkay *et al.*, 1996: 102, figs 4–6, 11; Clayton, 2001: 37–55; Clayton, 2005: 53–70, figs 1–9; Ng *et. al.*, 2008: 240.

Material examined. Red Sea. male [holotype] (MNHN-B11782). **Republic of Djibouti.** No further data, 2 males, 1 juv. male, 3 juv. females (ZMB 15639); — Tadjoura, 2 juv. males (ZMH-K2927). **Yemen.** Aden, 1 juv. male, 2 juv. females, 2 juvs. (ZMB 5878); male (USNM-64745); — Tauwahi (= at-Tawahi), East of Aden (12°47′N, 44°59′E), male (NHMW-24970), 1899, O. Simony. **Oman.** As Suwadi W of Masqat (23°46.57′N, 57°47.46′E - 12°47′N, 44°59′E), male (SMF-24530); male (SMF-24531); male (SMF-24532); — Golf of Masirah, peninsula Barr Al-Hikman, Khawr Al-Milh, South (20°22.22′N, 58°17.34′E), female (SMF-24533), 31.v.1995, D. Clayton.

Diagnosis. Middle- to small-sized species. Eyestalks not prolonged distally beyond cornea. Exorbital angles acutely triangular. Stridulating ridge composed of 41–79 tubercles and tubercles with striae. Smaller cheliped narrowing to pointed distal end. P2 propodus with a median row of setae on anterior surface. P3 propodus naked on anterior surface. Go1 narrowing distally, and slightly curved laterally in distal part, bearing a palp. Horny endpiece flat, longer than broad, and rounded at tip. Operculum of female genital opening rounded and protruding mesially.

Description. Carapace (Fig. 38) almost quadrate, and covered densely with fine tubercles on dorsal surface. Lateral half of orbital margin concave. Exorbital angles acutely triangular and protruding outward. Lateral margins of carapace directed slightly outward from base of exorbital angle in anterior third of carapace, and then directed inwards in posterior two-thirds, forming weakly protruding epibranchial angles. Carapace broadest at exorbital angles. Pterygostomial region coarsely tuberculate except along lateral sides of buccal cavern. P1 thoracic sternite (Fig. 16A) smooth and rimmed laterally with tuberculate carina, bearing scantily tuberculate humps. Palm of larger cheliped broad and covered densely with irregularly arranged tubercles on anterior surface, bearing a relatively small number of denticles on ventral margin. Stridulating ridge (Fig. 3A) composed of at least 41 (SMF-24530), 72 (NHMW), or at most 79 (holotype) elements; 15 tubercles in dorsal third and 26 closely spaced tubercles with striae in ventral two-thirds (SMF-24530). Smaller cheliped narrowing to pointed distal end. P2 propodus (Fig. 16B) with a median row of setae on anterior surface. P3 propodus (Fig. 16C) naked on anterior surface. Go1 (Fig. 16D–E) distinctly narrowing distally, and weakly curved laterally in distal part, bearing a distinct palp directed distally and located distant from distal end. Operculum of female genital opening (Fig. 16F) rounded and protruding mesially, posterior to which a large elevation present.

Juvenile specimen. In a young specimen (7.8×9.0 mm, ZMB 5878) carapace tuberculate. Orbital margin directed obliquely backward from front. Exorbital angles located distinctly backward. Stridulating ridge already characterised by elements, which are gradually transformed from tubercles into striae from the upper end downwards. P2 propodus with a median row of long setae on anterior surface. P3 propodus sparsely setose on anterior surface.

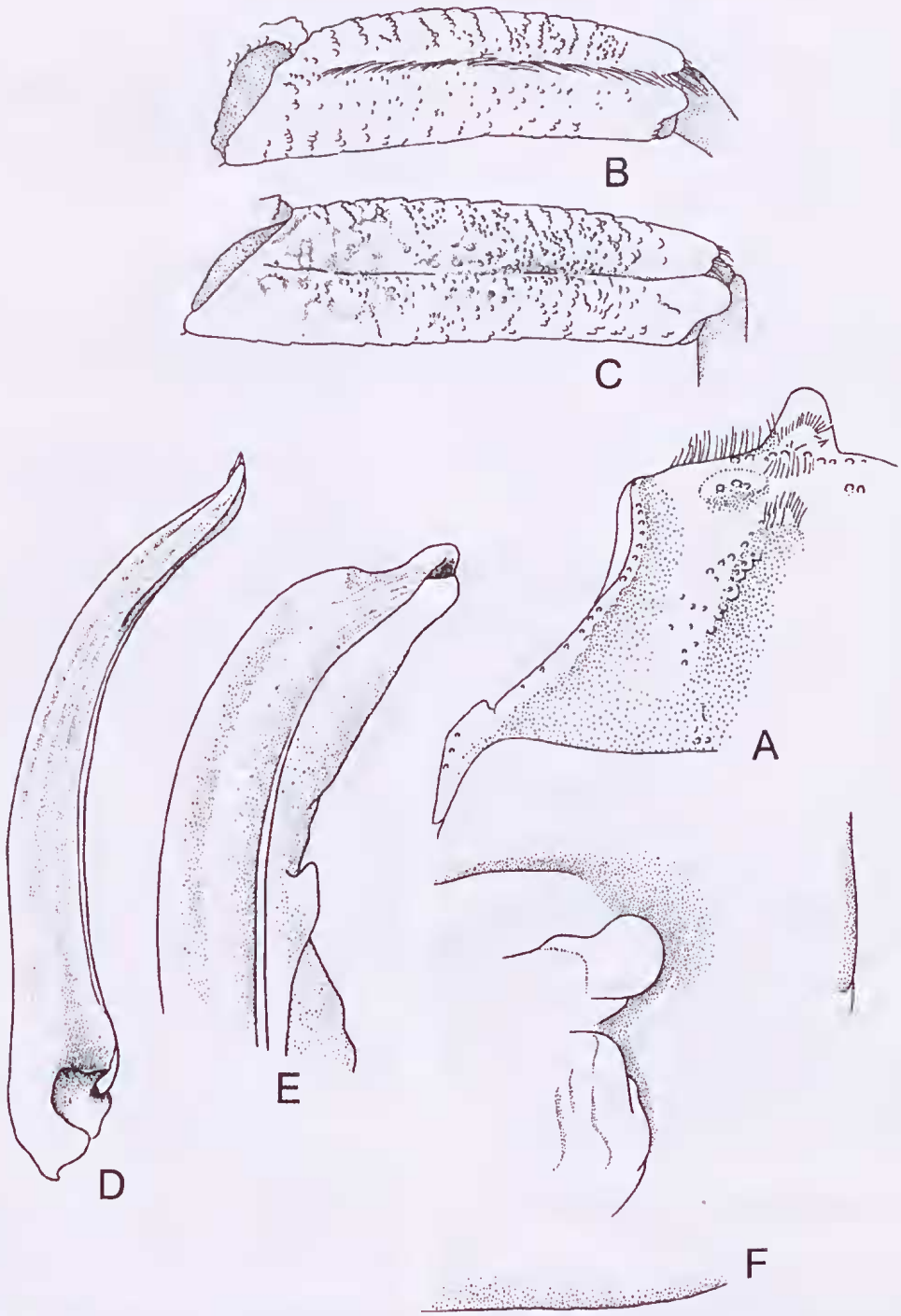

FIG. 16. *Ocypode jousseaumei*: **A**, P1 thoracic sternite; **B**, **C**, P2–3 propodi; **D**, **E**, Go1; **F**, female operculum.

Table 3. Differences between *O. fabricii* and *O. jousseaumei*.

O. fabricii	*O. jousseaumei*
Carapace covered with coarse tubercles becoming finer toward middle (branchial region).	Carapace covered densely with fine tubercles.
Male P2 propodus with two rows of setae on anterior surface.	Male P2 propodus with one row of setae on anterior surface.
Stridulating ridge composed of fine striae.	Stridulating ridge composed of tubercles and tubercles with striae.
Distributed in northern and western Australia.	Distributed in the Gulf of Aden.

Distribution. Only known from the Gulf of Aden (Yemen and Djibouti) and the Gulf of Oman (surroundings of Masqat). Though the holotype is labelled 'Red Sea', this might refer to the southern-most part, already in the straits of Bab el Mandeb. To date there are no records from the Red Sea proper. Type locality: Obock, Djibouti (Nobili 1906b).

Remarks. *Ocypode jousseaumei* from the Gulf of Aden seems very similar to *O. fabricii* from northern and western Australia. Those two species are, however, easily distinguishable from each other by the differences between them listed in Table 3.

Juvenile specimens of *O. jousseaumei* are also easily distinguishable from the potentially sympatric species *O. saratan* by the length of their stridulating ridge; in *O. jousseaumei* the stridulating ridge extends dorsally past a line corresponding the median line of the movable finger, while in *O. saratan* the stridulating ridge reaches the line but does not extend further.

The type locality of *O. jousseaumei* was corrected by Nobili (1906) from the Red Sea to Obock (now in the Republic of Jibouti), and there has been no evidence since that this species occurs in the Red Sea. The very small number of male specimens recorded from the Gulf of Aden, suggests that it is not well established there.

Ocypode kuhlii De Haan, 1835

(Figs 3B, 17, 39)

Ocypode (*Ocypode*) *kuhlii* De Haan, 1835: Fauna Japon. Crust., 29, 58; Herklots, 1861: 128.

Ocypode kuhlii — De Man, 1881: 250; Miers, 1882: 384 [in part: not pl. 8, 8a = O. convexa]; De Man, 1883: 156; Osório, 1888: 238; Crosnier, 1965: 101, figs 157, 164, 176-177, pl. 9, fig. 1; Holthuis, In Yamaguchi, 1993: 626, fig. 18; Davie, 2002: 358; Ng, Guinot & Davie, 2008: 240.

Ocypode kuhli — De Man, 1895: 570; Ortmann, 1897: 364 [in part]; Tesch, 1918: 36; Gordon, 1934: 9; Tweedie, 1947: 32.

Ocypoda Kuhli — Doflein, 1904: 126.

Ocypode ceratophthalma — Rathbun, 1910a: 321[in part].

? *Ocypode kuhli* — Stephenson, Endean & Benett, 1958: 269.

Ocypode cf. *kuhlii* — McNeill, 1968: 86.

Material examined. India. Kondul (7°12.92´N, 93° 42.6´E), Nicobar Islands, 1 juv. (SMF-8341). **Thailand.** NorthWest point of Phuket Is., female (RMNH-24992). **Indonesia.** Sumatera: Aceh, 6 males, 4 females (ZSM, originally from Natur Museum Lübeck) [det. De Man, 1895]; — Storm, male (ZMA-102367); male (RMNH-1615) [det. De Man, 1895]; — Padang, West Sumatera, 2 juv. males, 5 juv. females (RMNH-218); — Lsikin, Simeulue Is., off west coast of Sumatera, 2 juv. males (RMNH-2182); — Nias Island, off west coast of Sumatra, female (ZMA-102.336); — Luau vara, Nias Island, 2 males, 2 juv. females (MCG-147) [det. as *O. sp.*]; — Java: no further data, male [lectotype] (RMNH-D217), male [paralectotype] (RMNH-D 216), 2 dry males [paralectotypes], male, 6 juvs. (UZMK), 1 juv. (SMF-7850); — South coast, male, female (ZMA-102368); — Jakarta, male, female (ZMA-102365); — Semarang, male, dried (MNHN-3286); female (NHMW-1874) [det. as *O. cordimanus*], Pfason; — Madura I., 1 juv. male, 1 juv. (RMNH-15514-516); — Kangean Islands off East Java, male (ZMA-102363), 'Siboga Expedition', St. 51; — Poelo Pete, 3 males, 5 juvs., 1 broken specimen (IRSNB-9223) [det. Gordon, 1934]; — South coast, Karang Hawoe, 1 juv. male (IRSNB-9223) [det. Gordon, 1934 as *O. sp.*]; — Lesser Sunda Islands: Bali, South-West coast, Batu Belig Beach (8°40.96´N, 115°9.1´E), North-West of Legian, male (SMF-23298), x.1994, C. Tautz-Kopania; — Lombok, Ampenan, 1 juv. female, 2 juv. males (MCZ-7246) [det. Rathbun, 1910 as *O. ceratophthalma*]; — Flores, 7 males, 10 juv. males, 2 females, 19 juv. females (RMNH), 'Snellius Expedition'; — Flores, South coast, female (MS-t11431); — Flores, South-east coast, Paga (8°46.77´N, 122°2.67´E), female (SMF-7611); male (SMF-20288 [ex. WAM]), 2.vi.1973, R.W.

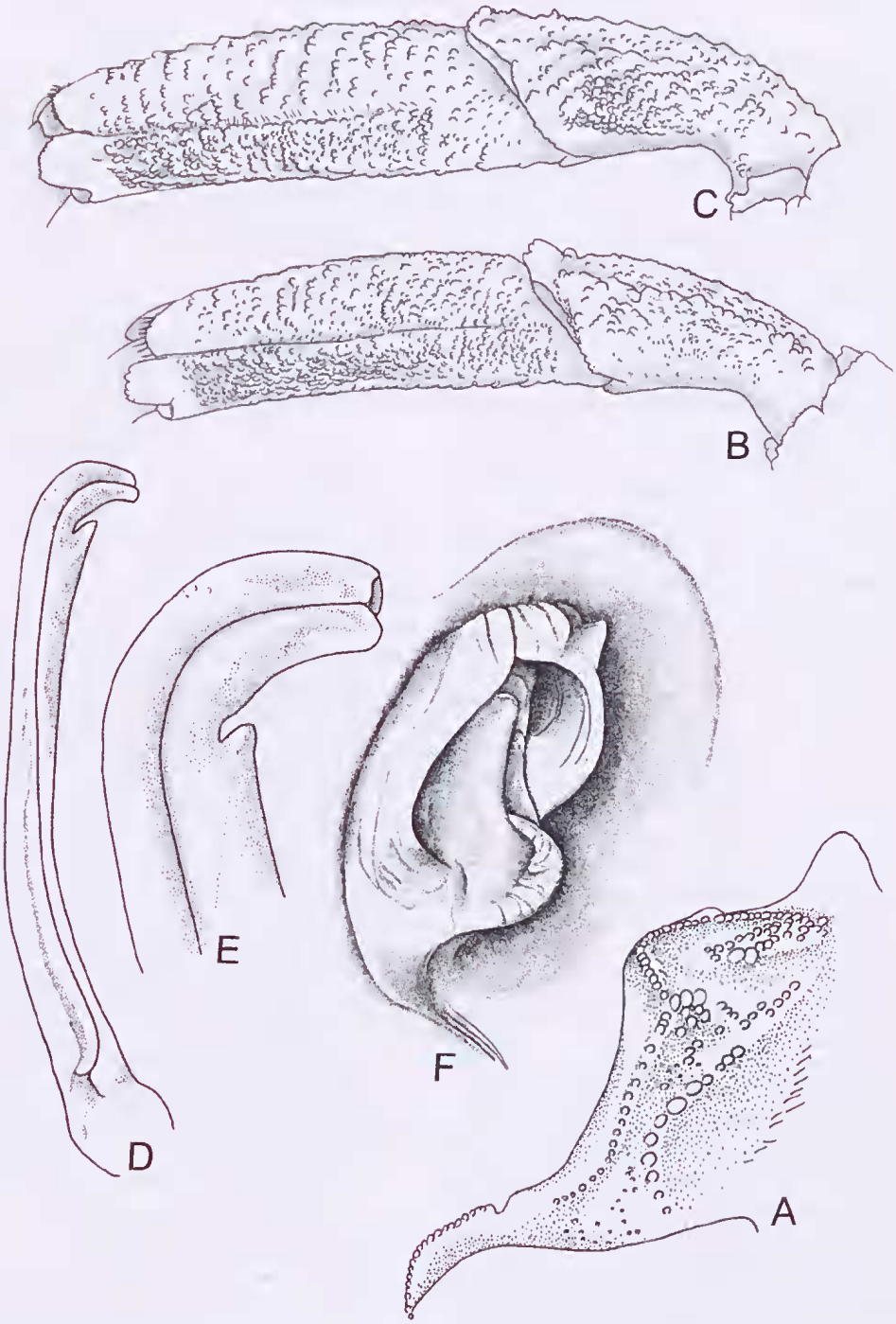

FIG. 17. *Ocypode kuhlii*: **A**, P1 thoracic sternite; **B, C**, P2–3 carpi and propodi; **D, E**, Go1; **F**, female operculum.

George; — Solor Island, Lamakera, male (ZMA-102.364) [det. Tesch, 1918]; — Timor, female (MBL-1852) [det. Osório, 1887]; — Moluccas: Ternate, 1 juv. (RMNH), 'Snellius Expedition'; — Irian Jaya, Western New Guinea: Sekru, north-west coast of New Guinea, 1 juv. male (RMNH-15514-516); — Kabupaten Nabire, male (RMNH-15513); — Kali Buaja near Holtekang, East coast of Humboldt Bay (= Yos Sudarso Bay), male (RMNH-16296); 1 juv. male (RMNH-15514-516); — Jayapura, Humboldt Bay (= Yos Sudarso Bay), 5 juv. males, 1 juv. female (RMNH-16297); — Haytefa, Humboldt Bay (= Yos Sudarso Bay), 2 juv. females (RMNH-15493-500). **Papua New Guinea**. Solomon Is, Bougaineville, female (ZSM); male (USNM-90874).

Diagnosis. Middle- to large-sized species. Eyestalks not prolonged distally beyond cornea. Exorbital angles acutely triangular. Stridulating ridge composed of *c.* 10 interspaced tubercles. P2–5 propodi naked on anterior and posterior surfaces. Go1 slightly narrowing distally, and curved laterally in distal part, bearing a palp. Operculum of female genital opening broadened.

Description. Carapace (Fig. 39) wider than long, and covered densely with fine tubercles, becoming larger toward lateral. Exorbital angles acutely triangular and protruding anteriorly. Lateral margins of carapace distinctly directed outwards from base of exorbital angle in anterior half of carapace, and then directed inwards in posterior half, and carapace broadest at its middle. Pterygostomial region with distinct tubercles, becoming smaller and indistinct towards lateral sides of mouth parts. P1 thoracic sternite (Fig. 17A) bearing tuberculate humps near anterior margin, and tuberculate carinae surrounding posterior two-thirds and on anterior margin. Palm of larger cheliped distinctly serrated on ventral margin. Stridulating ridge (Fig. 3B) composed of *c.* 10 interspaced tubercles arranged in a straight row at least in dorsal two-thirds. Smaller cheliped pointed at distal end. P2–3 carpi and propodi (Fig. 17B–C) naked on anterior and posterior surfaces. Go1 (Fig. 17D–E) three-sided proximally, slightly narrowing distally, and curved laterally in distal part, bearing a distinct cone-shaped palp directed distally. Operculum of female genital opening (Fig. 17F) broadened and posterior half of operculum reaching to caudal end of genital opening; median rim broad.

Juvenile specimens. In a specimen (10.0×12.9 mm, IRSNB-9223) stridulating ridge composed of *c.* 9 irregularly arranged indistinct granules. In a larger specimen (15.1×19.3 mm, MCZ-7246) stridulating ridge composed of distinct tubercles arranged in a straight row as in adult ones. Stridulating ridge easily distinguishable because of its smooth and flat surroundings. P2–3 propodi naked on anterior surface. Epibranchial angles very evident.

Distribution. Nicobars, southern Thailand, throughout Indonesia, Papua New Guinea. Type locality: 'Mari Indico'.

Remarks. *Ocypode kuhlii* had long been considered to be distributed widely in the Indo-West Pacific region until Sakai, K. & Türkay (1976) showed that the species considered as *O. kuhlii* by earlier authors is in reality heterogeneous. We found that *O. ryderi*, hitherto regarded as a synonym of *O. kuhlii*, was a valid species distributed in the western Indian Ocean. *O. kuhlii* is restricted to an area ranging from N. Sumatera and Timor to New Guinea and Bougaineville, North Solomon Islands (Papua New Guinea). Crosnier (1965) stated that one specimen of *O. kuhlii* reported by Miers (1882) from Madagascar had to be considered as belonging to his new species *O. madagascariensis* (Crosnier, 1965: 102). A specimen from New Hebrides, also attributed to *O. kuhlii* by Miers (1882) was identified as part of this study as *O. convexa* because of the number of tubercles on the stridulating ridge. The record of *O. kuhlii* by Stephenson *et al.* (1958) from the Great Barrier Reef is doubtful, because, according to McNeill (1968), the specimen from Low Isles of the Great Barrier Reef recorded by them, could not be traced. A subsequent revision of the *Ocypode* holdings of the Australian and Queensland Museums in 1980 by one of us (M. T.) also failed to find any specimens of *O. kuhlii* from Australia, and therefore, a misidentification of *O. ceratophthalma*, *O. cordimanus*, or *O. pallidula* as *O. kuhlii* is the most probable explanation.

Rathbun (1910b: 305) recorded *O. ceratophthalma* based on 7 juveniles from Lombok. Upon our re-examination her material has turned out to include 3 specimens of *O. kuhlii*, and therefore, only 4 specimens were correctly identified as *O. ceratophthalma*.

Ocypode macrocera H. Milne Edwards, 1837
(Figs 3C, 18, 40)

Ocypoda macrocera H. Milne Edwards, 1837: 49 [in part]; Lucas, 1840: 57; Heller, 1865: 42; Miers, 1882: 381, pl. 17, figs 2, 2a, 2b; Henderson, 1893: 387; Alcock & Anderson, 1894: 202; Ortmann, 1897: 360, 368; Alcock, 1900: 345, 347 [in part]; Kemp, 1915: 219, fig. 6; Gravely, 1927: 148; Chopra & Das, 1937: 419 [in part]; Nagabushanam & Rao, 1967: 1109; Nageswara Rao *et al.*, 1986: 1.

Ocypode macrocera — White, 1847: 35; H. Milne Edwards, 1852: 142; Kingsley, 1880: 181 [in part]; Altevogt, 1959: 130–133, fig. 3; Guinot-Dumortier & Dumortier, 1960: 136, 148, tab. 3; Rao, 1966: 257; Rajabai, 1974: 203; Sakai, K. & Türkay, 1977a: 178, Pl. 1; Nadarajalingam & Subramoniam, 1987: 43–53, tabs 2, 3, 5; Ng *et. al.*, 2008: 240.

Ocypoda portonovoensis Prem Kumar, 1964: 153, fig. 1, pl. 4, figs 1, 2.

Ocypode portonovoensis — Serène, 1968: 97.

Ocypode macrocerus — Serène, 1968: 97.

? *Ocypoda stimpsoni* — Baksi, Ray & De, 1980: 184–187, pl. 2 fig. 3.

Material examined. Myanmar. Yangon, male (USNM-106702), G. E. Gates. Arakan; — male (NHMW-2168). **India.** No further data, male (UZMK); — Nicobar Islands, female (NHMW-1627) [det. Heller, 1865), 1857-59, 'Novara Expedition'; — Ganjam, east coast of India, male (NHM); — Ennore, east coast of India, male, 2 females, larger cheliped (NHM-1892.7.15.26-28); — Puducherry (= Pondicherry), male [lectotype], female, dried [syntype] (MNHN-3304) [det. H. Milne Edwards, 1837], Leschenoult; male, dried (MNHN) [det. H. Milne Edwards, 1837], Reynaud; 3 males, 1 juv. male, female, 1 juv. female (MNHN), 1959, ldetmov; — Parangipettai (= Porto Novo), female [type specimen of *C. portonovoensis* Prem Kumar, 1964] (ZSI-C-4351/1); — Tharangambadi (= Tranquebar), 5 males, 4 females (UZMK); — Toothukudi (=Tuticorin) (8°44.64′N, 78°10.21′E), 3 males (NHM-1890.10.20.6-10), E. Thurston; male (SMF-6772). **Sri Lanka.** Trinkomali, female (UZMK); 2 females (NHMW), ix 1929, Zool. Inst. Wien, Nr. 384; male, dried (MHNG) [det. Sakai, K. & Türkay, 1977]; 2 males (MHNG-563a). **Pakistan.** Karachi, 3 males (NHM-82.278). **Wrong locality.** ? Tahiti, 2 males (NHMW) [det. Heller, 1865, locality confused], 1857, 'Novara Expedition'.

Diagnosis. Middle-sized species. Eyestalks prolonged distally beyond cornea in a stylus. Exorbital angles protruding laterally. Stridulating ridge composed of 36-56 tubercles with striae. Chela of smaller cheliped truncate distally. P2-3 propodi with setae on dorsal half of anterior surface. Go1 slightly curved laterally in distal part, bearing a palp. Operculum of female genital opening rounded and protruding mesially; lateral rim distinct.

Description. Carapace (Fig. 40) distinctly wider than long and covered dorsally with fine tubercles, which becoming distinct along anterolateral borders. Lateral half of orbital margin almost straight and directed obliquely backward. Exorbital corners angulate, tooth--shaped, and protruding outward in adult males, but not in females and young males. Lateral margins of carapace directed slightly outwards from base of exorbital corner in anterior third of carapace, and then directed inwards in posterior two-thirds in adult males, and carapace broadest at exorbital corners or anterior third, while in females and young males lateral margins of carapace directed straight backwards and parallel with each other. Pterygostomial region sparcely tuberculate, but smooth around buccal cavern. P1 thoracic sternite (Fig. 18A) smooth, bearing tuberculate carinae on anterior and lateral margins, and a transverse granulous carina at anterior third (SMF-6772). Palm of larger cheliped broad and densely tuberculate on anterior surface, and distinctively serrated on dorsal and ventral margins. Stridulating ridge (Fig. 3C) composed of 36–56 tubercles with striae; 9 slightly interspaced tubercles with striae in dorsal third and 27 closely pressed elongate tubercles with striae in ventral two thirds. Chela of smaller cheliped truncate distally. P2 propodus (Fig. 18B) with numerous short oblique rows of setae on dorsal half of anterior surface, bearing two median rows of setae. P3 propodus (Fig. 18C) with setae on dorsal half of anterior surface, bearing one median row of setae. P4–5 propodi naked. Go1 (Fig. 18D–E) three-sided proximally, slightly narrowing distally, and curved laterally in distal part, bearing protruding palp directed distally. Operculum of female genital opening (Fig. 18F) roundly protruding in mesial half; lateral rim distinct.

Distribution. Pakistan, India (including Nicobars), Sri Lanka, Myanmar. Type locality: 'Les Indes orientales, le Brésil etc.' (in error).

Remarks. As demonstrated by Sakai, K. & Türkay (1977: 178), the type locality of *Ocypode macrocera* is Pondicherry, India. These authors also discussed in detail the synonymy of *O.*

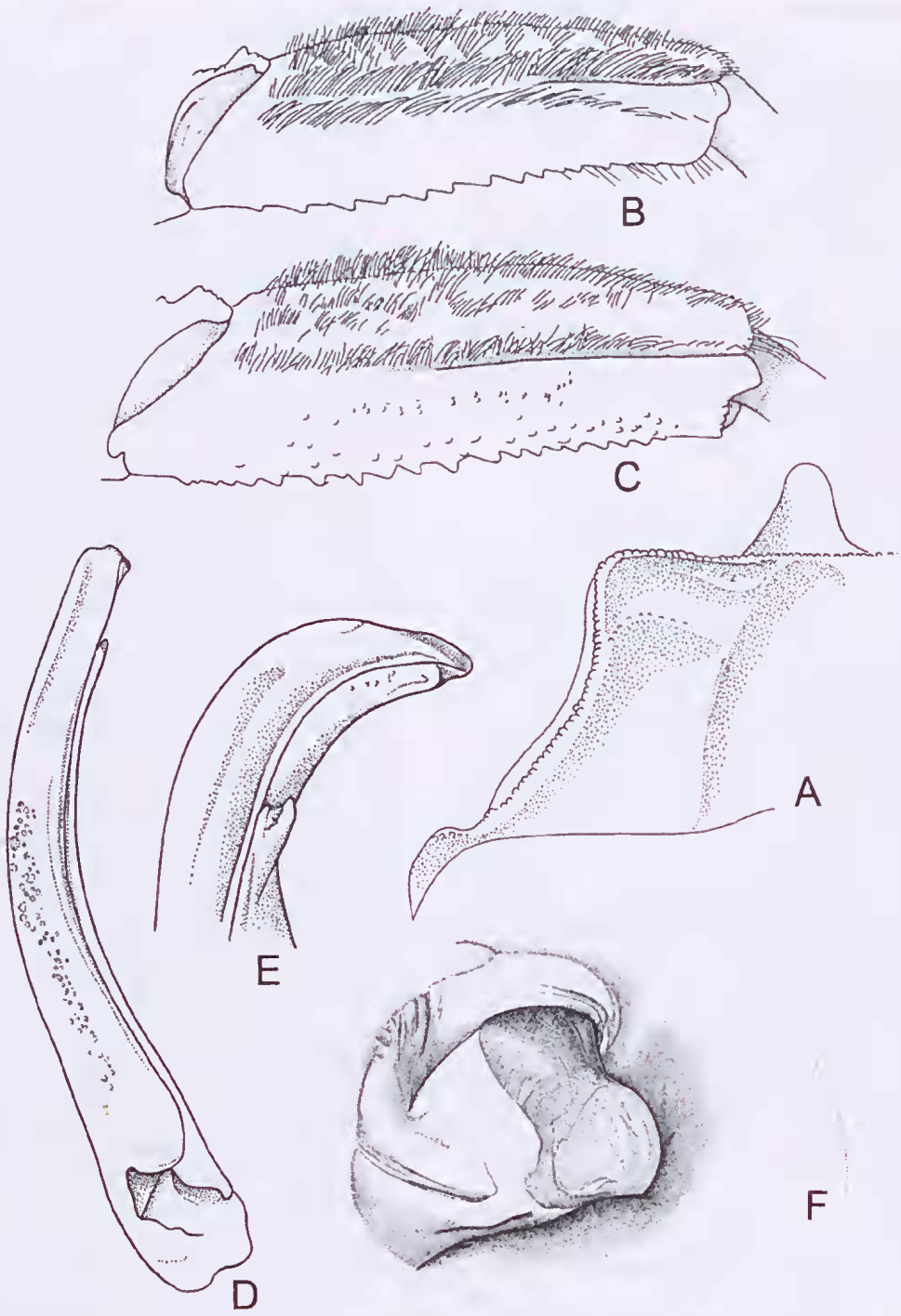

FIG. 18. *Ocypode macrocera*: **A**, P1 thoracic sternite; **B**, **C**, P2–3 propodi; **D**, **E**, G01; **F**, female operculum.

portonovoensis with *O. macrocera*, and concluded that the former was based on a specimen with regenerated chelipeds. The record of *O. macrocera* from Japan by Urita (1917) refers in reality to *O. stimpsoni* (see under that species).

Ocypode madagascariensis Crosnier, 1965
(Figs 3D, 19, 41)

Ocypode cordimana — Krauss, 1843: 41.
Ocypoda kuhlii — Miers, 1882: 385 [in part].
Ocypode madagascariensis Crosnier, 1965: 103–105 [in part: only specimen of Petit identified by Balss as *Ocypode* aff. *nobilii*], figs 159, 166, 180–181, pl. 9, fig. 3, pl. 11, fig. 2; Berry, Smale & Jackson, 1976: 29; Berry, 1976: 35–37, 1 unnumbered text-fig.; McLachlan, 1980: 57; Kensley, 1981: 49; Jackson, Smale & Berry, 1991: 280–286, tabs 1–3, text-fig. 1; Ng, Guinot & Davie, 2008: 240.

Material examined. Madagascar. Tuléar [= Toliara], male [holotype] (MNHN) [det. Crosnier]; — Lokaro Island near Fort Dauphin, East coast of Madagascar, male, female (MNHN) [det. Crosnier], 7.iii.1973; — Tamatave, East coast of Madagascar, 1 ovig. female [det. as *O.* sp]; male, female (NHM-82.6) [det. Miers, 1882 as *O. kuhlii*]; male (NHM) [det. Miers, 1882 as *O. kuhlii*]; female (NHM-1892.7.4.1). **Comores.** Grand Comore, Ngazidja, male (MNHN) [det. as *O. cordimana*], P. Fournanoir. **South Africa.** No further data, 1 juv. male (RMNH); female (NHM-1917.6.19.48); — KwaZulu-Natal: No further data, 2 males (SMF-7274); — Kosi Bay, female (NHM-1917.6.19.48); — Boteler Point (27°1.0′S, 32°51.92′E), male, 5 females (SMF-10931). **No definite locality.** male (ZMH-2969).

Diagnosis. Middle-sized species. Eyestalks not prolonged distally beyond cornea. Exorbital angles broadly triangular and distinctly protruding anteriorly. Stridulating ridge composed of 20–30 tubercles with striae. P2–3 propodi setose on dorsal half of anterior surface. Go1 strongly crooked at distal end, bearing a palp. Operculum of female genital opening broad and rounded; median rim with strong triangular tooth.

Description. Carapace (Fig. 41) slightly wider than long, and covered densely with coarse tubercles on dorsal surface. Eyestalks not prolonged distally beyond cornea. Lateral half of orbital margin regularly concave. Exorbital angles triangular and distinctly protruding forward. Lateral margins of carapace directed outwards from tip of exorbital angle in anterior third of carapace, and then directed inwards in posterior two-thirds, and carapace broadest at anterior third. Pterygostomial region distinctly tuberculate, but smooth along lateral sides of buccal cavern. P1 thoracic sternite (Fig. 19A) tuberculate irregularly on surface, bearing tuberculate carinae on anterior and lateral margins, and an obliquely running swelling with tubercles at anterior third. Palm of larger cheliped broad, bearing strong denticles on ventral margin and small denticles on dorsal margin. Both chelipeds scattered irregularly with coarse tubercles on anterior surface. Stridulating ridge (Fig. 3D) composed of 20–30 closely spaced tubercles with striae. Smaller cheliped pointed at distal end. P2–3 propodi (Fig. 19B–C) setose on dorsal half of anterior surface. P4–5 propodi naked. Go1 (Fig. 19D–E) three-sided proximally, slightly narrowing distally; strongly crooked at distal end; bearing a bulging, rounded palp at base of distal crook. Operculum of female genital opening (Fig. 19F) broad and rounded; median rim with strong triangular tooth.

Distribution. Madagascar; SE coast of Africa, Mozambique to Natal. Type locality: Tuléar, Madagascar [= Toliara].

Remarks. *Ocypode madagascariensis* Crosnier, 1965, had earlier been reported from Madagascar under the names *O. kuhlii* or *O. cordimana*. Crosnier (1965: 105) remarked that *O. kuhlii* described by Miers (1882: 385) based on a specimen (NHM-82.6) from Madagascar would probably prove to be identical with his species *O. madagascariensis*. Krauss (1843: 41) described two species, *O. cordimana* and *O. ceratophthalma* based on specimens from South Africa. However, his description of *O. cordimana*, especially the following part; 'Die Unterscheidungsmerkmale von letzter (*O. ceratophthalma* – Anm. Verf.) liegen aber hauptsächlich in einem mehr breiten als langen und in einem gewölbten Rückenschilde ... [= The characters to distinguish *O. cordimana* from *O. ceratophthalma* lie chiefly in the carapace which is more wider than long and more strongly vaulted ...]' suggests that Krauss' '*O. cordimana*' is not identical with *O. cordimanus* Latreille, 1818, because the carapace of *O. cordimanus* is not more wider than long than that of *O. ceratophthalma* and not strongly vaulted but as flat as *O. ceratophthalma*, so

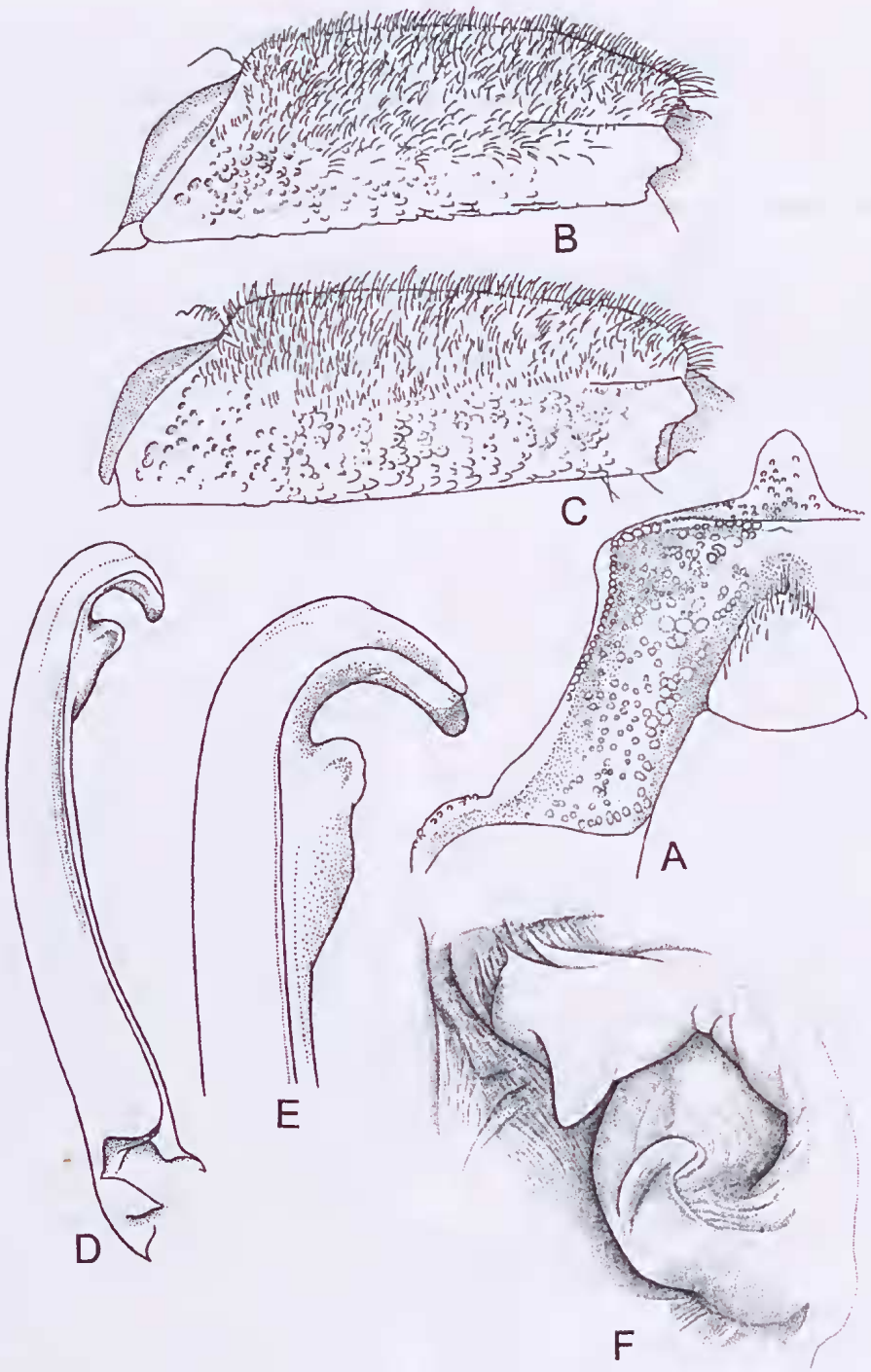

FIG. 19. *Ocypode madagascariensis*: **A**, P1 thoracic sternite; **B**, **C**, P2–3 propodi; **D**, **E**, Go1; **F**, female operculum.

Table 4. Comparison in characteristics among 6 species of *Ocypode*.

	O. cordimanus	*O. madagascariensis*	*O. ceratophthalma*	*O. pauliani*	*O. kuhlii*	*O. ryderi*
Carapace CW/CL (mm)	1.10	1.19	1.18	1.19	1.23	1.26
Anterolateral margin of carapace.	Rounded.	Rounded.	Straight.	Straight.	Rounded.	Rounded.
Eyestalks.	Not prolonged.	Not prolonged.	Prolonged.	Not prolonged.	Not prolonged.	Not prolonged.
Stridulating ridge.	Absent.	Composed of 20–30 closely spaced tubercles with striae.	Composed of 10–11 interspaced tubercles in dorsal third, 8 thick striae in middle third, and 20–30 closely spaced fine striae in ventral third.	Composed of 7–13 tubercles.	Composed of *c.* 10 interspaced tubercles.	Composed of *c.*15 irregularly arranged tubercles.
Pereiopod 2 propodus.	With transverse rows of setae on dorsal half of anterior surface, bearing a median row of setae.	Setose on dorsal half of anterior surface.	With oblique rows of setae on dorsal half of anterior surface, bearing two median rows of setae.	With setae on and along dorsal margin.	Naked on anterior surface.	Naked on anterior surface.
Pereiopod 3 propodus.	With thick setae along dorsal margin.	Setose on dorsal half of anterior surface.	With oblique rows of setae on dorsal half of anterior surface, bearing two median rows of setae.	With setae on and along dorsal margin.	Naked on anterior surface.	Naked on anterior surface.

Krauss' '*O. cordimana*' must be identical with *O. madagascariensis* occurring in almost the same area, whose carapace is always more wider than long and more strongly vaulted than that of *O. ceratophthalma*. Unfortunately Krauss' specimens are lost (H. Janus, Museum Stuttgart, *in litt.*), so this can never be confirmed. Crosnier (1965) indicated that one male of Petit's specimens from Tuléar determined by Balss as *O. affinis nobilii* is identical with *O. madagascariensis*.

O. madagascariensis is best characterised by the shapes of the Go1 and the female genital opening, which are diagnostic (a comparison of six species of *Ocypode* that have often been misidentified is presented in Table 4). However, it is very difficult to distinguish juvenile specimens of *O. madagascariensis* from *O. pauliani* of the same size, not only because they are very similar to each other in the carapace and the eyestalks, but also because they are both distributed in Madacascar. However, the former is distinguishable from the latter by the structure of the stridulating ridge and the pattern of setae on the anterior surfaces of the P2–3 propodi.

It is also to be added that in a male specimen examined (SMF-7274) the stridulating ridge is composed of as many as 30 closely spaced tubercles with striae, though Crosnier stated that it is composed of 20 tubercles with striae.

Ocypode mortoni George, 1982

(Figs 3E, 20, 42)

Ocypode mortoni George, 1982: 187–190, fig. 1C, 2C, pl. 3; Sakai K., 2000:1159, figs 2a–b, 3a–e; Ng, Guinot & Davie, 2008: 240; Wong, Shih. & Chan, 2012: 71–87, figs 1–8.

Ocypode macrocera — Dai *et al.*, 1985: 370, figs 1–7, pl. 1, figs 1–2; Yang, 1986: 153.

Material examined. China. No further data, 2 males (SMF-36912); — Tai Long Wan, Sai Wan, East New Territories, Hong Kong, 2 males, female (WAM-230–80); — Hainan, Sanya, Xishatan, female [23.3×27.5 mm] (SMF-36189, ex. Coll. IOAS), 19.iii.1958. **Japan.** Kochi Prefecture: Cape Muroto, Toyo-cho, sandy beach of Ikumi (33°31.68′N, 134°17.06′E), male [22.0×26.0 mm], female [24.4×28.2 mm] (SMF-36190, ex. BLT-6277), 4.x.1998, I. Mano.

Diagnosis. Small-sized species. Eyestalks prolonged distally beyond cornea in a stylus. Exorbital angles protruding outward. Stridulating ridge composed of 35–71 striae, not extending ventrally over median line of fixed finger. Smaller cheliped broadly rounded to truncate at distal end. P2–3 propodi with a median row of setae on anterior surface. Go1 slender, slightly narrowing distally, and curved laterally in distal part, bearing a small palp distant from distal end. Operculum of female genital opening directed obliquely forward at an angle of 45° relative to midline, without prominent lateral rims.

Description. Carapace (Fig. 42) slightly wider than long; covered densely with fine tubercles on dorsal surface. Lateral half of orbital margin directed obliquely backwards to exorbital corner. Exorbital corners protruding outward. Lateral margins of carapace directed slightly outward from base of exorbital corner in anterior third of carapace and then directed inward in posteior two-thirds, forming distinct epibranchial angles, where carapace broadest. Pterygostomial region spacious and finely tuberculate except along lateral sides of buccal cavern. P1 thoracic sternite (Fig. 20A) smooth. Palm of larger cheliped broad and beset with regularly arranged coarse tubercles on anterior surface, and serrated regularly on ventral margin and roughly on dorsal margin. Stridulating ridge (Fig. 3E) composed of 35–71 striae, terminating far from ventral margin of palm without extending ventrally over median line of fixed finger. Smaller cheliped rounded to truncate at distal end. P2 propodus (Fig. 20B) with a short row of setae along dorsal margin on anterior surface, bearing a median row of scanty setae. P3. propodus (Fig. 20C) setose on dorsal half of anterior surface, bearing a median row of short setae. Go1 (Fig. 20D–E) slender, slightly narrowing distally; curved laterally at distal end; bearing a small palp distant from distal end. Sperm-channel originating dorsally, running without torsion along distal curve into flat terminal part. Distal opening located terminally. Operculum of female genital opening (Fig. 20F) directed obliquely forward at 45° to sternal median line, without rim. Vagina deep anteriorly; sunken in shape of funnel.

Distribution. S. China (Hongkong, Quandong, Guangxi, and Hainan); southern Japan. Type locality: Sai Wan-Tai Long Wan, E. New Territories, Hongkong.

Remarks. The present species is closely related to the sympatric species *O. stimpsoni*, with

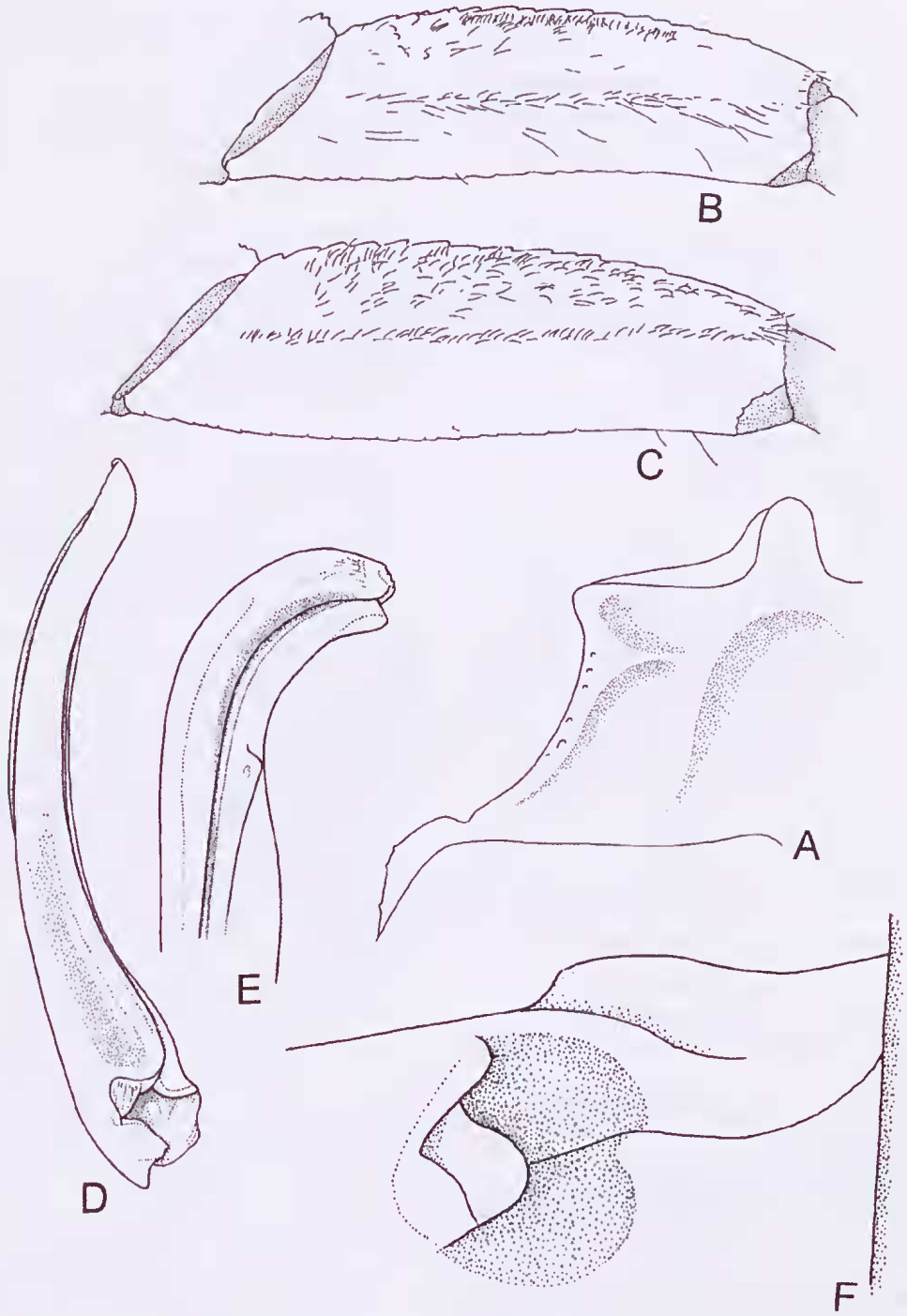

FIG. 20. *Ocypode mortoni*: **A**, P1 thoracic sternite; **B**, **C**, P2–3 propodi; **D**, **E**, Go1; **F**, female operculum.

which it shares an almost identical Go1, however, it differs from that species by having the eyestalks prolonged distally beyond the cornea in a stylus; a rather short stridulating ridge that does not extend over the median line of the fixed finger; and the palm of the larger cheliped coarsely tuberculate on the anterior surface. Conversely, the eyestalks of *O. stimpsoni* are not prolonged distally beyond the cornea, the stridulating ridge is longer, always over-reaching the median line of the fixed finger, or even almost reaching the ventral margin of the palm, and the palm of the larger cheliped is finely tuberculate.

Wong *et al.* (2012) mention that 'It [*O. mortoni*] was always sympatric with the common *O. ceratophthalmus* (Pallas, 1772) at the same tidal level, and there appeared to be no clear habitat/niche distinction. Relative abundance of *O. mortoni* vs. *O. ceratophthalmus* was at most in the ratio of 31:69% based on quantitative transect survey data from Sai Wan', and '... our results do not support George's preliminary ecological hypothesis.' In Toyo-cho, on the sandy beaches of Ikumi, Kochi Pref., Japan, facing the the Pacific Ocean, *O. ceratophthalma* is also common, whereas *O. mortoni* was recorded only once (Sakai, K. 2000). Nevertheless they can also be considered to be sympatric at this locality, and the low incidence of *O. mortoni* may be the result of the lower tidal zone being often effected by typhoons (in litt. Mano).

Ocypode nobilii De Man, 1902

(Figs 4A, 21, 43)

Ocypoda convexa — Nobili, 1900: 518.
Ocypode ceratophthalma — Lanchester, 1900a: 258 [in part].
Ocypode convexa — Lanchester, 1900b: 548.
Ocypoda nobilii De Man, 1902: 47, pl. 19, figs 2–3; Nobili, 1903: 20.
Ocypoda macrocera — Rathbun, 1910a: 322.
Ocypode macrocera — Suvatti, 1950:153.
Ocypode nobilii — Guinot-Dumortier & Dumortier, 1960: 135, fig. 17; Serène, 1968: 97; Ng *et al.*, 2008: 240.

Material examined. Malaysia. Borneo: No further data, 2 males (NHM); — Sarawak, male (NHM-1895 10.10.2-3); 3 males, female (MCSNG) [det. Nobili, 1899]; — estuary of Sarawak River (1°39.7′N, 110°28.72′E), Sarawak, 2 males, female (SMF-7273), 1967, W. Macnae; — Baram River (4°35.68′N, 113°58.93′E), Sarawak, male [holotype] (SMF-5412), W. Kükenthal; 2 females (NHM-1895.7.2.23-24); 4 males, 2 females (NHM-1895.2.7.17-22); — E-Buntal, Santubong Peninsula, Sarawak, male (NHM); — Sarawak, Baka Beach, female (ZRC-199.0683) [det. Lanchester, 1900], vi.1999, P. Ng *et al.*; — Malacca, male (UZMK). **Cambodia.** Island Kaoh Kong, Gulf of Thailand, female (UZMK) [det. Rathbun, 1910].

Diagnosis. Small-sized species. Eyestalks not prolonged distally beyond cornea. Exorbital angles broadly triangular with tips directed behind. Stridulating ridge composed of 99–120 closely spaced fine striae. Smaller cheliped rounded to truncate at distal end of chela. P2 propodus setose along dorsal margin, bearing two rows of setae on anterior surface. P3 propodus setose on dorsal half of anterior surface, bearing a median row of setae. Go1 strongly curved laterally in distal part; broadened at distal end; bearing a palp. Horny terminal endpiece much wider than long. Operculum of female genital opening protruding mesially; rounded distally. Vaginal slit oval.

Description. Carapace (Fig. 43) distinctly wider than long and beset densely with fine tubercles. Orbital margin with a median bulge, its lateral half directed obliquely backwards. Exorbital angles broadly triangular and directed slightly anterolaterally with tips directed behind, and located clearly posterior to median convexity of orbital margin. Lateral margins of carapace directed outward from base of exorbital angle in anterior third of carapace, and then directed inward in posterior two-thirds, forming epibranchial angle, where carapace broadest. Pterygostomial region with distinct tubercles except along lateral sides of buccal frame. P1 thoracic sternite (Fig. 21A) smooth on surface, bearing tuberculate carinae on anterior and lateral margins. Palm of larger cheliped broad, beset densely with fine tubercles on anterior surface, and finely serrated on ventral margin. Stridulating ridge (Fig. 4A) composed of 99–120 closely spaced fine striae. Smaller cheliped rounded to truncate at distal end of chela. P2 propodus (Fig. 21B) setose along dorsal margin, bearing a median row of long setae and another short row of long setae just below on anterior surface. P3 propodus (Fig. 21C) with transverse rows of setae on dorsal half of anterior surface, bearing a median row

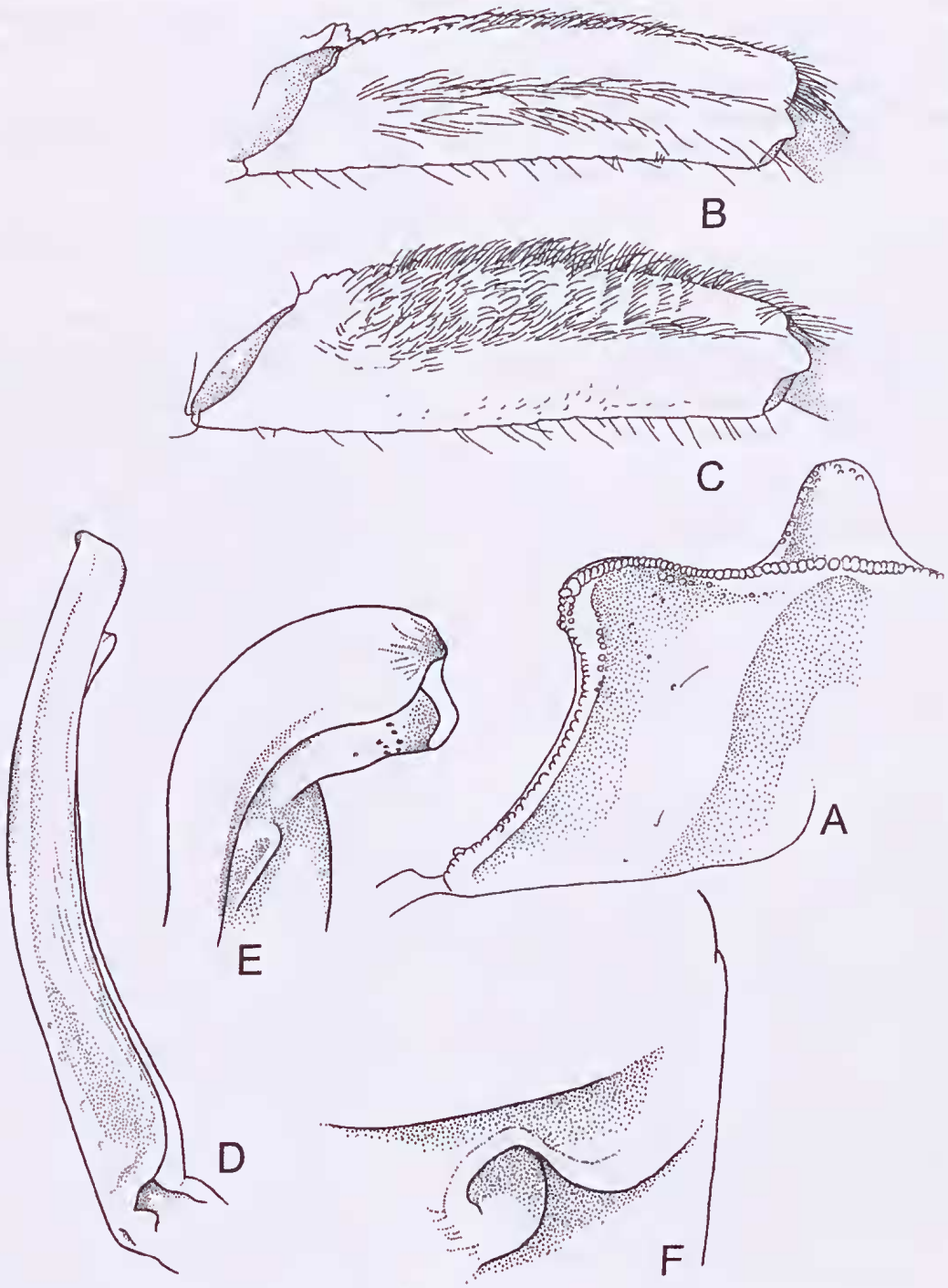

FIG. 21. *Ocypode nobilii*: **A,** P1 thoracic sternite; **B, C,** P2–3 propodi; **D, E,** Go1; **F,** female operculum.

of setae. Go1 (Fig. 21D–E) strongly curved laterally in distal part; broadened at distal end; bearing a cone-like palp. Sperm-channel originating dorsally and running dorsally without torsion into short, broad terminal endpiece. Distal opening located terminally. Operculum of female genital opening (Fig. 21F) protruding mesially and rounded distally. Vaginal slit oval.

Distribution. Malay peninsula and northern Borneo. Type Locality: Baram River, Sarawak, Malaysia.

Remarks. This species was reported for the first time by Nobili (1899) under the name of *Ocypode convexa*, however, De Man (1902) recognised the earlier record was not a typical *O. convexa* and named it as a separate species *O. nobilii* in honour of the Italian carcinologist. Nevertheless, this species seems to have continued to confuse later authors. Rathbun (1910) recorded *O. macrocera* based on a specimen (UZMK) from Koh Kong, Cambodia in the Gulf of Thailand, but our re-examination shows this was a mis-identification of *O. nobilii*. Thus, it is likely that *O. macrocera* reported from Lem Sing in Thailand by Suvatti (1950) is also *O. nobilii*, because his identification was based on Rathbun's definition.

Ocypode nobilii is very similar to *O. stimpsoni*, as suggested by De Man (1902), especially in the rounded to truncate distal end of the smaller cheliped, and the eyestalks without a distal projection. However they differ from each other in the pattern of setae on the P2–3 propodi, and in the morphology of the stridulating ridge and the sexual organs. *O. nobilii* is sympatric with both *O. ceratophthalma* and *O. cordimanus*, but it appears to prefer a different habitat. *O. nobilii* has been collected on muddy beaches near estuaries (De Man 1902; Sérene 1968), while Rathbun's (1910) '*O. macrocera*' is said to have come from a sandy beach. Further fieldwork is needed to better understand the ecological preferences of this interesting species.

Ocypode pallidula Hombron & Jacquinot, 1846

(Figs 4B, 22, 44)

Ocypode rhombea — Randall, 1840: 123 [not *O. rhombea* Fabricius, 1798: 348 a *nomen dubium* – *fide* Rathbun 1906: 834].

Ocypoda pallidula Hombron & Jacquinot, 1846, Atlas, pl. 6, fig. 1.

Ocypoda laevis — Dana, 1852: 325; Dana, 1855: pl. 20, fig. 2; Stimpson, 1858: 100 [not *Ocypode laevis* Fabricius, 1798: 348 which is here considered *nomen dubium*].

Ocypoda cordimana (junior) — Jacquinot & Lucas, 1853: 65 [only locality, not the description; description = *O. ceratophthalma* (Pallas, 1772), not *O. cordimanus* Latreille 1818]; Kingsley, 1880: 185 [in part].

Ocypoda kuhlii — Miers, 1882: 386 [in part; only material from New Hebrides].

Ocypoda ceratophthalma — Miers, 1886: 238–239 [in part; only specimens from Hilo, Hawaii].

Ocypoda urvillei — Ortmann, 1897: 366–367; Lenz, 1901 Zool. Jb. Syst., 14: 476–477; Bouvier, 1915: 122 [not *O. urvillei* Guérin, 1829].

Ocypode laevis — Rathbun, 1906: 834, pl. 7, fig. 2; Stimpson, 1907: 110; Edmondson, 1962: 16, figs 6–7; Crosnier, 1965: 105; Fellows, 1966: 1–78; Serène, 1968: 97; Horch & Salmon, 1972: 9, fig. 6; Fellows, 1975a: 257–258, fig. 1; 1975b: 1–158.

Ocypoda Urvillei — Nobili, 1907: 407 [not *O. urvillei* Guérin, 1829].

Ocypoda ceratophthalma — Pesta, 1911: 54–55 [in part; material from Mauritius].

? *Ocypode kuhli* — Stephenson, 1958: 269, 273.

Ocypode urvillei — Michel, 1964: 12 [not *O. urvillei* Guérin, 1829].

? *Ocypode* cf. *kuhlii* — McNeill, 1968: 86.

? *Ocypode cordimana* — Ooishi, 1970: 94.

Ocypode pallidula — Sakai, K. & Türkay, 1976: 87–91, figs 14–15, pl. 2; Jones, 1988: 33; Poupin, 1996: 73; Clark & Crosnier, 2000; 417, tab. 4; Holthuis, 2002: 420; Ng, Guinot & Davie, 2008: 240.

Ocypode aff. *pallidula* — Poupin *et al.*, 2011: 18.

Material examined. Madagascar. No exact locality, 3 juvs. (SMF-36209), 1971, H. Kurokawa [ex. Sakai, T.]; — West coast, male (MNHN). **Mauritius.** No exact locality, male, 3 females (NHMW); 5 males (MNHN); female (MNHN-B32895); 5 males, female (MI); — Tombeau Bay, 6 males, female (MI); — Flic en Flac, 1 juv. male, 2 females (MI); — Wolmar near Flic en Flac, 2 males, 3 females (MI); — Mahébourg, 2 males (RMNH-16293); male (MI); — Belle Maré, male (MI); — NW-coast Cannoniers Point [often previously cited as 'Cannonius Point' which is a spelling error] (20°0.02´S, 57°33.14´E), sandy beach, 11 males, 1 juv. (UZMK); 2 males, 2 females (SMF-7849), x.1929, Dr. Th. Mortensen's South Africa Expedition 1929/30. **Réunion.** Beach near La Saline des Bains (21°05.68´S, 55°14.08´E), male, 6 females (SMF-18278), 28-30.i.1989,

H. G. Müller; — Pointe des Avirons, N of l'etang Salé de Bains (21°15.11′S, 55°19.23′E), sandy beach, male, 2 females (SMF-18279), 31.i.1989, H.G. Müller; — St. Paul beach (21°00.53′S, 55°16.1′E), 3 males (SMF-18280), 1.ii.1989, H.G. Müller. **Indonesia.** Pulau Binongko, the Tukangbesi group, Banda See, 5 males (RMNH-30272); — Pulau Wetar near Timor, female (RMNH-15558); — North of Jayapura, Yos Sudarso Bay (formerly known as Humboldt Bay), Western New Guinea (= Irian Jaya), 1 juv. male (RMNH-15493–15500). **Australia.** Queensland: South Inlet, Willis Island off Cairns (16°17.25′S, 149°57.95′E), Coral Sea, female (SMF-10919), viii-ix. 1975, Z. Števčić; female (SMF-10920); female (SMF-10921); male (SMF-10922); male (SMF-10923); male (SMF-10924); male (SMF-10925); — Holmes Reef, Coral Sea, 2 juv. males (AMS-P17033); — Herald Cay, NE Cay (16°56.48′S, 149°11.89′E), Coral Sea, male, female (SMF-6871), 8.xii.1964, McMichael & Yaldwyn; 3 males, 3 females (QM-W2508); — Diamond Island, West Cay (17°26.88′S, 150°58.6′E), 2 males, female (SMF-6870), x.1964, McMichael & Yaldwyn; 8 males, female (AMS-P16888); 4 males, 2 females (AMS-P16889); — Swains Reefs, Great Barrier Reef, 14 males, 5 females (AMS-P16894); female (AMS); — NW-End of Gillett Cay, Swains Reefs, 3 males, 3 females (AMS-P16894); — Lady Musgrave Island, Capricorn Group, 4 males, 2 females (NHM); 5 males, female (AMS-P14969); — N-Riff, Heron Island, male (ZMH-K32283); — South Gladstone, Lady Elliot Island, Great Barrier Reef, male, 3 females (AMS-P17087); — Sand Cay, Wreck Reef, male (AMS-P13511). **Norfolk Island.** male (MNHN); 3 males (AMS-P4099); — Emile Bay, Norfolk Island, sandy coast of upper tidal zone, 2 males (AMS-P17310). **Cook Islands.** Rarotonga, female (NHM-2382); male (NHM-3219); male (BMH-3301); — Manuae, female (NHM-71.201). **French Polynesia.** Rurutu (22°27.25′S, 151°19.71′E), Austral Islands, 2 males, female (MNHN), v.1980, P. Fourmanoir; male (SMF-9408); — Gambier Islands, Tuamotu Archipelago, 5 males (MNHN); — Mangareva I., Gambier Is, Tuamotu Archipelago, male (MNHN); — Rikitea, Mangareva I., Gambier Is, Tuamotu Archipelago, female (MNHN). **Johnston Atoll.** 5 males, 5 females (BMNH 1336). **USA.** Hawaii: 1 juv. (NHM-84.31); — Oahu, Hawaii, 3 males, 2 females (UZMK); 4 juvs. (ZMH-K27846); male (NHM-224); male (NHM-6936); 1 juv. (NHM-223); 6 juvs. (NHM-226); — Waimea, Hawaii, 3 juvs. (USNM-171297); — Paia, Maui, 1 juv. male, 2 juvs. (RMNH-19068). **Midway Island.** male (NHM-4933); — Laysan, 1 damaged specimen (NHM-225); 4 males, female, 2 juvs. (ZMH-K27732).

Diagnosis. Small- to middle-sized species. Eyestalks not prolonged distally beyond cornea. Exorbital angles triangular and distinctly protruding anteriorly. Stridulating ridge composed of 30–42 (in male) or 17–29 (in female) thick striae. Smaller cheliped pointed at distal end. P2–3 propodi sparsely setose on anterior surface. Go1 slightly narrowing distally; slightly curved laterally in distal part; lacking palp. Terminal part longer than broad. Operculum of female genital opening directed obliquely forward; protruding anteromesially; mesial rim evident at caudal end.

Description. Carapace (Fig. 44) slightly wider than long and beset densely with fine tubercles on dorsal surface. Lateral half of orbital margin distinctly concave. Exorbital angles triangular and directed anteriorly. Lateral margins of carapace directed straight backward from tip of exorbital angle in anterior third of carapace and then directed inwards in posterior two-thirds, forming distinct epibranchial angles where carapace broadest. Pterygostomial region spacious, and distinctly tuberculate except along lateral sides of buccal cavern. P1 thoracic sternite (Fig. 22A) shallowly concave in shape of triangle and rimmed anterolaterally with tuberculate carina. Palm of larger cheliped distinctly wider than long, and scattered coarsely with tubercles of different sizes on anterior surface, bearing denticles on ventral margin. Stridulating ridge (Fig. 4B) composed of 30–42 (in male) or 17–29 (in female) rather interspaced thick striae. Smaller cheliped pointed at distal end. P2 propodus (Fig. 22B) sparsely setose on anterior surface, bearing a short median row of scanty setae, and setae along dorsal margin, which expanded distally onto anterior surface. P3 propodus (Fig. 22C) sparsely setose on dorsal half of anterior surface, bearing setae and spinules on dorsal margin. Go1 (Fig. 22D–E) slightly narrowing distally, slightly curved laterally in distal part, lacking a palp. Sperm channel originating dorsally and running without torsion into flat terminal part. Distal opening located terminally. Operculum of female genital opening (Fig. 22F) directed obliquely forward; protruding anteromesially; mesial entrance sunken and concave, vagina slightly sunken at mesial entrance, mesial side rim evident in caudal half and obscure towards frontal side.

Juvenile specimens. In a juvenile (5.5×6.7 mm, USNM-171297) carapace distinctly wider than long, and beset densely with fine granules.

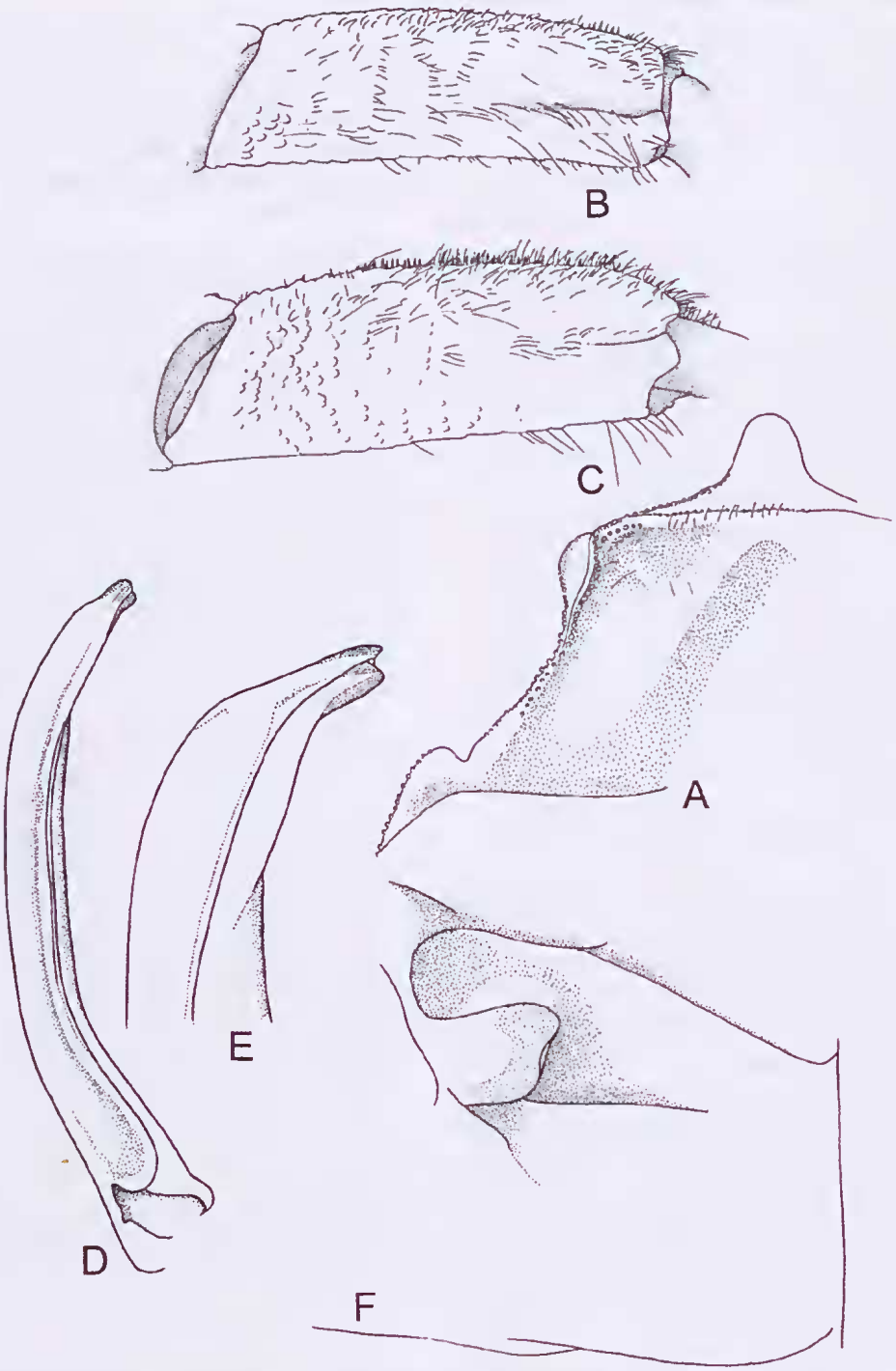

FIG. 22. *Ocypode pallidula*: **A**, P1 thoracic sternite; **B, C**, P2–3 propodi; **D, E**, Go1; **F**, female operculum.

Exorbital angles broadly triangular and less protruding. Carapace not broadening but keeping same width to epibranchial corners located at short distance from base of exorbital corners, and then narrowing. Palm of larger cheliped less wider than long and scattered more roughly with granules on anterior surface than in adult specimens. Stridulating ridge not yet distinct, but weakly developed as faint elevation. P2–3 propodi with scanty setae on dorsal margin, and P2 propodus with a median row of scanty setae on anterior surface. In a slightly larger specimen (8.0×9.5 mm, RMNH-30272) palm of large cheliped wider. Stridulating ridge already composed of interspaced striae as in adult specimens. P2 propodus with scanty setae on dorsal margin, which already expanded distally onto anterior surface, bearing a median row of setae on anterior surface, while P3 propodus naked on anterior surface.

Distribution. A relatively wide distribution: Hawaii Islands in the Central Pacific, the Great Barrier Reef in Australia (Fellows 1975b), the Cook Islands in the southern Pacific, and also in the Banda See, Indonesia, Ogasawara (= Bonin) Is, and Madagascar and Mauritius in the western Indian Ocean. Type locality: Mangareva, Gambier Islands, Tuamotu Archipelago.

Remarks. The taxonomic and nomenclatural problems associated with *Ocypode pallidula* have already been discussed by Sakai, K. & Türkay (1976), showing as *O. pallidula* Jacquinot [? 1842–47], however Holthuis (2002) cited that 'This name was published on pl. 6. g. 1 by Hombron & Jacquinot (February 1846).' As noted above this species, as presently conceived, has a wide Indo-Pacific distribution, however it is interesting that there is such a wide gap in distribution in the Indian Ocean from Mauritius to Indonesia. The small size of the Mauritius specimens is not particularly unusual, because specimens from south Pacific are also typically smaller (Fellows 1975; personal observations). Similar sized males from Mauritius and Indonesia have a stridulating ridge composed of more striae than those from Hawaii; however, two male specimens from the Cook Islands are intermediate in the number of striae. There is no obvious geographic differentiation in females, and all the other characters (gonopods, pereiopods, orbits, eyestalks) do not show any geographically meaningful groupings. Therefore, on present evidence we are unable to recognise any obvious consistent geographical populational structure that may indicate there are two cryptic species present, however, further investigation using more sophisticated molecular methods may prove interesting.

Ooishi (1970: 94, pl. 16–1) reported *O. cordimana* from Futami Bay, Bonin (= Ogasawara) Islands, however, in Ooishi's material, as shown by her photo 'Pl. 16-1', the lateral margin of the carapace is directed straight backward from the tip of the exorbital angle in the anterior third of the carapace, and then directed inwards in the posterior two-thirds as in *O. pallidula*, which makes it clear that her specimen belongs neither to *O. cordimanus* nor to *O. stimpsoni* which are both distributed in the southern part of the Japanese and Ryukyu Islands, but has to be attributed to *O. pallidula*. In *O. cordimanus* the lateral margin of the carapace is not straight but convex from the tip of the exorbital angle in the anterior third of the carapace; and in *O. stimpsoni* the lateral margin of the carapace is directed straight and slightly outward from the base of the exorbital angle in the anterior third of the carapace.

The type specimens of *Ocypode laevis* Fabricius, 1798 and *Ocypode minuta* Fabricius, 1798, are lost (*in litt.*, J. Olesen, Zoological Museum, University of Kopenhagen and D. Brandis, Zoological Museum, University of Kiel), so we consider it best to treat these two species as 'nomen dubium', because Fabricius' descriptions are too short and ambiguous for species separation.

Ocypode pauliani Crosnier, 1965

(Figs 4C, 23, 45)

Ocypode fabricii — Lenz & Richters, 1881: 423 [in part].
Ocypode pauliani Crosnier, 1965: 102, figs 158, 165, 178–179, pl. 9, fig. 2, pl. 11, fig. 1; Ng, Guinot & Davie, 2008: 240.

Material examined. Madagascar. Tany Kely Island, male [holotype] (MNHN-B 11776), 1962, A. Crosnier; — Nosy Iranja, 2 males, 4 females [paratypes] (MNHN-B 11823), 25.i.1959, A. Crosnier; — Nosy Bé (13°23.78′S, 48°12.33′E), 2 males, 2 females (SMF-

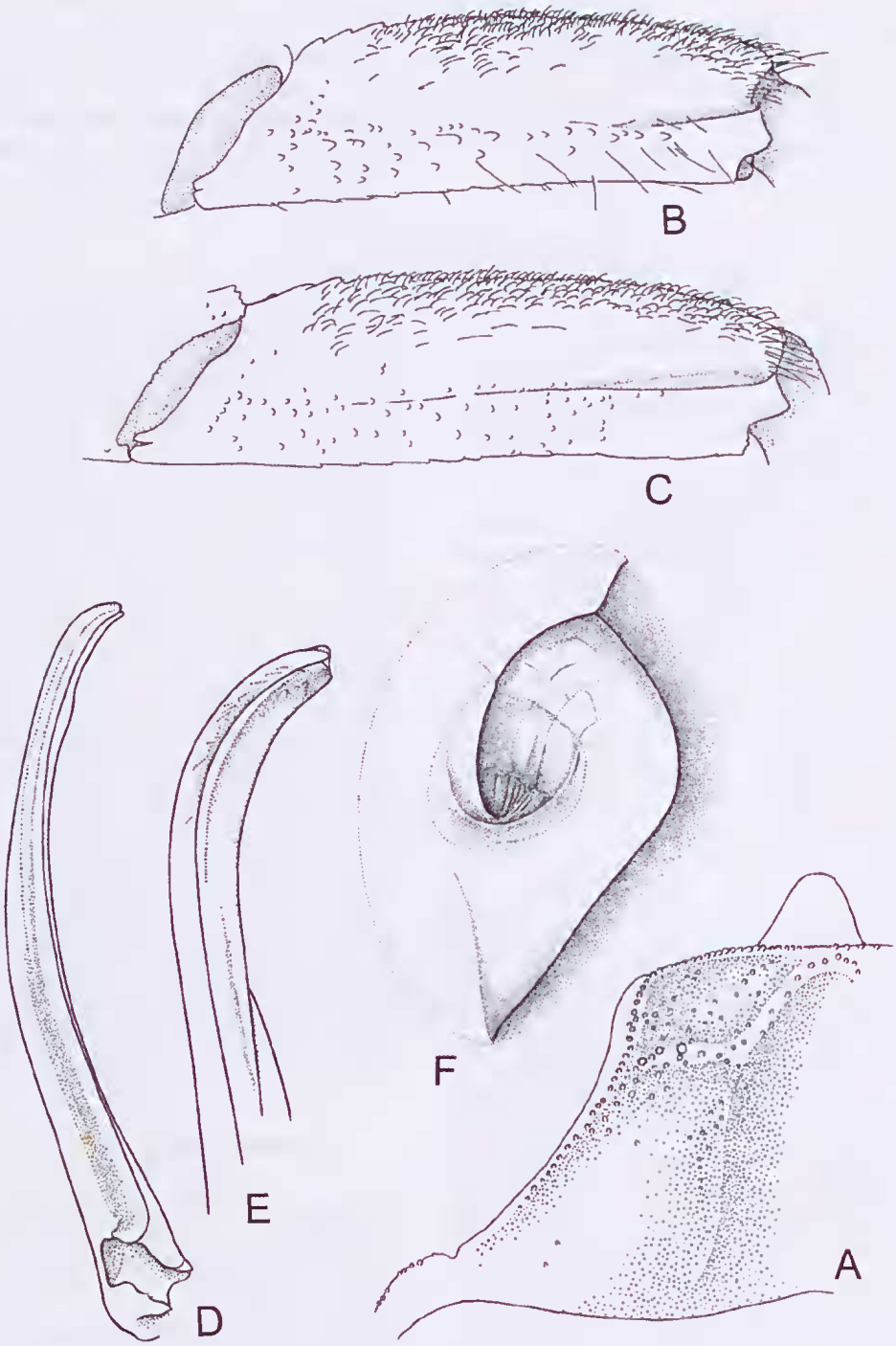

FIG. 23. *Ocypode pauliani*: **A**, P1 thoracic sternite; **B**, **C**, P2–3 propodi; **D**, **E**, Go1; **F**, female operculum.

1958) [det. Lenz & Richters, 1881 as *O. Fabricii*], C. Ebenau. **No locality**. male (UZMK).

Diagnosis. Middle-sized species. Carapace wider than long. Eyestalks not prolonged distally beyond cornea. Exorbital angles broadly triangular. Stridulating ridge composed of 7–13 tubercles. Smaller cheliped pointed at distal end. P2–3 propodi with setae on and along dorsal margin. Go1 tubelike distally and circular in cross section, bearing no palp. Operculum of female genital opening protruding mesially; median rim curved slightly and regularly.

Description. Carapace (Fig. 45) distinctly wider than long, and densely beset with fine tubercles, becoming larger near anterolateral margin of carapace. Lateral half of orbital margin broad and concave. Exorbital angles broadly triangular. Lateral margins of carapace directed straight backward from tip of exorbital angles in anterior third of carapace, and then directed inwards in posterior two-thirds. Pterygostomial region tuberculate except around buccal cavern. P1 thoracic sternite (Fig. 23A) with a granulated transverse crest at anterior third, to be connected to lateral carina of respective sternite. Palm of larger cheliped broad, and scattered sparsely with tubercles of various sizes on anterior surface as in palm of smaller cheliped; distinctly serrated on ventral margin. Stridulating ridge (Fig. 4C) composed of 7–13 irregularly spaced tubercles. Smaller cheliped pointed at distal end. P2–3 propodi (Fig. 23B–C) with setae on and along dorsal margin, extending distally onto anterior surface. Go1 (Fig. 23D–E) slender and three-sided proximally, tube-like distally, circular in cross section; slightly curved laterally in its distal part; bearing no palp. Sperm-channel originating dorsally and running along distal curve without torsion to terminal part; distal opening terminal. Operculum of female genital opening (Fig. 23F) protruding mesially; median rim curved slightly and regularly, lateral rim narrow.

Distribution. Madagascar. Type locality: Tany Kely Island, NW coast of Madagascar.

Remarks. *Ocypode pauliani* is similar to *O. ryderi* in the shape of the carapace, but they are easily distinguishable by the setae on the P2–3 propodi. *O. pauliani* is also similar to *O. madagascariensis* in the pattern of setae on the P2–3 propodi, but those two species can be differentiated by the structure of the Go1, the female operculum, the stridulating ridge, and the carapace granulation. In *O. pauliani* the carapace is much more finely and densely tuberculate on the dorsal surface than in *O. madagascariensis*, whose carapace is scattered with coarse and rough tubercles. Lenz & Richters (1881: 3) described *O. fabricii* based on specimens from Madagascar, and their report was supported by Crosnier (1965), who also considered their specimens to belong to *O. fabricii* without examining them. However, we have now re-examined that original material (SMF-1958) and found that they are actually *O. pauliani*, so *O. fabricii* is excluded from the fauna of Madagascar.

Ocypode quadrata (Fabricius, 1787)
(Figs 4D, 24, 46)

Cancer arenarius Catesby 1771: 35, pl. 35, caption [ICZN Opinion 262; name 18 on the Official Index of Rejected and Invalid Specific Names in Zoology] [Not *Cancer arenarius* Zimmermann, in Cavolini, 1792 = *Eriphia verrucosa* (Forsåke, 1775); and not *Cancer* (*Gammarellus*) *arenarius* Herbst, 1793 = *Gamarellus homari* (Fabricius, 1779)].
Cancer albicans minor littoralis Fermin, 1765: 73.
Cancer albicans minor Fermin, 1769: 276; 1770: 249.
'Witte Krab', Hartsinck, 1770: 118.
Cancer quadratus Fabricius, 1787: 315; 1793: 439.
Ocypode quadrata — Fabricius, 1798: 347; Latreille, 1803: 49; Smith, 1880: 254.
Ocypoda quadrata — Bosc, 1801–1802: 194; 1830: 247; Latreille, 1818: 199.
Ocypode albicans Bosc, 1802: 196, pl. 4, fig. 1 [in part]; Latreille, 1802: 48; Olivier, 1811: 414, 417; Lamarck, 1818: 253; Latreille, 1818: pl. 285, fig. 1; Latreille, 1818: 198, pl. 15, fig. 4; Desmarest, 1825: 121; H. Milne Edwards, In Lamarck, 1838: 463.
Ocypode arenarius — Say, 1817: 69.
Monolepis inermis — Say, 1817: 157.
'Landkrebse' Sack, 1821: 230.
Ocypoda albicans — Bosc, 1830: 249, pl. 4, fig. 1 [in part]; Lucas, 1840: 58.
Ocypode (*Ocypode*) *albicans* — De Haan, 1835: 29.
Ocypode (*Ocypode*) *quadrata* — De Haan, 1835: 29.
Ocypoda arenaria — H. Milne Edwards, 1837: 44, pl. 19, figs 13–14; Lucas, 1840: 58; Guérin-Méneville, 1856: 7; Desbonne & Schramm, 1867: 44; Kingsley, 1878: 322; Kingsley, 1880: 184 [in part]; De Man, 1881: 248; Miers, 1882: 378, 384, pl. 17, fig. 7, 7a, 7b; Miers, 1886: 240; Leidy, 1888: 333; Ives, 1891: 179; Benedict, 1892: 77; Aurivillius, 1893: 24; Ortmann, 1897: 359, 362; Doflein, 1899: 190; Cowles, 1908: 1–41, pl. 1, fig. 10; Luederwaldt,

1919: 435; A. Milne-Edwards & Bouvier, 1923: 351; Luederwaldt, 1929: 51.

Ocypoda rhombea H. Milne Edwards, 1837: 46; Dana, 1852: 322; Guérin-Méneville, 1856: 7; Saussure, 1858: 440; Heller, 1865: 42; Desbonne & Schramm, 1867: 44; Smith, 1869: 35; Cunningham, 1871: 493.

Ocypoda macrocera H. Milne Edwards, 1837: 49; Lucas, 1840: 57 [in part, only material from Brasil].

Ocypode arenaria — White, 1847: 34; Gibbes, 1850: 180; H. Milne Edwards, 1852: 143; Gerstäcker, 1856: 136; Hilgendorf, 1869: 81; von Martens, 1872: 103; Gundlach, 1887: 334; Ortmann, 1894a: 761, 765; Rathbun, 1898a: 287; 1898b: 603.

Ocypode rhombea — White, 1847: 58; Gibbes, 1850: 180; H. Milne Edwards, 1852: 143 [in part]; Gundlach, 1887: 335.

Monolepis inermis — White, 1847: 65.

? *Ocypoda rhombea* — Streets, 1871: 240.

Ocypode albicans — Rathbun, 1901: 6; 1918: 367, pls 127–128; 1919: 342; Pearse, 1915: 555; Crane, 1940: 70, figs 2, 3A, 4B, 4C, 4D, 5A, 6B, 6C, 6D, 7A–7N, 8A–I; 1941: 309, fig. 7C–D, pl. 2 fig. 6; Chace & Holthuis, 1948: 22, 27; Ferguson & Jones, 1949: 442; Buitendijk, 1950: 278; Monod, 1951: 398; Bott, 1955: 67.

Ocypode arenarius — Verrill, 1908a: 306, fig. 1; 1908b: 491.

Ocypoda albicans — Balss, 1922b: 79.

Ocypoda quadrata — Milne, 1946: 362–380; Milne & Milne, 1946: 224–230.

Ocypode occidentalis — Jones, 1968: 159, pl. 4.

Ocypode quadrata — Chace, 1956: 159; Holthuis, 1959: 259, pl. 9, fig. 3; Schöne, 1964: 107, unnumbered text-fig; Williams, 1965: 225, fig. 208; Jones, 1968: 159, pl. 4; Chace & Hobbs, 1969: 204, fig. 68; Holthuis, 1969: 13; Coêlho, 1971a: 81; 1971b: pl. 1; Coêlho & Ramos, 1972: 198; Bright & Hogue, 1972: 10; Diaz & Costlow, 1972: 120; Gomes-Corrêa, 1972: 12; Haley, 1972: 1; Horch & Salmon, 1972: 10; Henning & Klaassen, 1973: 67; Fates, 1976: 65; Powers, 1977: 141; Wolcott, 1978: 67–82; Fisher & Tevesz, 1979: 31–36; Leber, 1981: 110–112; Robertson & Pfeiffer, 1981: 165–177; Steiner & Leatherman, 1981: 111–122; Hill, 1982: 23–34; Williams, 1984: 468, text-fig. 375; Abele & Kim, 1986: 66, fig. 716a; Melo, Veloso & Oliveira, 1989: 25; Melo, 1996: 484, 1 text-fig.; 1998: 504; Alberto & Fontoura, 1999: 95–108; Weinstein & Full, 2000: 33; Rosenberg & Langer, 2001: 345–353; Fransozo *et al.*, 2002:189–195; Portell *et al.*, 2003: 712–722; Vallero-Pacheco, *et al.*, 2004: 466–475; Sabine, Meyers & Schweitzer, 2005: 295; Turra, Goncalves & Denadai, 2005: 2163–2177; Blankensteyn, 2006: 870–876; Neves & Bemvenuti, 2006: 431–435; Martin, 2006: 57–67; Maccarone & Mathews, 2006: 51–60; Valero-Pacheco, *et al.*, 2007: 313–325; Hobbs, *et. al.*, 2008: 1450–1458; Rosa Da. *et al.*, 2008: 383–388; Souza *et al.*, 2008: 139–145; Ng, Guinot & Davie, 2008: 240; Vilar de Araujo, *et al.*, 2008: 73–80, figs 1–5; López-Greco *et al.*, 2009: 41–50, figs 1–4; Maccarone & Matthews, 2008: 51–60; Teixeira, Torres & Capitoli, 2008: 9, 10, text-figs 9.1, 10A; López-Greco, *et al.*, 2009: 41–50, figs 1–4; McDermott, 2009: 637–646, figs 1–2; Perry *et al.*, 2009: 673–683; Magalhnes *et al.*, 2009: 149–152, fig. 2; Arteta-Bonivento, 2009: 149, 1 text-fig.

Material examined. Bermuda Islands. No exact locality, female (NHM-84.31), Challenger Expedition. **USA**. Massachusetts: Harraganserr Pier, Rhode Island, 1 juv. female (USNM-92129), 2.ix.1950, C.J. Fish; — New York: Long Island, 2 juvs. (MNHN) [det. Smith, 1899 as *O. arenaria*]; 2 juvs. (NHM), not registered; — New Jersey: no exact locality; — Carolina: no exact locality, 1 dry female (MNHG) [det. as *O. arenaria*]; — North Carolina: Beaufort, male, female (MZT-1107); — *ibid.*, 1 juv. male (SMF-5507), 1904, Reichard; — Georgia: Sapelo Island, 2 males, 4 females, 5.iv.1964, Mus. Copenhagen; — *ibid.*, 2 males (SMF-6847), J. Dörjes; — *ibid.*, tidal flat, 3 males, 1 juv. (SMF-22177), 23.v.1969, J. Dörjes; — Florida: Cay Biscayne, male (MNHG-147); — Key West, female (NHM-1898.5.7.536–537); — Dry Tortugas, male (ZMH-2800) [det. as *O. arenaria*]; 3 males, female (NHM-1938.3.19.61–63); — Sarasota, Siesta-Key, male (SMF-5404), x.1963, W. Klausewitz; — *ibid.*, male (SMF-6851), ix.1963; — Santa Rosa I. near Pensacola, beach with white sand, 2 juvs. (SMF-22175), 17.ix.1972, J. Dörjes; - Texas: no exact locality, female (NHMW) [det. as *O. rhombea* Fabricius], 20.i.1882, Stind. **Mexico**. No exact locality, 1 juv. female (NHMW-1957) [det. as *O. occidentalis*], 1884, Bilimek; — East coast of Mexico, 5 males, female, 1 juv. female (NHMW), 5.v.1883, Bilimek; — Estado de Veracruz: Veracruz, male (NHM-81.29); — Barra de Tuxpam (20°58.55´N, 97°18.54´W), male (SMF-7495), 5.xi.1973, E.G. Burmeister; 1 juv. (SMF-7506). **Belize**. No exact locality, male, 1 ovig. female (NHM-1967.7.1.93–94). **Honduras**. Puerto Cortés, strand (15°51.92´N, 87°56.54´W), 2 females, 1 juv. (SMF-2341), 19.ix.1951, H.M. Peters; — *ibid.*, 2 males, female (SMF-2075), 21.ix.1951, H.M. Peters; — Coast of Tela (15°46.98´N, 87°27.33´W), 1 juv. female (SMF-2206), 24.i.1953, O. Schuster. **Costa Rica**. No further data, 3 females (ZMH-2799) [det. as *O. Arenaria*]. **Bahamas**. No further data, male (MZT-1104). **Cuba**. No further data, 1 dry female (MNHG) [det. as *O. arenaria*]; male (ZMH-25495); — Cárdenas (23°3.08´N, 81°12.14´W), male, female (ZMH-2742). **Cayman Islands**. Grand Cayman, 1 juv. (NHM-1955.10.6.34). **Jamaica**. No exact locality, male (NHMW-1955) [det. *O. albicans* Bosc], xi.1929, Schmarda; — Saint Thomas Parish: near Port Morant, male (NHM-1912.7.13.3); — Trelawny Parish: Falmouth, Mangrove near Glistening Waters (18°29.67´N, 77°40.01´W), 1 juv. female (SMF-19578), 18.ii.1987, R. Diesel. **Haiti** . No exact locality, male (SMF-1946), 1904, A. Reichardt. **Dominican Republic**. No exact locality, 1 juv.

female (ZSM), 8.xii.1903, Heitz; — Monte Christi, 3 males, 2 females (ZMH-25171) [det. as *O. arenaria*]; — Beata Island, male (UZMK) [det. as *Ocypode* sp.], 22.iii.1922. **USA, Puerto Rico**. Mona Island between Dominican Republic and Puerto Rico, male (MNHN) [det. Bouvier, 1907 as *O. arenaria*]. **U.S. Virgin Islands**. No exact locality, male, 1 juv. male, female (MCZ), 1911; — St. Thomas, male (ZMH-2808) [det. as *O. ceratophthalma*]; 3 males, female, 1 juv. female, 6 juvs. (ZMH-2788); female (MZT-1098); — *ibid.*, Salmin, female (ZSM) [Vend]; — Water Island, St. Thomas, female (MCZ) [det. as *O.* sp.], 3.xii.1910; — Smiths Bay, St. Thomas, male (MCZ) [det. *Ocypode* sp.], 1.xii.1933; — St. Croix, Bay beach, 1 juv. male (SMF-22176), 5.xii.1972, J. Dörjes. **St. Kitts and Nevis**. St. Kitts, female (NHM-441b); — Nevis I., male, 1 juv. male, 1 juv. female (NHM-1938.3.29.97–99). **French Antilles**. Martinique: no exact locality, 1 dry male (MNHN-3263) [det. as *O. arenaria*]; — *ibid.*, male, female, dry (MNHN) [det. as *O. arenaria*], Plee; — *ibid.*, male [18.0×23.3 mm], female [27.4×28.4 mm] (SMF-36242), 8-16.i.2004, M. Türkay; — St. Anne, male, female (ZSM), 1898, F. Doflein; — Martinique, Dizac near Diamant (14°28.707′N, 61°1.767′W), sandy beach, taken at night, 2 males [34.0×41.4, 30.4×37.2 mm] (SMF-36241), 13.i.2004, M. Türkay; — Guadeloupe: no exact locality, 1 dry female (MNHN-3264) [det. as *O. arenaria*]; — *ibid.*, female (SMF-9409), 1960, Merkel; — District Basse Terre, NW-coast close to Deshaies (16°1.09′N, 61°47.68′W), 2 males, 2 females (SMF-21573), x.1991, M. Gutmann. **Trinidad and Tobago**. Mt. Irvine Bay, SW-coast of Tobago Island, 2 juv. males (NHM, unregistered). **Colombia**. Depto Bolivár: Cartagena, sandy beach near Boca Grande (10°24.21′N, 75°33.41′W), male (SMF-6849), 16.i.1968, Sturm; — Depto Magdalena: Isla de Salamanca, male (SMF- 6848), viii-xii.1969, F. Klaassen; — *ibid.*, Pueblo Viejo, cimitary, 2 juv. males (SMF-7036), viii.1969, F. Klaassen; — Beach at Hotel Irotama, 15 km SW Santa Marta (11° 8.94′N, 74° 13.58′W), female (SMF-16597), 12.x.1978, M. & H. Türkay; — Ensenada Grande, N of Santa Marta, sandy beach, male (SMF-16596), 20.x.1978, M. & H. Türkay; — Bahia Concha, *c.* 10 km NE of Santa Marta (11°17.8′N, 74°9.1′W), sandy beach, 1 juv. male (SMF-5141), 24.ix.1967, F. Riemann; — *ibid.*, male, female (SMF-16593), 7.x.1978, M. & H. Türkay; — *ibid.*, male (SMF-16594),14.x.1978, M. & H. Türkay; — Bahia Nenguangue *c.* 25 km NE of Santa Marta (11°18.92′N, 74°4.96′W), muddy mangrove, male (SMF-6861), xii.1974, H. Schmalfuß; — *ibid.*, male (SMF-16595), 8.x.1978, M. & H. Türkay; — *ibid.*, male (SMF-17994), 11.x.1978, M. & H. Türkay; — Playa del Muerto c. 25 km NE of Santa Marta (11°19.65′N, 74°4.63′W), sandy beach, male, 1 juv. (SMF-16598), x.1978, M. & H. Türkay; — *ibid.*, female (SMF-18687), 1.xii.1978, D. Rodriguez; — Rio Buritaca (11°15.81′N, 73°46.14′W), 4 females (SMF-6850), viii-ix.1970, F. Klaassen. **Venezuela**. No exact locality, male (ZMH-2794); — *ibid.*, male (NHMW-9776) [det. O. Pesta], 1930, Koller, Costa Rica Expedition; — Valencia [This locality is clearly wrong, as Valencia, the capital of the Carbobo State, lies far inland. Probably the collector meant the coast of Carbobo State], female (ZMK-1537), 1815, Werner; — Isla Los Roques (11°51.63′N, 66°45.19′W), female (SMF-2440), I. Eibl. **Republic of Guyana**. No exact locality, male, female (MNHN) [det. Guinot as *O. arenaria*], 1953, J. Duraud. **Brazil**. No exact locality, 1 dry male [CL 21 mm] (MNHN) [det. as *O. rhombea* Fabricius]; 1 damaged male (ZMH-2744); 3 males, female (NHMW) [det. *O. rhombea*], Nallere; — North Brazil, female, (ZMH-2786); — Estado de Pará: Belem, female (NHMW-1952); 2 females (NHMW-1632), Nallere; — Estado de Maranhno: Tutoia, 2 ovig. females (ZMH-2785); — Estado de Pernambuco: Fernando de Noronha, 4 males, female (NHM-88.19); — Estado de Bahia: Salvador, male, juv. female, 1 juv. (ZMH-25276); 1 juv. (ZMH-2949); male (NHM-84.31); — Estado de Espirito Santo: no exact locality, 2 males (SMF-9822); — Estado Rio de Janeiro: Rio de Janeiro, male (NHM-69.37); male (NHMW-1951) [det. as *O. albicans*]; female (NHMW-1954) [det. as *O. albicans*]; — *ibid.*, male (NHMW), 1.xi.1931, Ryrt, Kurl & Klelle Son; — *ibid.*, male (NHMW-1399) [det. Heller, 1865 as *O. rhombea*], 'Novara Expedition'; female (NHMW-1434); — Rio de Janeiro, Penha, 6 males, female (SMF-1947), 24.vi.1914, Breslau; — Estado Sno Paulo: São Paulo, male, 1 damaged female (ZMH-13817) [det. as *O. Arenaria*]; — Estado de Santa Catarina: Praia Grande, Sno Francisco do Sul, 3 males, 2 females (USNM-70947), 6.x.1925, W.L. Schmitt; — Estado de Rio Grande do Sul: Torres, 2 males, female (SMF-5075), 12.ii.1966, Lise; — 7 km N of Tranandai (30°00′S, 50°15′W), 4 males (SMF-21987), 3–4.iii.1993, Ha. Langer; 4 males (SMF-21987); — Pinai (30°10′S, 50°15′W), E of Porto Alegre, 6 males, 2 females (SMF-21988), 9.iii.1993, H. Langer. **Incorrect localities**. Altata, West coast of Mexico, Pacific Ocean, 1 damaged female (ZMH-2743); — West coast of Mexico, Pacific Ocean, female (ZMH-2787); — Indian Ocean, male (ZMK-1538) [det. as *O. Cordimanus*]; — West Africa, 1 damaged female (ZMH-2796). **No locality**. 2 males (ZSM) [from Natur Museum Lübeck 817]; male (ZMH-2797); male (NHM); — 'America', male, female (SMF-7153); male (SMF-36886), J. Dörjes; — 'West Indies', 2 males, 2 females, 1 juv. (ZMH-25373) [det. as *O. arenaria*]; male, 2 females (ZMH-2793); 1 juv. male (NHM- 1967.4.4.142); — *ibid.*, male (SMF-16567 [ex. Mus. Heidelberg]), 1865, Salmin.

Diagnosis. Mid-to large-sized species. Eyestalks not prolonged distally beyond cornea. Lateral half of orbital margin concave. Exorbital angles acutely triangular and directed anteriorly. Stridulating ridge composed of 15–18 tubercles. P2–3 propodi with median rows of setae on

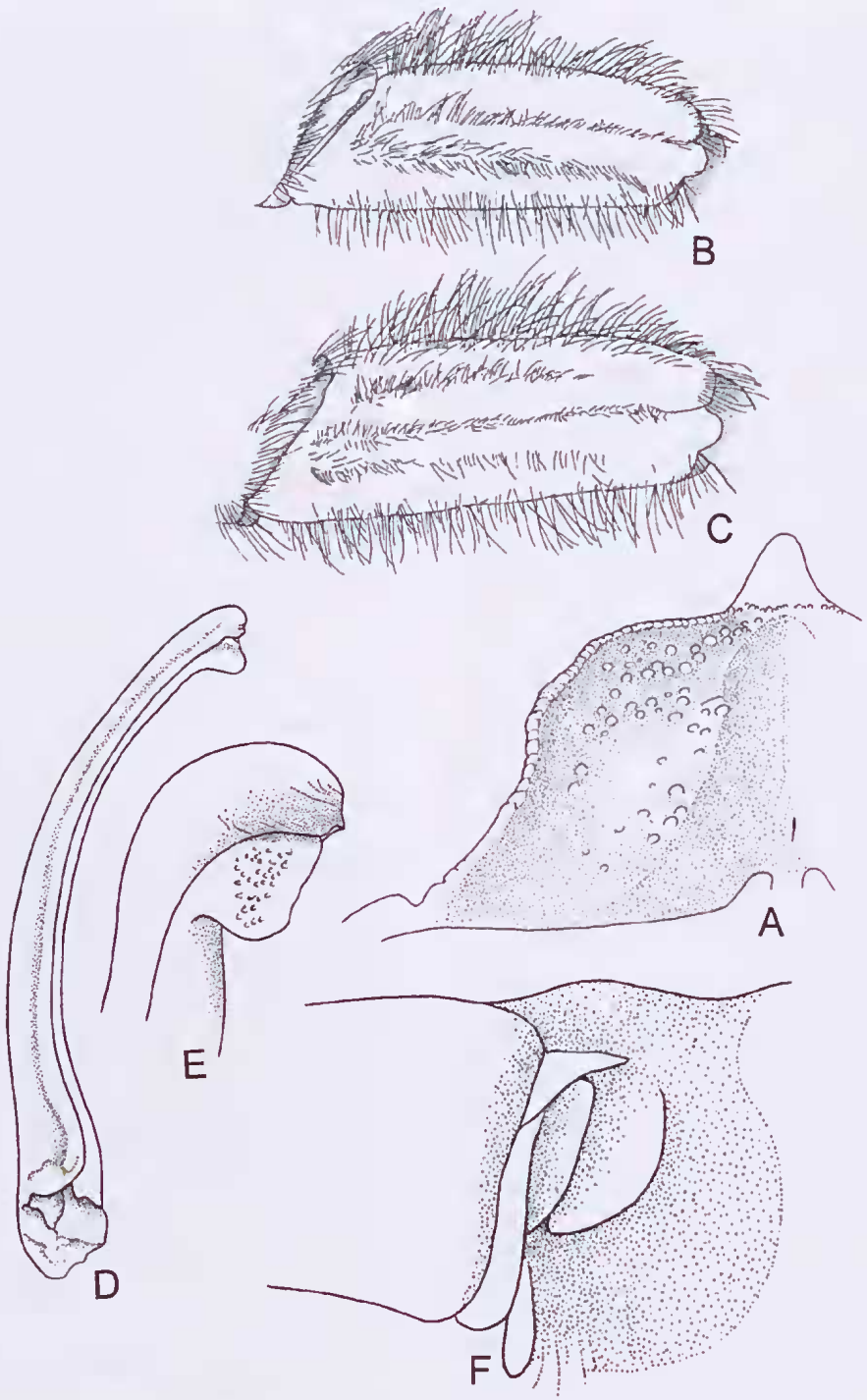

FIG. 24. *Ocypode quadrata*: **A**, P1 thoracic sternite; **B**, **C**, P2–3 propodi; **D**, **E**, Go1; **F**, female operculum.

anterior surface, bearing long setae on dorsal and ventral margins. Go1 deepened on both sides of sperm channel; broadened at distal end; lacking palp. Operculum of female genital opening very narrow and long.

Description. Carapace (Fig. 46) wider than long and beset densely with fine tubercles on dorsal surface, which becoming larger towards lateral sides. Lateral half of orbital margin concave. Exorbital angles acutely triangular and directed anteriorly. Lateral margins of carapace directed slightly outwards from tip of exorbital angle in anterior third of carapace, and then directed mesially in posterior two-thirds, so that carapace broadest at anterior third. Pterygostomial region distinctly tuberculate except along smooth lateral sides of buccal cavern. P1 thoracic sternite (Fig. 24A) rounded at anterolateral angle and slightly sunken around corner, and hemmed anteriorly and laterally with tuberculate carinae, and roughly tuberculate in anterior third. Palm of larger cheliped elongate and scattered sparsely with coarse tubercles on anterior surface, bearing irregularly arranged obtuse teeth on ventral margin and denticles on dorsal margin. Smaller cheliped pointed distally. Stridulating ridge (Fig. 4D) composed of 15–18 interspaced tubercles. P2–3 propodi (Fig. 24B–C) with median rows (two in P2 and three in P3) of setae on anterior surface, bearing long setae on dorsal and ventral margins. P4–5 propodi with long setae on dorsal and ventral margins. Go1 (Fig. 24D–E) three-sided proximally; deepened on both sides of sperm channel; curved laterally at broadened distal end with lateral bulge; lacking palp. Operculum of female genital opening (Fig. 24F) very narrow and long; median rim elevated, acutely triangular.

Distribution. Western Atlantic: From Block I., Massachusetts to Rio Grande do Sul, Brazil. Type locality: Jamaica.

Remarks. The name of the only *Ocypode* species reported from the Atlantic coast of North and South America was settled as *Ocypode quadrata* through ICZN opinion 262 (1954). Which name to apply to the species had been ambiguous and confused before this act, by which most of the historical problems regarding its nomenclature were solved. It must especially be pointed out that, though *Ocypode rhombea* has been used for Atlantic specimens by a number of authors in the past, after examination of their respective specimens it is clear that this Atlantic material is all *O. quadrata*, and that *O. rhombea* Fabricius, 1798, is restricted to the Pacific. Also, as mentioned earlier, we have examined the holotype of *O. rhombea* in the ZMUC and although it is a juvenile, and in poor condition, we are confident that it is a junior synonym of *O. ceratophthalma* and not *O. quadrata* as has long been supposed.

Ocypode rotundata Miers, 1882

(Figs 5A, 25, 47)

Ocypoda rotundata Miers, 1882: 378, 382, pl. 17, fig. 4; Ortmann, 1897: 360, 364; Alcock, 1900: 348; Chhapgar, 1956: 508; 1957: 46, pl. 13 figs g–i; Hashmi, 1963: 240.

Ocypoda rotundata var. *arabica* Nobili, 1906a: 152, pl. 5. fig. 26; Ng *et al.*, 2008: 240.

Ocypode aegyptiaca — Laurie, 1915: 416 [in part, only record from Persian Gulf].

Ocypoda aegyptiaca — Stephensen, 1945: 188, fig. 55.

Ocypode rotundata — Pretzmann, 1971: 480, pl. 4, figs 8–10; 1974: 453; 1975: 15; Tirmizi, 1980: 109; Titgen, 1982: 152; Tirmizi & Kazmi, 1983: 371, 377; Türkay *et al.*, 1996: 104, text-figs 7–8, 12, pls 1–3; Clayton, 2001: 37–55; Yousuf *et al.*, 2007: 110, figs 7–8; Ng *et al.*, 2008: 240; Hosseini, 2009: 37–46.

Ocypode saratan — Basson *et al.*, 1977: 38, 40, 56, 60, 126, 140, 145, text-fig. 14; Jones, 1986: 157, pl. 42; Hogarth, 1989: 103, 115; Kazemiyan, 2008: 404–409.

Ocypode ceratophthalma — Yousuf *et al.*, 2007: 108, figs 1–2.

Ocypode macleayana — Yousuf *et al.*, 2007: 109, figs 5–6.

Ocypode gaudichaudii — Yousuf *et al.*, 2007: 108, figs 3–4.

Material examined. Pakistan. Karachi, female (NHM-1897.9.12.2); 2 specimens (NHM-1911.1.17.72–73); 1 juv. male (USNM-216684); 1 juv. (UZMK); — Sandy beach at Horst Point, W of Karachi, male (UZMK); — Clifton, Karachi, female (NHM); — Indus-Delta, Waddi Khuddi Creek [= 'Khudi Creek'] (24°34.52′N, 67°12.4′E), 3 males, female (SMF-6748), xii.1970; — *ibid.*, male, female (SMF-17728), i.1974, G. Pilleri. **Oman.** Island Al Hallaniyah (17°30′N, 56°01′E), Oman, Arabian Sea, male [holotype of *Ocypoda rotundata* var. *arabica*] (MNHN); — Masqat, Gulf of Oman, 2 males (NHM-1898.4.14.3–4); — Al Bustan (23°34.37′N, 58°36.72′E), South of Masqat, male [9.9× 12.8 mm] (SMF-36245), 6.ix.1983, P.J. Hogarth; — Al Chasab, male (NHM-1973.167); female (NHM-1973.170); — Al Khuwayr, Batinah (23°36′N, 58°25′E), 1

juv. male, 2 females, 2 juv. females (SMF-18285), 28.vi.1988, M. Gallagher; — Suwadi, West of Masqat (23°47´N, 57°47´E), Sandy shoal, female (SMF-24534), 26.v.1995, D. Clayton; — Seeb, W of Masqat, male (SMF-24535), 29.v.1995, D. Clayton. **Persian Gulf.** No further data, female (NHM-1962.8.30.5). **Iran.** No further data, 4 males, 3 females (NHMW); — Bushehr, Persian Gulf coral reef, 2 males (UZMK) [det. Stephensen, 1945]; — Jazireh-ye Shotur (= Jazireh-ye Shitwar), Persian Gulf (26°47´N, 53°25´E), 2 females (UZMK) [det. Stephensen, 1945]; — Bandar Abbas, male, female (NHMW-3804), 1970, Pretzmann & Bilek; 2 males (NHMW-3805); 1 juv. male, 5 juv. females, 2 juvs. (NHMW-3806); females (NHMW-9870); 5 males, female, 1 juv. (NHMW-10793). **Saudi-Arabia.** Ras at Tannurah, male (RMNH-15616); male (USNM-207674); — Jazirat Abu Ali (27°20´N, 49°33´E), 2 males, 2 females (NHM-1974.386); — *ibid.*, (27°21´N, 49°30´E), North coast, sandy beach, male (SMF-23028), 2.xi 1992, M. Apel; 2 males, 3 females (SMF-23029), 11.vi.1992; male, female (SNMNH-13), 16.v.1995; — *ibid.*, North coast behind ARAMCO-camp, sandy beach covered with tar, male, female (SNMNH-12), 30.x.1992, M. Apel; — *ibid.*, (27°18´N, 49°42´E), eastern tip, close to coast guard camp, male, 2 females (SMF-23030), 29.v.1992; male, 2 females (SMF-23031); 2 males, 2 females (SNMNH-11), 28.vi.1992; — *ibid.*, (27°18´N, 49°41´E), north coast close to eastern tip, sandy beach with scattered rocks, 2 males, 2 females (SMF-23033), 16.v.1995, M. Apel; — *ibid.*, South-West tip, sandy beach, female (SMF-24534); male, 3 females (SNMNH-14), 20.v.1995, M. Apel; — Ras Az Zawr (27°27´N, 49°18´E), sandy beach, female (SMF-23032), 17.v.1995, M. Apel; — Jazirat Karan (27°43´N, 49°48.48´E), sandy beach with scattered rocks, female (SMF-23027), 12.vii.1992, M. Apel; —*ibid.*, 2 males, 2 females (SMF-23034). **Qatar.** Dukhun, male [holotype] (NHM-79.32). **United Arab Emirates.** Ash Shariqah, female (NHM-1971.32); — Jazirat Abu Ali (27°20´N, 49°33´E), 2 males, 2 females (NHM-1974.386); — Fujairah, N of Khor Fakkan (25°30´N, 56°22´E), 4 males, 9 females (SMF-23035).

Diagnosis. Large-sized species. Eyestalks prolonged distally beyond cornea in a stylus. Exorbital angles rounded. Stridulating ridge composed of 10–15 tubercles with striae. Smaller cheliped pointed at distal end. P2 propodus with two median rows of setae on anterior surface. P3–5 propodi naked. Go1 broadened, curved laterally at distal end, with distinct palp. Operculum of female genital opening rounded distally, protruding mesially in button-shape. Vaginal slit directed lengthwise.

Description. Carapace (Fig. 47) wider than long and beset densely with coarse tubercles, becoming less densely scattered toward lateral sides. Lateral half of orbital margin directed obliquely backwards, so that exorbital corners located far posterior to median convexity of orbital margin. Exorbital corners broadly rounded. Lateral margins of carapace convex from rounded exorbital corners to anterior third of carapace, and then directed inwards in posterior two-thirds, forming broad and rounded epibranchial corners, at which carapace broadest. Pterygostomial region sparsely tuberculate except along lateral sides of buccal cavern. P1 thoracic sternite (Fig. 25A) triangular at anterolateral corner and slightly sunken mesially, and indistinctly tuberculate in posterior two-thirds, bearing tuberculate carinae on setose anterior and naked lateral margins. Palm of larger cheliped broad and densely beset with fine tubercles on anterior surface, among which scanty coarse tubercles present, and roughly serrated on ventral margin. Stridulating ridge composed (Fig. 5A) of 10–15 irregularly spaced elongate tubercles with striae. Smaller cheliped pointed at distal end. P2 propodus (Fig. 25B) with two median rows of setae on anterior surface, all other surfaces of P3 (Fig. 25C) to P5 propodi naked. Go1 (Fig. 25D–E) broadened with lateral bulge and curved laterally at distal end, bearing thumb-like palp branching from stem near genital opening; sperm channel originating dorsally and running without torsion to broad distal part. Operculum of female genital opening (Fig. 25F) rounded distally; protruding mesially in button-shape. Vaginal slit directed lengthwise, almost parallel to sternal median line. Lateral rim well developed, increasing in height toward median part.

Juvenile specimens. In a small specimen (13.8×15.8 mm, NHMW-3806) eyestalks not yet prolonged distally beyond cornea, but in larger specimens (19.7×22.9, 22.5×26.6 mm, NHMW-3806) eyestalks already prolonged distally beyond cornea in a short stylus. Lateral half of orbital margin concave, and exorbital angles distinct. Lateral margins of carapace directed straight backwards, and then directed inwards, forming more distinct epibranchial corners than in adult specimens. Palm of larger cheliped more longer than broad than in adult ones. Stridulating ridge composed of 10–11 interspaced striae. P2 propodus with a median

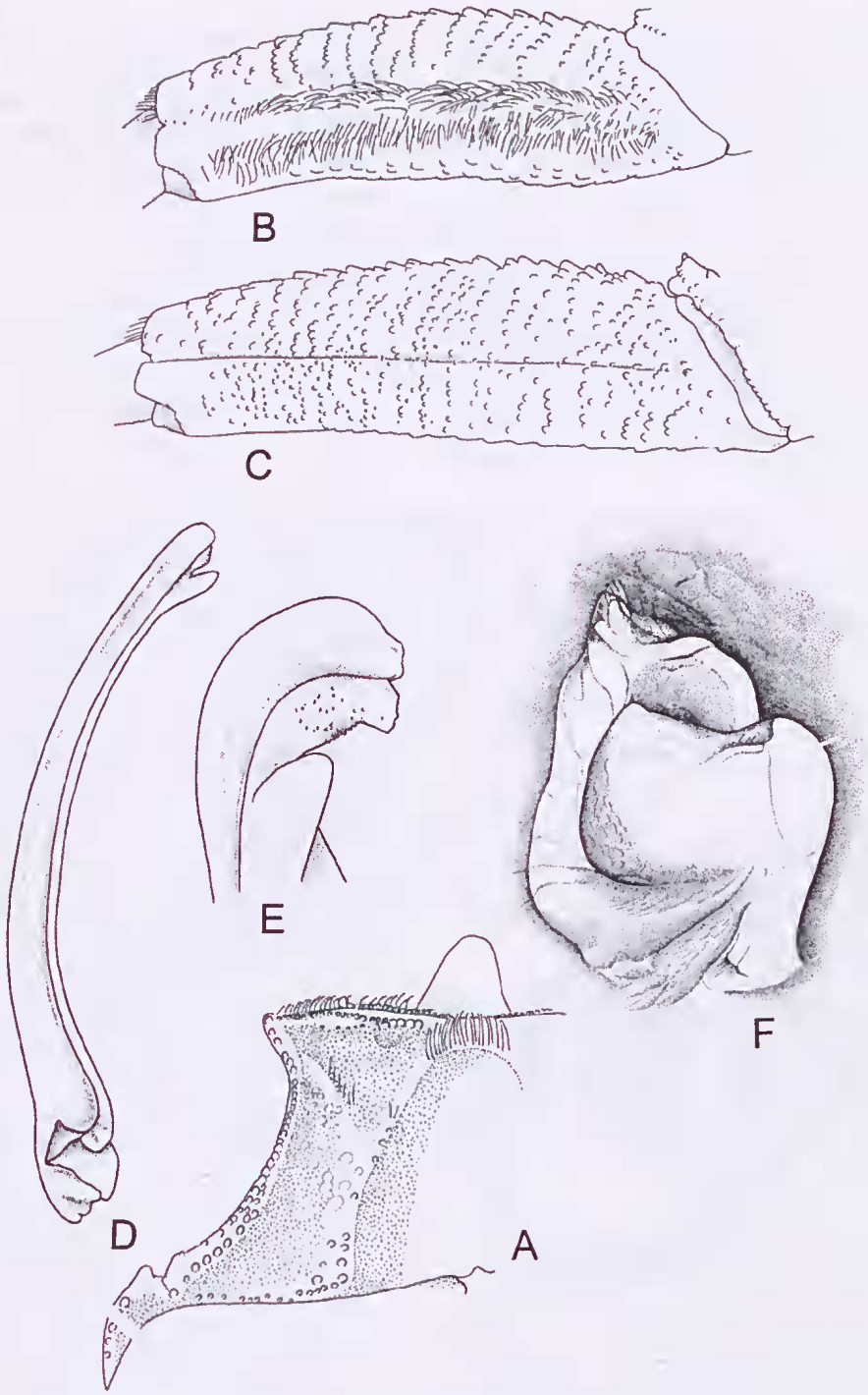

FIG. 25. *Ocypode rotundata*: **A,** P1 thoracic sternite; **B, C,** P2–3 propodi; **D, E,** Go1; **F,** female operculum.

row of scanty setae on anterior surface, and yellowish setae at distal end of dorsal margin.

Distribution. South coast of Arabian Peninsula (Oman) to North India (Bombay State), including the Persian Gulf. Type locality: 'Dukhun' (probably Dukhan, Qatar, see Remarks)

Remarks. *O. rotundata* is similar in morphology to *O. saratan* from the Red Sea and its adjacent regions, and they have often been confused. However, in *O. rotundata* the stridulating ridge of the chela is composed of 10–15 irregularly spaced elongate tubercles with striae, and the Go1 bears a stout thumb-like palp; whereas in *O. saratan* it is composed of 67–87 fine striae and the Go1 bears a palp which is slenderly triangular in its distal half.

Different names were used by earlier authors, and this caused some sonfusion. *O. rotundata* var. *arabica* described by Nobili (1906) was characterised by its typical triangular exorbital angles; however, this is also observed in young specimens of *O. rotundata*, and is simply related to growth. We re-examined the type specimen of *O. rotundata* var. *arabica* and here confirmed that it is conspecific with *O. rotundata*. Stephensen (1945) reported *O. aegypticae* from the Persian Gulf, because he considered his specimen to be similar to *O. aegypticae* described by Gerstaecker (1856) (later synonymised with *O. saratan*), however, his specimen too has been re-identified as *O. rotundata*.

Some uncertainty exist regarding the type locality of *O. rotundata*. Miers (1882) stated: 'The specimen, which is much mutilated, is labeled "Dukhun, Col. Sykes" (coll. Indian Museum), and was probably obtained at some locality on the western coast of India.' 'Dukhun' is presumed to be Dukhan located on the coast of Qatar in the Persian Gulf.

Yousuf *et al.* (2007) recorded *Ocypode ceratophthalma*, *O. gaudichaudii*, *O. macleayana*, and *O. rotundata*, based on specimens collected from the sandy beach of Sonmiani on the Makran coast (Baluchistan Province, Pakistan) and published figures of the specimens. However, it is evident from their figures and distribution that the first two species are rather to be identified as *O. rotundata*, because their '*O. ceratophthalma*' and '*O. gaudichaudii*' are shown to have the carapace rounded at the exorbital corners, though *O. ceratophthalma* and *O. gaudichaudii* have the carapace triangular at the exorbital corners. It must also be added that *O. gaudichaudii* is not distributed in Pakistan but in the eastern Pacific. *Ocypode macleayana* is also impossible as it is a synonym of *O. ceratophthalma*, and their '*O. macleayana*' can also be attributed to *O. rotundata*.

Ocypode ryderi Kingsley, 1881
(Figs 5B, 26, 48)

Ocypode Urvillei — A. Milne-Edwards, 1868: 71 [in part].

Ocypode ryderi Kingsley, 1881: 183; Sakai, K. & Türkay, 1976: 82, figs 2, 5, 6, 9, 10, 12, pl. 1; Berry *et al.*, 1976: 29; Berry, 1976: 35–37, 1 un-num. text-fig; Vannini, 1980: 171–183, figs 1–4; McLachlan, 1980: 57–58, fig. 1; Vannini & Valmori, 1981: 206, figs 1C, 2C, 3C, 4C; Kensley, 1981: 49; Rivera & Langner, 1982: 228; Henning & Langner, 1986: 213–214; Jackson *et al.*, 1991: 280–286; Vetter, 1992: 2, 6, 33, 61, 65, 66, 67, 85, fig. 9; Rosenberg & Langner, 2001: 345–353, fig. 1; Rosenberg *et al.*, 2001: 53–70, figs 1–7; Bruyn, 2002: 28–34, figs 1–2, 4, 6–9; Ng *et al.*, 2008: 240.

Ocypoda Kuhlii — Pfeffer, 1889: 30; Lenz, 1912: 6.

Ocypoda Kuhli — Lenz, In: Voeltzkow, 1910: 558.

Ocypoda cordimana — Pfeffer, 1889: 30 [in part]; Bouvier, 1921: 58.

Ocypode kuhli — Ortmann, 1894a: 761; Stebbing, 1910: 327; Rathbun, 1933: 260, pl. 7, fig. 2; 1935: 26; Chace, 1942: 202; Barnard, 1950: 87, fig. 17e–g; Barrass, 1963: 73; Guinot, 1967: 281; Jones, 1972: 31–43, tab. 1, figs 3, 4b, 4d, 4f, 4h, 5; Evans, 1976: 121–135, tabs 1–4, figs 1–4).

Ocypode Kuhli — Ortmann, 1894b: 59.

Ocypoda kuhli — Ortmann, 1897: 359 [in part]; Lenz, 1905: 365; Cott, 1929: 755.

Material examined. No locality. male (ZMH-K2963). **Eastern Africa.** No further data, male (ZMH-K25451). **Yemen**. Suqutra, South coast centre (12°18.7′N, 53°48.29′E), 3 males, female (SMF-36170), 9.iv.1999, M. Apel; 2 males, 2 females (NHCY-86); — Abd el-Kuri island, 3 female, 1 juv. (NHM-1906.5.29.23–25). **Somalia**. Mogadischu, beach (2°2.68′N, 45°22.1′E), male (SMF-9981), xi-xii.1976, M. Vannini; — Marka, South of Mogadischu, female, 1 juv. female, 3 juvs. (MCSNM); — Sar Uanle, 20 km S of Kisimayo (= Kismaayo), 2 males (RMNH-25852); male, female (AMS-P24831). **Kenya**. female (MHNG); — Lamu I., male (NHM-1893.11.9.11); — Malindi (3°12.72′S, 40°7.35′E), 2 males (SMF-9831), xii.1980, W. Sudhaus; — Watamu (3°21.2′S, 40°1.5′E), S of Malindi, male (RMNH-15852); — *ibid.*, 1 juv. male, 1 juv. female

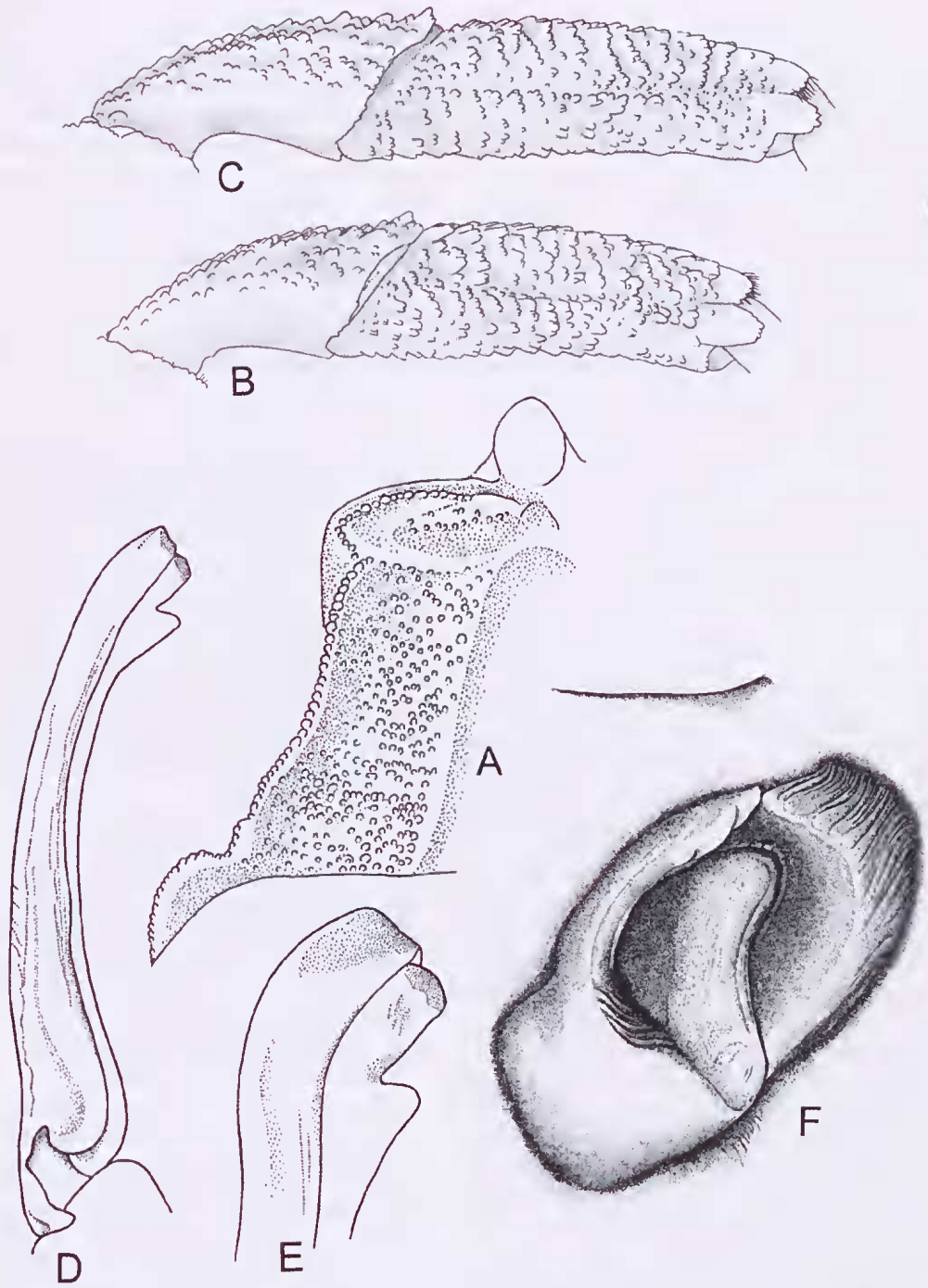

FIG. 26. *Ocypode ryderi*: **A**, P1 thoracic sternite; **B, C**, P2–3 propodi; **D, E**, Go1; **F**, female operculum.

(SMF-9315), x.1978, M. Grasshoff; — Mida Creek, S of Watamu, Swatami Mangrove (3°24.05′S, 39°57.95′E), 1 juv. (SMF-18281); — Kilifi Creek (3°38.27′S, 39°51.58′E) between Malindi and Mombasa, male (SMF-18286), xii.1985, W. Baumeister; — Kikambala (3°49.65′S, 39°49.71′E), 3 males, female, 4 juvs. (SMF-6110), 20.iii–5.iv.1971, Z. Števčić; — *ibid.*, male (SMF-6354), 1.ix.1973, W. Sudhaus; — Mombasa, 1 juv. male, 2 females (ZSM); female (ZSM); 2 males, 3 females (ZSM); male (NHM); 2 juv. females (NHM-1955.6.9.38–39); — Mombasa, Nyali, male (UZMK); — Mombasa, Bamburi, 10 males, 3 females, 1 juv. (RMNH-26015). **Tanzania**. Zanzibar, male (ZMH-K2839) [det. Pfeffer, 1888 as *Ocypode cordimana*]; — Zanzibar, Mkokotoni, female (ZSM) [det. Lenz, 1905]; — Dar es Salaam, 2 males, 1 juv. male, female, 2 juvs. (NHM-1973.41); 2 males (NHM-1964.7.10.9–10); male, female (ZMH-K2964). **Mozambique**. No further data, male (NRMS-t5972); — Inhambane, male, 2 females (ZMH-K29813); — Xai-Xai, 3 males, 2 females (ZMH-K29816). **South Africa**. Boteler Point (27°1.0′S, 32°51.92′E), Kosi Bay, 2 males, 2 females (SMF-10932); — Durban, male, female (NRMS-t6526); female, 1 juv. female (RMNH-73801); female (ZMUA-102.369); — Amanzimtoti, S of Durban, 1 juv. female (NMG-2235) [det. Lenz, 1912]; — Port Alfred, 1 specimen (NHMW). **Seychelles**. Mahé, 1 juv. (NHMW-24971) [det. Koelbel as *Ocypode fabricii*], Korvette Frundsberg Expedition.

Diagnosis. Middle-sized species. Eyestalks not prolonged distally beyond cornea. Exorbital angles broadly triangular. Stridulating ridge composed of *c.* 15 tubercles. Smaller cheliped pointed distally. P2–3 propodi naked on anterior surface. P1–5 bases, carpi, and dactyli each bearing a distinct narrow red band along proximal margin. Go1 broadly bulging, slightly curved laterally in distal part, bearing a distinct palp. Operculum of female genital opening strongly protruding anteromesially with distinct rim; vaginal slit directed lengthwise.

Description. Carapace (Fig. 48) slightly wider than long and beset less densely with coarse tubercles than in other species of *Ocypode*, gradually becoming larger toward lateral sides. Lateral half of orbital margin broadly concave. Exorbital angles broadly triangular and directed slightly anteriorly. Lateral margins of carapace directed slightly outwards from base of exorbital angle in anterior third of carapace, and then directed inwards in posterior two-thirds, forming distinct epibranchial angle, and carapace broadest at anterior third. Pterygostomial region distinctly tuberculate except along lateral sides of buccal cavern. P1 thoracic sternite (Fig. 26A) protruding roundly at anterolateral corner and concave inside, and distinctly tuberculate in posterior two-thirds, bearing a pair of distinct humps with roughly arranged tubercles, and tuberculate carinae on anterior and lateral margins. Palm of larger cheliped longer than broad and scattered with distinct and coarse tubercles on anterior surface, and irregularly denticulate on ventral and dorsal margins. Stridulating ridge (Fig. 5B) composed of *c.* 15 irregularly arranged tubercles. Smaller cheliped pointed distally. P2–3 carpi and propodi (Fig. 26B–C) naked on anterior surface. P1–5 bases, carpi, and dactyli each bearing a distinct narrow red band along proximal margin. Go1 (Fig. 26D–E) broadly bulging, curved laterally in distal part, bearing distinct cone-like palp: terminal projection wider than long; sperm channel originating dorsally and running without torsion along distal curve to short terminal projection; last part of channel in median line of terminal projection; distal opening located in flat median concavity of distal margin. Operculum of female genital opening (Fig. 26F) strongly protruding anteromesially with rounded distal end; vaginal slit directed lengthwise, almost parallel to sternal median line; lateral rim well developed.

Juvenile specimens. In a small specimen (12.4× 15.1 mm, NHMW) stridulating ridge not distinguishable among tubercles around. In a slightly larger specimen with a carapace width of 17.5mm (SMF-9315) stridulating ridge not yet distinguishable either, however in a still larger specimen with a carapace width of 18.0 mm (SMF-6111) stridulating ridge distinguishable. P2–3 propodi naked on anterior surface, bearing sparse setae on dorsal margin.

Distribution. East coast of Africa from Abd El Kuri and South Somalia to Port Elizabeth (South Africa), Seychelles. Type locality: Natal.

Remarks. *O. ryderi* is common on the eastern to southern coasts of Africa. It was identified by earlier authors under such different names as *O. kuhlii*, *O. cordimanus*, or *O. urvilleii*, which turned out later, however, to be based upon misidentified specimens. Pfeffer (1889), Ortmann (1894, 1897), Lenz (1905, 910), Barnard (1950), *etc.* identified specimens from eastern to

southern Africa as *O. kuhlii* instead of *O. ryderi*. So *O. ryderi* had remained confused with *O. kuhlii*, until Sakai, K. & Türkay (1976) clarified that they were two species which are clearly separable by their individual distribution area. Specimens examined since 1976 have proven, as suggested by us in 1976, that it is only *O. ryderi* of the two species that occurs on the eastern to southern coasts of Africa (vs. *O. kuhlii* is known to be distributed only in Indonesia), and therefore, there is no doubt that their material from the eastern to southern coasts of Africa is conspecific with the type specimen of *O. ryderi*, which seems to have been lost (S.H. Fuller, *in litt.*).

O. urvilleii described by A. Milne-Edwards (1868) based on a specimen from among Grandidier's collection, has turned out to be identical with *O. ceratophthalma*, however the P3 and P5 that have been glued to the left side of the specimen are not those of *O. ceratophthalma*, but of *O. ryderi*, and this has caused confusion.

O. ryderi is easily distinguishable from all the other eastern to southern African species by the morphology of the stridulating ridge, the naked P2–3 propodi, and the structure of the Go1. Recognition in the field is easy because of the striking red band along the proximal margins of the P1–5 bases, carpi, and dactyli, which even persists in ethanol for many years.

Juvenile specimens of *O. ryderi* are characterised by the scanty setae on the pereiopods when compared with the sympatrically ocuuring *O. madagascariensis*, *O. ceratophthalma*, and *O. cordimanus*, which have dense setae on the legs.

Ocypode saratan (Forskål, 1775)

(Figs 5C, 27, 49)

Cancer saratan Forskål, 1775: 87.

Ocypode saratan — Olivier, 1811: 414, 416 [in part, Red Sea except Suez Canal]; Holthuis, 1958: 52; George & Knott, 1965: 19; Crosnier, 1965: 92, 95 [in part], figs 153, 161, 169–170, pl. 8, fig. 2, pl. 10, fig. 5; Linsenmair, 1967: 403–456; Serène, 1968: 97; Carli, 1969: 57, 62, 63–76; Lewinsohn, 1977: 48; Vannini & Valmori, 1981: 205, figs 1 B, 2 B1–2, 3 B, 4B; Eshky, 1985: 1–451; Eshky *et al.*, 1988: 341–358; Al-Waissa *et al.*, 1988: 106P; Al-Waissa *et al.*, 1989: 755–764; Whiteley *et al.*, 1990: 261–273; Eshky *et al.*, 1990: 237–248; Türkay *et al.*, 1996: 107, figs 9–10, pls 4–6; Clayton, 2001: 37–55; Ng *et al.*, 2008: 240.

Ocypode (*Ocypode*) *saratan* — De Haan, 1835: 29.

Ocypode Fabricii — White, 1847:35 .

Ocypode cursor — White, 1847: 35 [in part: only material from the Red Sea].

Ocypode aegyptiaca Gerstäcker, 1856: 134; Miers, 1878: 409; De Man, 1881: 247; Ortmann, 1894a: 762, 769; Laurie, 1915: 416, 467 [in part: not material from the Persian Gulf]; Balss, 1924: 14 [material from the Gulf of Aqaba but not the Red Sea]: 14 [in part: including *O. cordimanus* from Noman I.]; Ramadan, 1936: 37; Monod, 1937: 18 [in part]; Monod, 1938: 146 [in part]; Holthuis, 1956: 328; 1960: 316, figs 1–5, 8.

Ocypoda aegyptiaca — Heller, 1861a: 16; 1861b: 361; 1862: 292; Miers, 1882: 381, pl. 17, figs 3, 3a; Ortmann, 1897: 360, 366; Nobili, 1901a: 16; 1906b: 309, 310; Lenz, 1912: 4.

Ocypoda cordimana — Heller, 1861a: 17; 1861b: 361; 1862: 292.

Ocypoda cursor — Heller, 1861a: 17.

Ocypode ceratophthalma — Von Martens, 1866: 381; Kossmann, 1877: 55; Neumann, 1878: 26.

Ocypode ceratophthalma var. *Ceratophthalma-aegyptiaca* — Paul'son, 1875: 64.

Ocypoda ceratophthalma var. *aegyptiaca* — Kingsley, 1880: 180.

Ocypoda ceratophthalma — Nobili, 1906b: 310; Parenzan, 1931: 1001, fig. 1, pl. 14, figs 1–6, pl. 15, figs 7–8.

Ocypode aegypticus [sic.] — Serène, 1968: 97.

Material examined. Red Sea (no exact locality). Male, female (MNHN-3296); male (USNM-43333); male (ZMH-K2960); male, 4 juv. females (SMF-1935), Rüppell; female (SMF-6746), Rüppell; female (SMF-1961), Bannwarth; 1 juv. [vend. Kapt. Pöhl], female (MNHN-3295); 2 males (MNHN), 'Companie de l Isthme Suez'; male (MNHN), 'Calypso'; 1 specimen (MNHN-3281), Clot Bey; 2 specimens (NHN-3282), Clot Bey; 2 specimens (MNHN-3283), Beaudoin; male, female (RMNH-237); 5 males (NHMW); 2 juvs [18.7×21.7, 22.5×25.7 mm] (RMNH-D2720); — Sinai Peninsula, female (RMNH-17722); — *ibid.*, male (SMF-18277), W. Baumeister; — Gulf of Aqaba, male (NHM-78.25). **Egypt**. Gulf of Suez: No exact locality, 2 males, female, 1 juv. female (NHM-69.49) [det. Miers, 1882]; — El Bilaiyim, female (RMNH-SLR 2672); male (RMNH-SLR 2702); 6 males (RMNH-SLR 2891); 1 juv. female (RMNH-27748); female, 10 juvs. (RMNH-27228); — Et-Tur (28°14.07′N, 33°36.21′E), male [40.7×44.5 mm]; 3 females [42.0×46.8 – 36.0×40.1 mm] (SMF-9711), 1874-75, R. Kossmann; — Et-Tur, 2 males, 2 females (SMF-6747), 21.ix.1967, L. Fishelson; male (ZSF); male (RMNH-SLR 262); male, female (RMNH-1990); female (RMNH-SLR 2156); — At-Tur, Abu Galambo, 4 females (NRMS-t6012); — Kad el Hamden, 2 males (MNHN); — Mersa Tal Kad Yayah, 2 females (MNHN); — Umm el Kyaman, female (MNHN); — Shadwan Island, 2 males, female

(RMNH-21934); male, female (NHMW); — Gulf of Aqaba: Dahab, male, female (RMNH-29236); 1 juv. (NHMW), S.M.S. 'Pola'; — Abu Zabad, 40 km south of Dahab, male (RMNH-12169); female (RMNH-SLR 892); — Sharm el Sheikh, 1 juv. male, 1 juv. female (RMNH-12168); — Ras Muhammad, female (RMNH-SLR 728); male, female (RMNH-11930); — Red Sea coast: Al Ghardaqa (= Hurghada) (27°16.12´N, 33°48.09´E), 4 males, female (UZMK); male, 6 females (RMNH-SLR 2361); — *ibid.*, male (SMF-7154), vii.1965, E. Linsenmayr; — Ras Abu Soma, male (NHMW), S.M.S. 'Pola'; — Beach at *c.* 20 km South of Safaga (26°30´N, 34°05´E), sand bottom near mangrove, male (SMF-23036), 23.iv.1995, M. Apel; — Al-Qusayr (= Kosseir), many specimens (RMNH-17546); female, 2 juvs. (NHMW), S.M.S. 'Pola'; — Port Berenice (= Barnis), male (MNHW), S.M.S. 'Pola'; — Mersah Dhiba, 2 juv. males (NHMW), S.M.S. 'Pola'. **Sudan.** No specific locality, 1 specimen (NHM-1934.1.17.118); — Mersa Halaib, male, female (USNM-97952); 5 males, 6 females (NHMW), S.M.S. 'Pola'; — Port Sudan, female, 2 juvs. (NHM-1955.6.9.37). **Saudi Arabia.** Bir al Mashi, male, 1 juv. female (NHMW), S.M.S. 'Pola'; male, 5 juvs. (ZSM); — Sanafir-Island, 2 males (NHMW); — Mersah Duba, 2 juv. males (NHMW), S.M.S. 'Pola'; — Habban (26°44´N, 36°32´E), male (MNHW), S.M.S 'Pola'; — Jeddah, 3 males, 2 juv. females (RMNH-236); 2 juvs. (RMNH-2720); — 50 km South of Jeddah (21°00´N, 39°12´E), 3 males, 4 females, 10 juvs (SMF-23037), 1.iv.1995, M. Apel; — Shoiba Beach, 120 km South of Jeddah (20°48.71´N, 39°25.58´ E), male (SMF-10700), 21.viii.1982, W. John; — Farasan Islands, Sarso, 1 juv. (ZMH-K28635) 'Meteor-1 Expedition' 1964, W. Schäfer, W. Klausewitz *et al.*; 1 juv. male (SMF-5417). **Eritrea.** Difnen Island, 2 males, female (MCSNG); — Mitsiwa (= Massawa, Massaua), male, female (MNHN); 3 males, 4 females (MCSNG-136–142); male, female (MCSNG-147); 2 males (MZT-1108); female (MZT-1111); — Massawa, Adbelkader Peninsula, 2 males, 3 females (MZT-1106); — Shēk Seyd (= Sheikh Sa'id I. = Green I.) near Massawa, 1 juv. male, 1 juv. (RMNH-26863); female (MZT-1101); — Dahlak Archipelago: Shumma-Island, female (MCSNG-147); — Madote Island, male, 3 females (MCSNG); — Dissei Island, Dahlak Achipelago, 3 males (MCSNG-147); — Entedebir Island near W coast of Dahlak Kebir, male, 2 females (RMNH-17822), male, 1 juv. male, 1 juv. female (RMNH-25846); — Cundabilu I. *c.* 2 km West of Entebebir Island, male (RMNH-24767); — Museri Island near SE point of Dahlak Kebir, 1 juv. male, 2 juv. females (RMNH-25847); 2 females (RMNH-25847); 2 females (RMNH-25849); — Seil Anbar Island, E of Museri, male (RMNH-25848). — Assab (= Aseb), 2 males (MNHN), 1 juv. (RMNH-26864); 2 juv. males, 4 juv. females, 1 juv. (RMNH-25846); 3 males (RMNH-25566). **Yemen.** Red Sea: Kamaran Island, 2 males (NHMW), S.M.S. 'Pola'; — Jazirat Zabarjad (= Zebayir Island), female (MNHW), S.M.S. 'Pola'; — Gulf of Aden: Aden, female (USNM-19040); female (USNM-43295); 2 males, 3 females (MNHN); 1 juv. male (RMNH-15504); 3 juvs. (RMNH-15505); male, female (RMNH-15506); 2 juvs. (NHMW); female (MCSNG-143); male, 3 juvs. (MCSNG); — Al-Mukalla, male, 1 juv. female (NHM-1894.10.31.13); female (MNHN); — Suqutra (= Socotra), male, 3 females (NHM-1906.5.18–22); — Suqutra (= Socotra), Soc/It-157a (12°18.698´N, 53°48.285´E) –(12°18.698´N, 53°48.285´E), sandy beach, male cheliped (SMF-36171), 9.iv.199, M. Apel. **Republic of Djibouti.** Ras Siyahn (12°28.59´N, 43°18.89´E), Mangrove, Lagoon, 4 males, female, 1 juv. (SMF-24495), 24.vi.1996, U. Zajonz & F. Krupp; — Godoriyah (12°9.97´N, 43°24.73´E), behind northern Mangrove, male (SMF-24499), 2 juv. males (MZUT-1097); male, 5 juvs. (MNHN), 24.vi.1996, U. Zajonz & F. Krupp; — Gulf of Tadjoura, Obock, Tadjoura, male (MNHN); — Djibouti, male, 2 juvs. (MNHN); male (MNHN). **Somalia.** Berbera, male (ZMK-1540); — Kasim, male, 4 females (MCSNM-2155). **Oman.** Gulf of Masirah, peninsula Barr Al-Hikman, Khawr Al-Milh, southern part (20°23´N, 58°17´E), male (SMF-24539), 31.v.1995, D. Clayton; 1 damaged female (SMF-24540).

Diagnosis. Middle- to large-sized species. Eyestalks prolonged distally beyond cornea in a long slender stylus. Exorbital angles slightly protruding forward. Stridulating ridge composed of 67–87 fine striae. Smaller cheliped pointed distally. P2 propodus with a broad median row of setae on anterior surface. P3 propodus naked. Go1 distinctly curved laterally at bulging distal end, bearing a distinct palp at base of distal curve; terminal projection wider than long. Operculum of female geital opening rounded distally and protruding mesially; vaginal slit directed anteromesially.

Description. Carapace (Fig. 49) wider than long; densely beset with fine tubercles, becoming larger towards sides of carapace. Lateral half of orbital margin directed obliquely backward. Exorbital angles slightly protruding forward as a small pointed tip. Lateral margins of carapace directed distinctly outwards from base of exorbital angle in anterior third of carapace, and then directed inwards in posterior two-thirds, so that carapace broadest at anterior third. Pterygostomial region distinctly tuberculate except around buccal cavern. P1 thoracic sternite (Fig. 27A) smooth on surface and triangular at anterolateral corner, bearing tuberculate carina on lateral margin. Palm of larger cheliped broad, densely beset with fine tubercles on

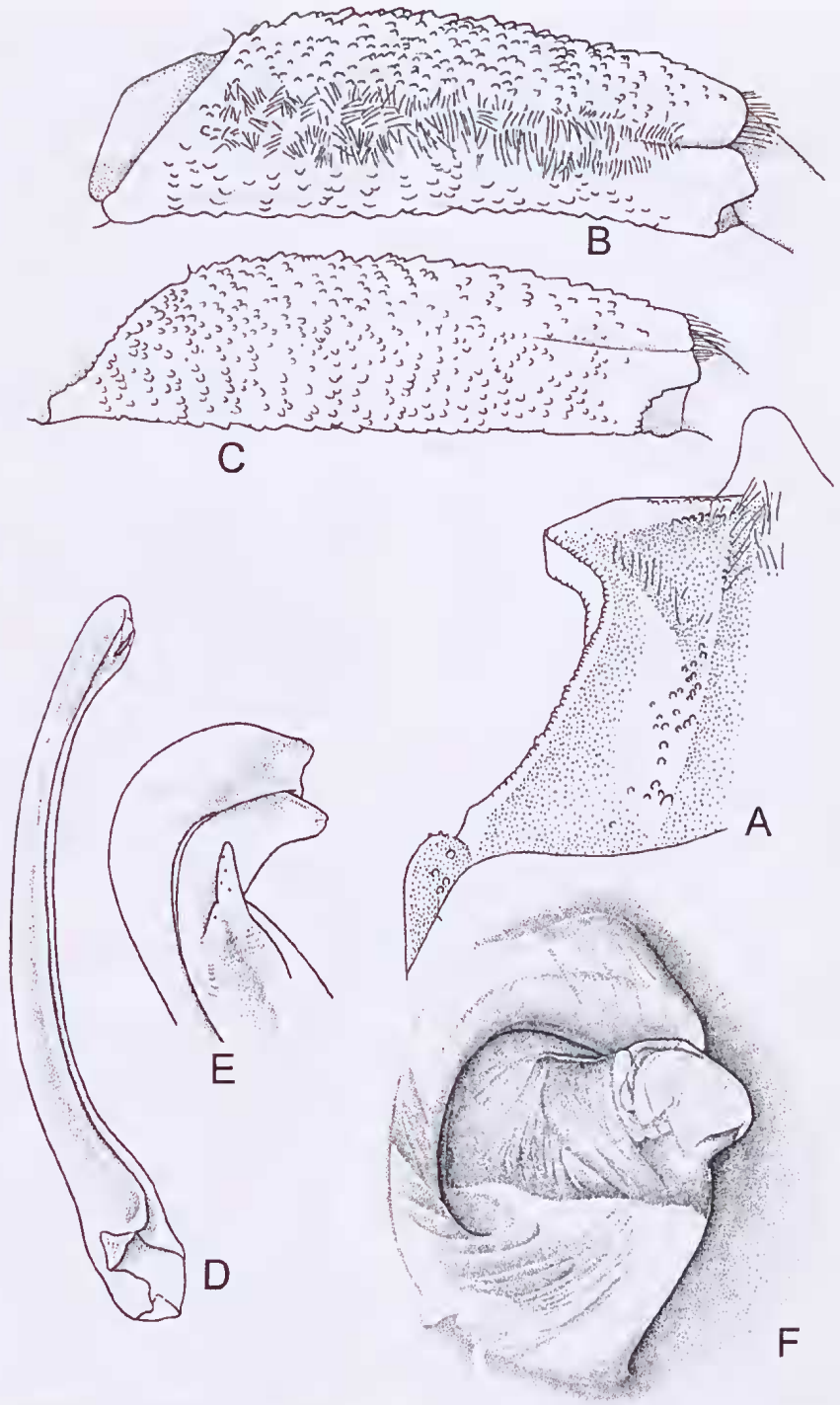

FIG. 27. *Ocypode saratan*: **A**, P1 thoracic sternite; **B**, **C**, P2–3 propodi; **D**, **E**, Go1; **F**, female operculum.

anterior surface. Stridulating ridge (Fig. 5C) composed of 67–87 fine striae. Smaller cheliped pointed distally. P2 propodus (Fig. 27B) with broad median row of setae on anterior surface. P3 propodus (Fig. 27C) naked. Go1 (Fig. 27D–E) three-sided proximally, distinctly curved laterally at bulging distal end, bearing palp with slenderly triangular distal half at base of distal curve. Operculum of female genital opening (Fig. 27F) protruding mesially in globular shape; mesial part of rim distinct.

Juvenile specimens. In a small specimen (5.7×6.3 mm, RMNH-15505) eyestalks not yet prolonged distally beyond cornea. Exorbital angles broadly triangular, located far backward, and slightly protruding forward. Carapace quadrate. Stridulating ridge not yet developed, but low elevation already present. P2–3 propodi with scanty spinules on dorsal margin and yellowish short distal setae at distal end, bearing (only in P2 propodus) a median row of scanty setae on anterior surface. In a larger specimen (18.7×21.7 mm, RMNH-D2720) eyestalks not yet prolonged distally beyond cornea, but slightly protruding at distal end of cornea. In a still larger specimen (22.5×25.7 mm, RMNH-D2720) eyestalks prolonged distally beyond cornea in a small stylus. In those larger specimens lateral margins of carapace curved outwards from base of exorbital angle. P2–3 propodi naked on dorsal margin, but yellowish short setae at distal end, bearing (only in P2 propodus) a median row of scanty setae on anterior surface. Stridulating ridge already composed of more than 50 fine striae.

Distribution. All coasts of the Red Sea, African coast of the Gulf of Aden and northeastern coast of Somalia up to Bedei, southern Arabian coast to southern Oman. Type locality: the Red Sea, but without specific locality.

Remarks. *Ocypode saratan* is common on the coast of the Red Sea and on the African coast of the Gulf of Aden. Another species *O. cordimanus* is also found, though rarely, in the Red Sea. Earlier records of some species, especially of *O. ceratophthalma* have turned out to be incorrect, and those records can be considered to be based upon mis-identified specimens, especially of juveniles. Juvenile specimens reported by Von Martens (1866), Kossmann (1877), Neumann (1878), Kingsley (1880), Nobili (1906) and Parenzan (1931) have all been re-examined and found to be *O. saratan*. Monod (1937, 1938) identified specimens from the Suez Canal as *O. aegyptica*, and this was later cited by Holthuis (1956). However, the reexamination of Monod's specimens shows them to be all *O. saratan*, except one, which we identified as *O. cursor*. A good number of records of *O. saratan* from areas outside the Red Sea and the African coast of the Gulf of Aden exist in the literature. Hoffmann (1874) reported *O. saratan* from Madagascar, and was followed by Miers (1878), Ortmann (1894, 1897), and Nobili (1906). Lipke Holthuis examined Hoffmann's material at our request, and determined it to be *O. ceratophthalma* as suggested by Crosnier (1965). The reports of *O. aegyptiaca* (= *O. saratan*) by Laurie (1915) and Stephensen (1945) based on the material from the Persian Gulf, have turned out to be incorrect, because their material is clearly identifiable as *O. rotundata*. We have also reidentified *O. aegyptiaca* (= *O. saratan*) reported by Balss (1935) from Shark Bay, Western Australia as *O. fabricii*.

Ocypode stimpsoni Ortmann, 1897

(Figs 5D, 28, 50)

Ocypode (*Ocypode*) *cordimana* — De Haan, 1835: 57–58, pl. 15, fig. 4.

Ocypode convexa Stimpson, 1858: 100; 1907: 110, pl. 15, fig. 2 [Junior homonym of *Ocypode convexa* Quoy & Gaimard, 1824]; Ortmann, 1894a: 769, pl. 23, fig. 21.

Ocypoda stimpsoni Ortmann, 1897: 367–368 [Nomen nudum for *Ocypode convexa* Stimpson, 1858. – type locality therefore: Japan, Shimoda]; Sakai, T. 1934: 319; 1935a: 211, pl. 58, fig. 4; 1947: 664, fig. 1915; 1939: 613, pl. 104, fig. 1; 1940: 50; 1956: 53; 1965: 189, pl. 90, fig. 1; Kamita, 1936a: 318; 1936b: 33; Horikawa, 1940: 28; Shen, 1940: 91; Kamita, 1941a: 241; 1941b: 80; 1941c: 154; Lin, 1949: 26; Kim, 1958: 11; 1962: 53; 1970: 18; Ono, 1959: 146; Kikuchi, 1959: 51; Park, 1964: 17; Kim & Rho, 1971: 13; Muraoka, 1974: 48–51, tab. 1, figs 1–2.

Ocypode macrocera, Urita, 1917: 72.

Ocypoda stimpsonii — Balss, 1922a, 88A (11): 142.

Ocypode stimpsoni — Urita, 1926a: 435; 1926b: 27; Shen, 1932: 268–272, figs 164, 166, pl. 9, fig. 3; 1937b: 309; Sakai, T., 1935b: 72; 1976: 599–600, fig. 327a, pl. 206, fig. 3; Shen, 1936: 76; 1937: 184; Miyake *et al.*, 1962: 130; Inaba, 1963: 170; 1988: 102; Utinomi, 1976: 89, pl. 45, fig. 5; Kim, 1977: 206; Miyake & Takeda, 1978: 43; Dörjes, 1978: 121;

Terada, 1979: 58, 60–62, 68, 69, figs 1–2; Fukuda, 1980: 1–8, figs 1–3; Yang, 1986: 153; Dai & Yang, 1991: 454, text-fig. 230, pl. 58 (2); Gamo & Kosakai, 1991: 27, 30, fig. 1; Huang *et al.*, 1992: 144, fig. 3, pl. 1C, tab. 1; Wang *et al.*, 1998: 65, figs 53–59; Kitaura *et al.*, 1998: 627, 628, 630, 632, 633; Ng *et al.*, 2001: 36; Imafuku, Habu & Nakajima, 2001: 197–211, tabs 1–3, figs 1–5; Marumura, & Kosaka, 2003: 69; Yodo *et al.*, 2006: 2–3, figs 2–4; Mano *et al.*, 2008: 2, 5–8, figs 2–8; Ng *et al.*, 2008: 240; Wada, 2009: 1–7, figs 1–3.

Ocypoda cordimana Desmarest, Nakazawa, 1927: 1124, fig. 2166 (misidentified)

Material examined. China. Unknown locality (NHM-1935.3.19.8); — Shandong Prov.: Shandong Peninsula, female (MCSNM); — Qingdao, 5 females (ZSM-128/1); — Qingdao, Xuejidao, sandy beach (35°58.54′N, 120°17.68′E), 8 males, 4 females (SMF-18283), 22.viii.1987, M.Türkay & Y.-L. Wang; — Suzhou, 1 juv. (USNM-168468); — Shanghai: Beidaihe District, Gulf of Liaotung, male, 3 females, 1 juv. (USNM-55712); 1 juv. female (USNM-50469); — Fujian Province: Fuzhou, 7 males, 5 females, 3 juv. males, 6 juv. females (ZMH-K2869); 18 males, 11 females, 3 juvs., 2 carapaces (ZMH-K2874); 3 males, 5 females (ZMH, K2887); — Xiamen, male (UZMK); female (RMNH-228); female (RMNH-2007); male (MNHN); — Taiwan: No exact locality, 5 males (SMF-8808); — East coast, no exact locality, 4 males, 5 females (SMF-10674). **Japan.** No exact locality, male (RMNH-227); — Akita Prefecture: Oga (39°52.09′N, 139°49.71′E), 2 juvs. (SMF-36199), T. Sakai; — Niigata Pref.: Sado-Island, Mano Bay, Kawaharada (38°0.1′N, 138°18.87′E), male, female (SMF-36196)[ex. coll. T. Sakai], 24.x.1924; — Tokyo Pref.: Tokyo Bay, 3 specimens (MNHN); — Kanagawa Pref.: Sagami Bay, 2 males, 2 females (SMF-6752); — Enoshima, Sagami Bay, female (NHRMST-6531); — Shizuoka Pref.: Suruga Bay, male (MCSNM); — Hamana-ko, beach (34°40.62′N, 137°36.78′E), 5 males (SMF-36198), T. Sugano; — Tokushima Pref.: Tokushima, Yoshino-gawa, 2 males [21.5×24.3, 20.8×23.1 mm] (SMF-36211), 19.vii.1990, S. Shinomiya, K. Sakai & Yoshida; — Tokushima Pref., Okinosu, Yoshino-gawa, male (SMF-36197) [det. K. Sakai, 1993]; — Kochi Pref.: Toyo-cho, Ikumi (33°31.73′N, 134°17.06′E), female (SMF-37066), 7.vii.1986, K. Matsuzawa; male, 1 juv.; — *ibid.*, male, 1 juv. (SMF-37067), 8.viii.1985; — *ibid.*, 1 juv. (SMF-37068), 23.ix.1986; — Toyo-cho, Noné (33°30.12′N, 134°16.15′E), 4 males, 1 juv. female (SMF-37062), 10.x.1989, K. Matsuzawa; — *ibid.*, male (SMF-37063), 4.xi.1989; — *ibid.*, 3 juv. males (SMF-37064), 24.ix.1984; — *ibid.*, 1 juv. male, 1 juv. female (SMF-37065), 2.xi.1989; — Kochi City, Kagamigawa estuary (33°30.44′N, 133°34.44′E), 2 males, female (SMF-37061), 6.ix.1987, K. Matsuzawa; — Tosa Bay, Tosa city, Usa-Inoshiri (33°26.34′N, 133°26.5′E), inlet-beach, 5 males, 3 females (SMF-6843); — Uranouchi Inlet, South-West area, Nakanoura (33°24.47′N, 133°21.66′E), sandy beach, male (SMF-16610), 24.x.1979, M. & H. Türkay & K. Sakai; — Susaki-city, Awa (33°21.97′N, 133°15.54′E), female (SMF-37069), 9.viii.1989, K. Matsuzawa; — Ohgata-cho, Irino, Matsubara (33°1.19′N, 133° 0.88′E), 5 males [26.4×31.0–18.6×20.9 mm], 3 females [23.7×27.4–24.4×27.4 mm], 5 juvs. (SMF-36210), 6.viii.1994, T. Shimeno; — *ibid.*, 1 juv. female, 1 juv. (SMF-37070), 28.viii.1988, K. Matsuzawa; — Kumamoto Pref.: Amakusa I., Beach near Ushibuka (32°10.79′N, 130°1.14′E), 4.ix.1989, T. Yamaguchi; — Kagoshima Pref.: Kagoshima, male (USNM-48365); female (USNM-48328); — Beach north of Tarumizu at river mouth in the northern part of port (31°29.85′N, 130°41.98′E), male (SMF- 16611), 2.xi.1979, H. & M. Türkay & K. Sakai.

Diagnosis. Small-sized species. Eyestalks not prolonged distally beyond cornea. Exorbital angles acutely triangular, directed anterolaterally, located slightly backward. Stridulating ridges composed of 44–57 narrow striae, extending ventrally over mid line of fixed finger. Smaller cheliped broadly rounded to truncate distally. P2–3 propodi with median row of setae on anterior surface. Go1 slightly narrowing distally, curved laterally in flattened distal part. Operculum of female genital opening rounded distally, protruding mesially; rim undeveloped.

Description. Carapace (Fig. 50) slightly wider than long, and densely beset with fine tubercles on dorsal surface. Lateral half of orbital margin concave. Exorbital angles acutely triangular, directed anterolaterally, their tips posterior to median convexity of orbital margin. Lateral margins of carapace directed slightly outwards from base of exorbital angle in anterior third of carapace, then directed inwards in posterior two-thirds, forming broadly rounded, less protruding epibranchial corner, where carapace broadest. Pterygostomial region spacious, weakly tuberculate except along lateral sides of buccal cavern. P1 thoracic sternite (Fig. 28A) smooth, hemmed with tuberculate carinae on anterior and lateral margins, bearing shallow concavity at triangular anterolateral corner. Palm of larger cheliped broad, beset densely with fine tubercles on anterior surface, regularly serrated on ventral margin. Stridulating ridge (Fig. 5D) composed of 44–57 narrow striae, reaching (in most females) or overreaching (in very few females) mid-line of fixed finger, or extending (in males) to near ventral margin of palm. Smaller cheliped broadly rounded to

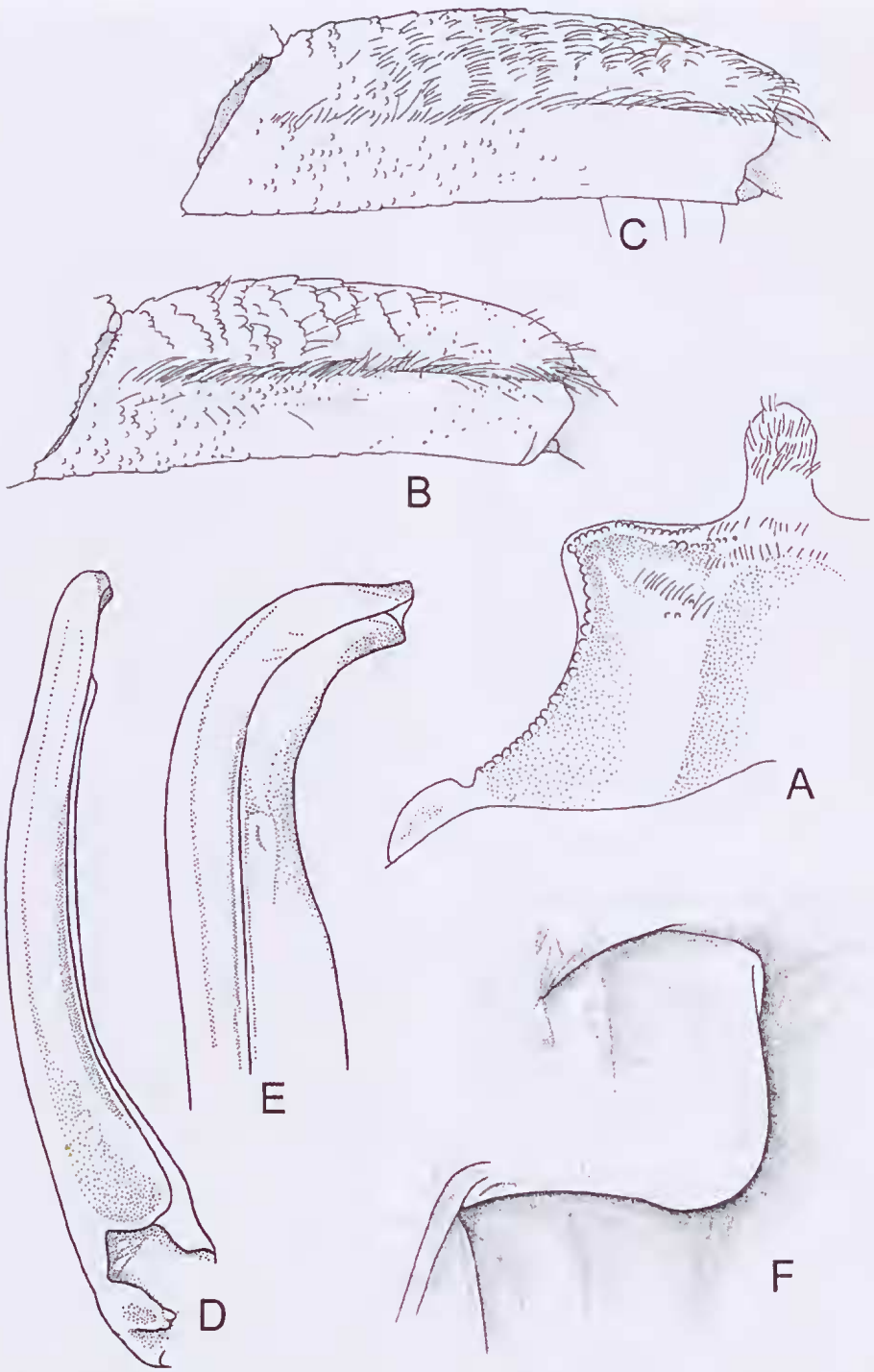

FIG. 28. *Ocypode stimpsoni*: **A,** P1 thoracic sternite; **B, C,** P2–3 propodi; **D, E,** Go1; **F,** female operculum.

truncate distally. P2 propodus (Fig. 28B) with median row of thick setae on anterior surface. P3 propodus (Fig. 28C) with transverse rows of setae on dorsal half of anterior surface, bearing a median row of setae. Go1 (Fig. 28D–E) slightly narrowing distally, curved laterally in flattened distal part, bearing small palp distant from distal end; groove originating dorsally, running along curved stem without torsion to flattened distal part; sperm-channel in middle line of stem. Operculum of female genital opening (Fig. 28F) rounded distally and protruding mesially in button-shape; rim undeveloped; entrance of vaginal slit sunken, forming deep funnel.

Juvenile specimens. In a small specimen (5.3×6.2 mm, USNM-168468) carapace wider than long, sparsely beset with granules on dorsal surface. Stridulating ridges distinctly developed, composed of striae, becoming finer and curved in S-shape in ventral part. P2 propodus with a median row of interspaced scanty setae on anterior surface. In a larger specimen (9.0×11.0 mm, ZMH-K2869) carapace densely tuberculate on dorsal surface. Stridulating ridge developed as distinctly as in adult specimens. Smaller cheliped pointed distally. In specimens with a carapace width of less than 17 mm, smaller cheliped always pointed distally, but gradually transformed into rounded to truncate adult shape in accordance with growth. In specimens with a carapace breadth of 19 mm, smaller cheliped already beginning to develop into characteristic adult shape, and in specimens with a carapace width of more than 20 mm, smaller cheliped in characteristic adult shape.

Distribution. China, Korea, and Japan. Type locality: Shimoda, Japan.

Remarks. This species was first reported from Japan by De Haan (1835) under the name of *Ocypode (Ocypode) cordimana*, but due to his precise figures, later authors quickly realised that his specimen did not belong to *O. cordimanus* Latreille, 1818. McLeay (1838: 64) stated: '*O. cordimana* of De Haan appears to be a different species', and Kraus (1843: 41) also noticed the peculiarity of De Haan's specimen, though he remarked more reservedly that the figures probably represented a juvenile specimen. White (1847: 34) stated very clearly that 'De Haan's material does not belong to *O. cordimana*.' Stimpson (1858) finally described it as a new species, *Ocypode convexa*, but Ortmann (1897) realised this was a junior homonym of *Ocypode convexa*, Quoy & Gaimard, 1824, and proposed the replacement name *Ocypode stimpsoni* Ortmann, 1897.

Ocypode stimpsoni seems most similar to *O. mortoni*, but the differences between them have already been enumerated under the remarks to *O. mortoni*. Juvenile *O. stimpsoni* are liable to be confused with the sympatric species *O. ceratophthalma* and *O. cordimanus*, however, they are easily identified by their stridulating ridges. *Ocypode stimpsoni* already has its distinctive stridulating ridge of fine striae fully developed from a carapace width as little as 10 mm, whereas in *O. ceratophthalma* of the same size the stridulating ridge is composed of irregularly arranged tubercles, and in *O. cordimanus* it is absent.

Urita (1917: 72) reported *O. macrocera* from Kagoshima, Japan, but his figures of the carapace and the stridulating ridge clearly indicate his specimens are identical with *O. stimpsoni*. Baksi *et al.* (1980) also recorded *O. stimpsoni* from India, where it definitely does not occur, and we suspect that his specimens belong to *O. macrocera*, a species that resembles *O. stimpsoni* in the shape of the smaller chela.

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Many individuals have helped us over the years to complete the study. We would like to thank especially Dr. Daniele Guinot of the Museum national d'Histoire naturelle, Paris,

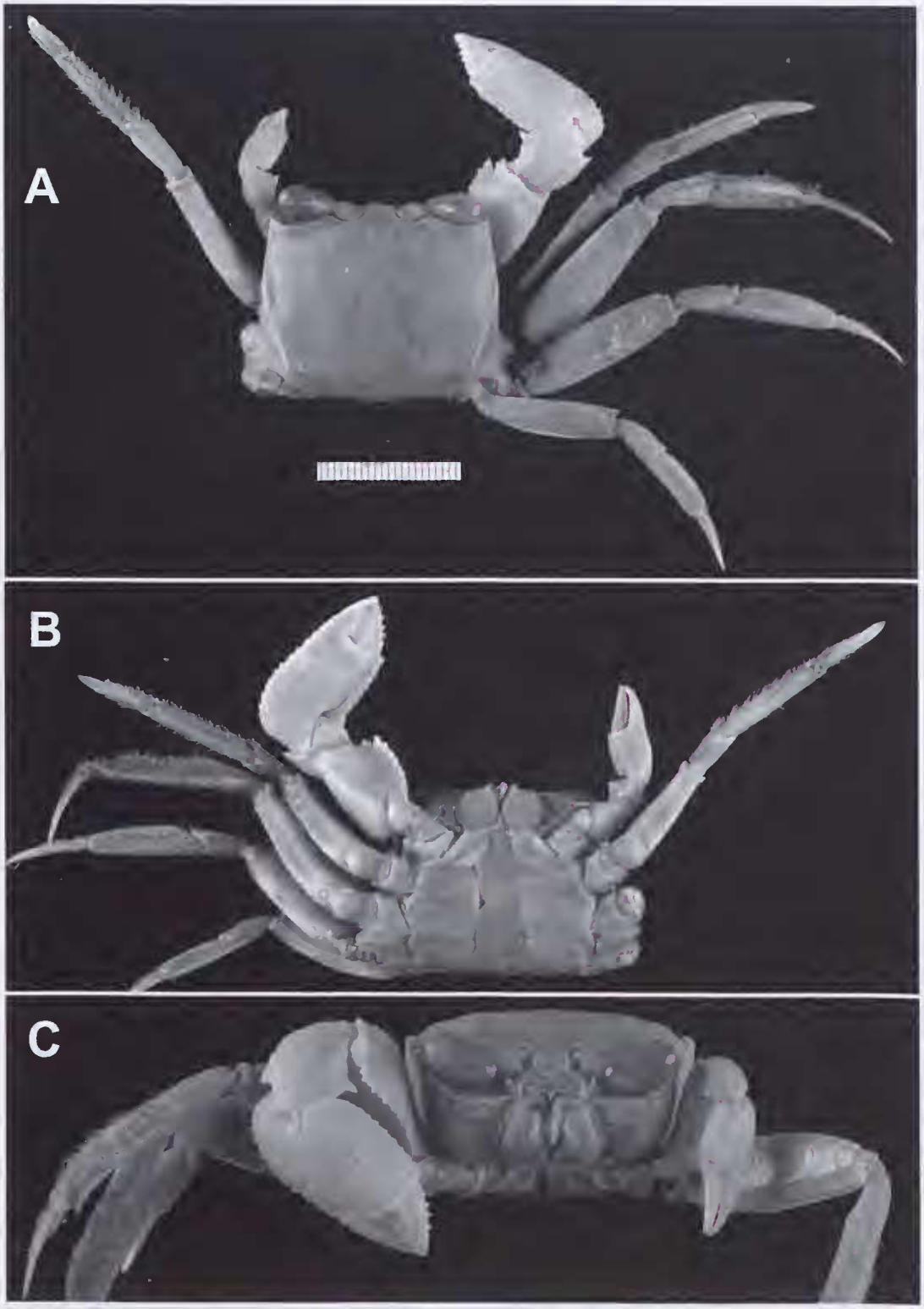

FIG. 29. *Hoplocypode occidentalis* (SMF-4104); dorsal, ventral and frontal aspects.

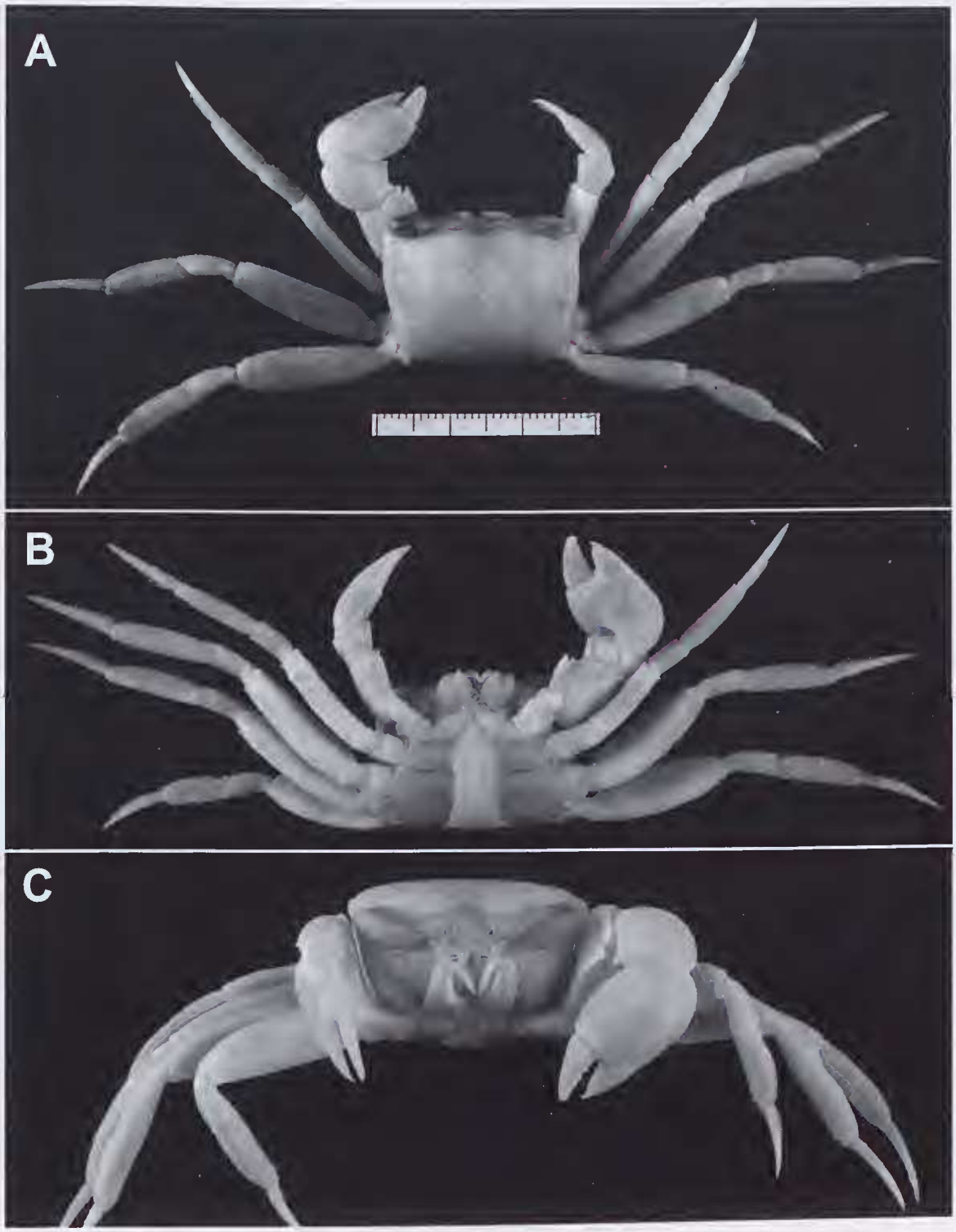

FIG. 30. *Ocypode africana* (SMF-1960); dorsal, ventral and frontal aspects.

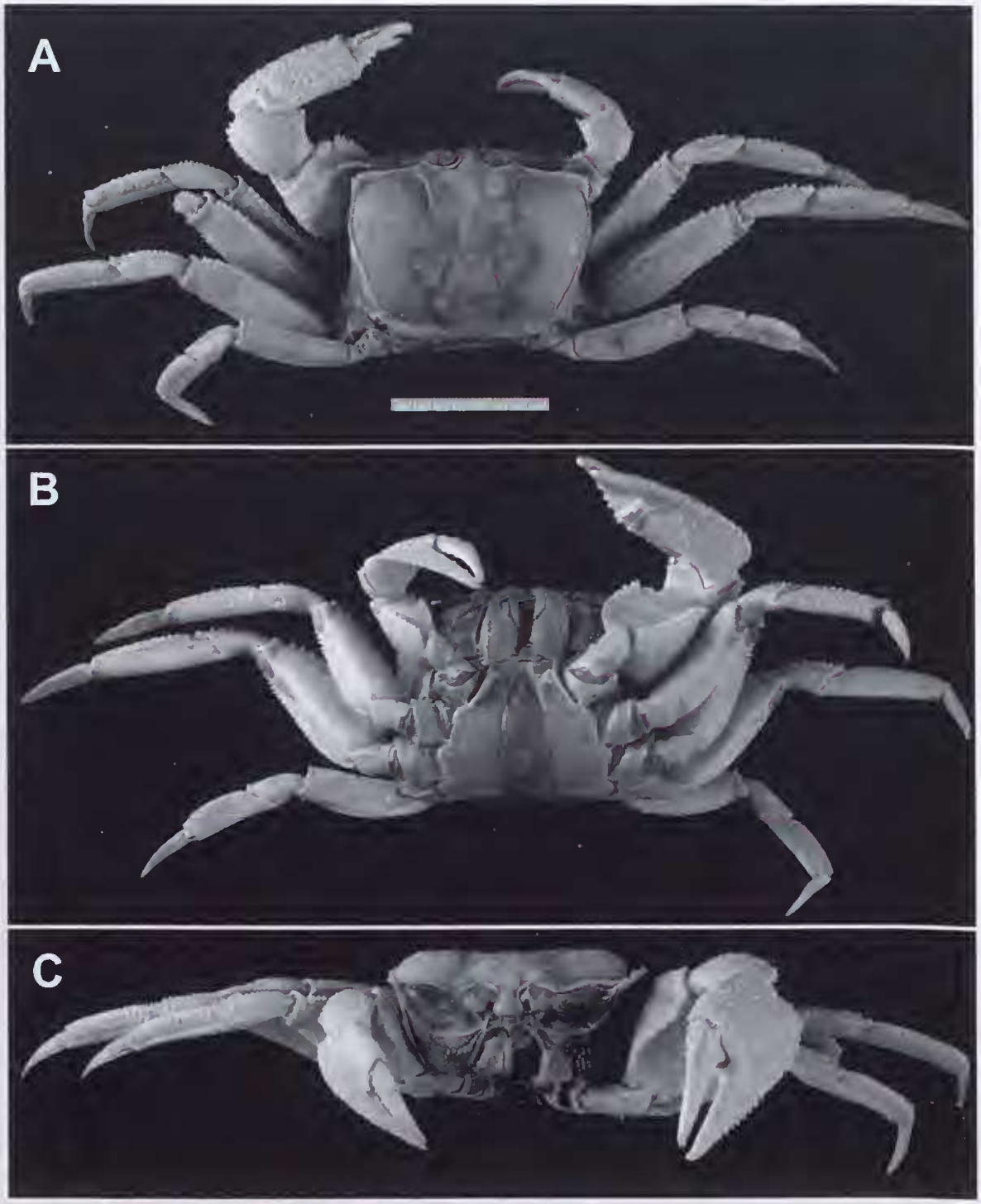

FIG. 31. *Ocypode brevicornis* (SMF-24536); dorsal, ventral and frontal aspects.

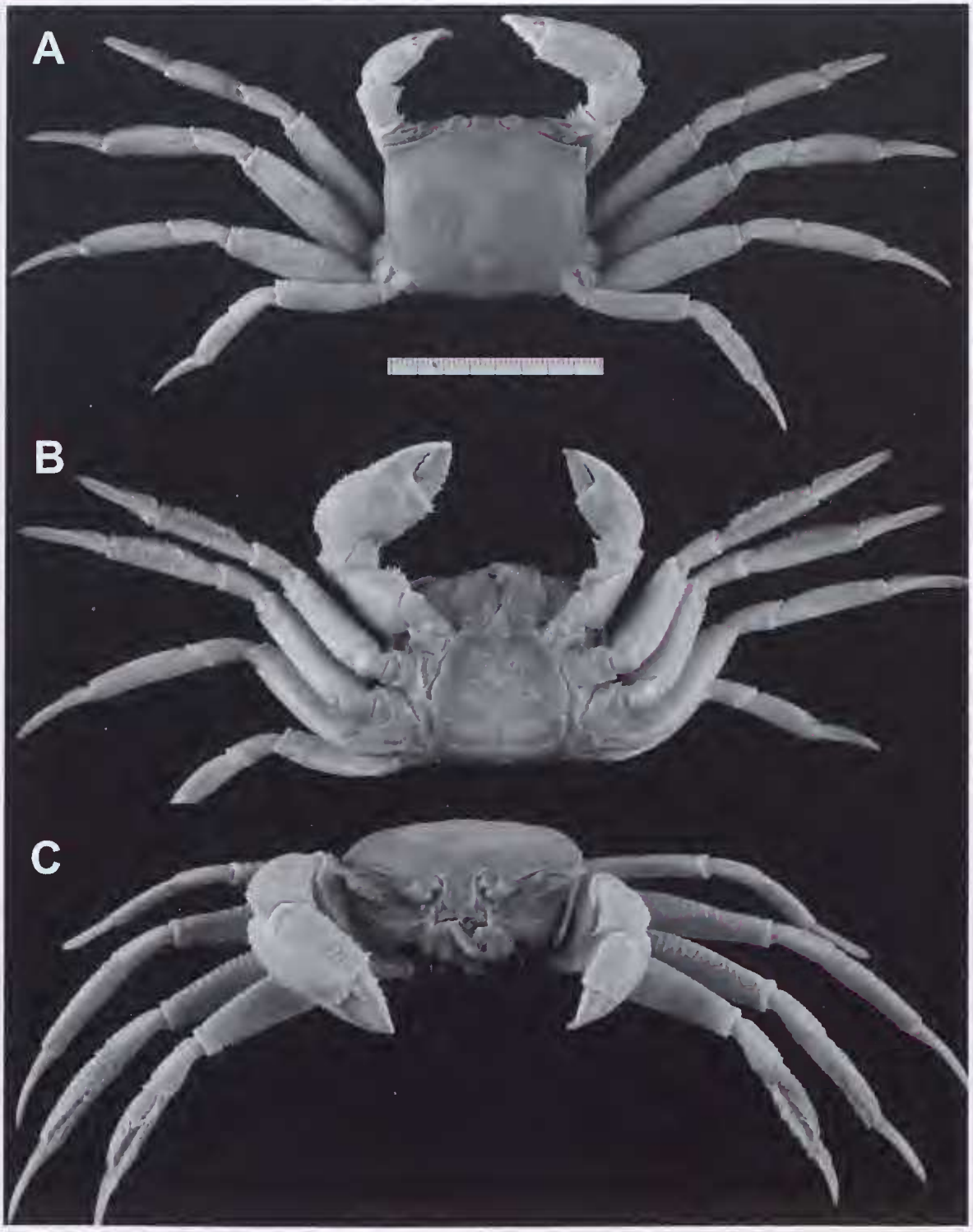

FIG. 32. *Ocypode ceratophthalma* (ZMG-124); dorsal, ventral and frontal aspects.

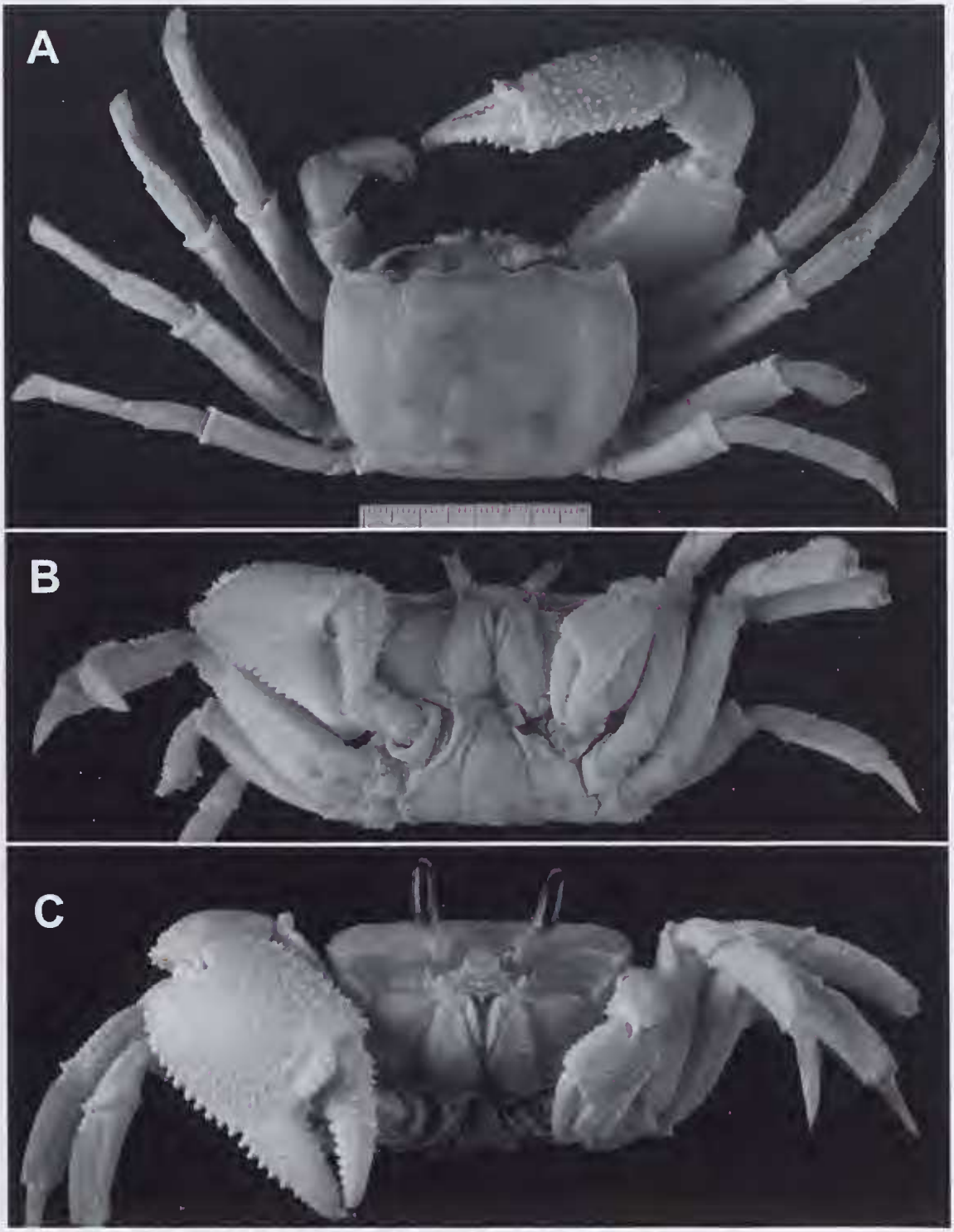

FIG. 33. *Ocypode convexa* (SMF-7609); dorsal, ventral and frontal aspects.

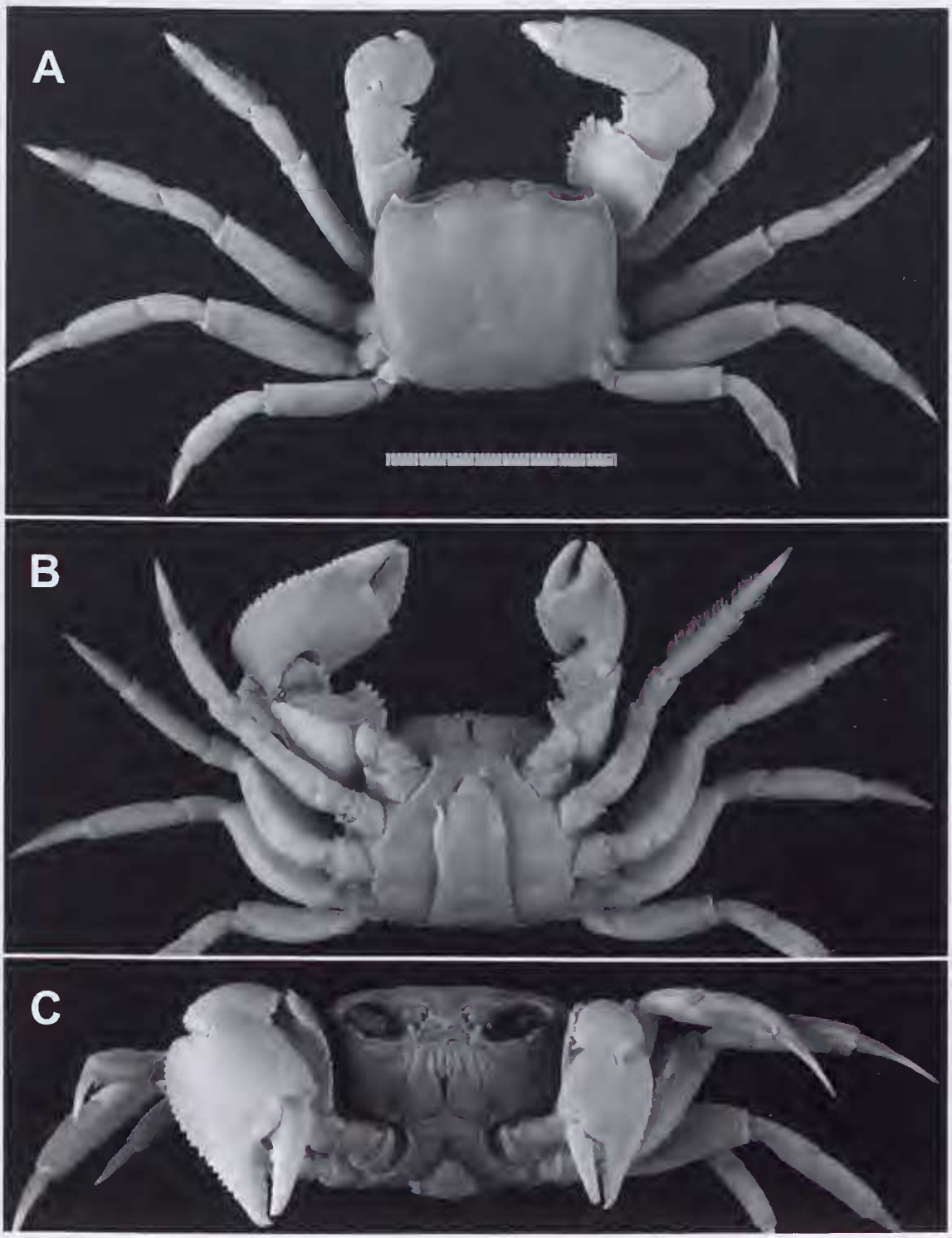

FIG. 34. *Ocypode cordimanus* (SMF-9983); dorsal, ventral and frontal aspects.

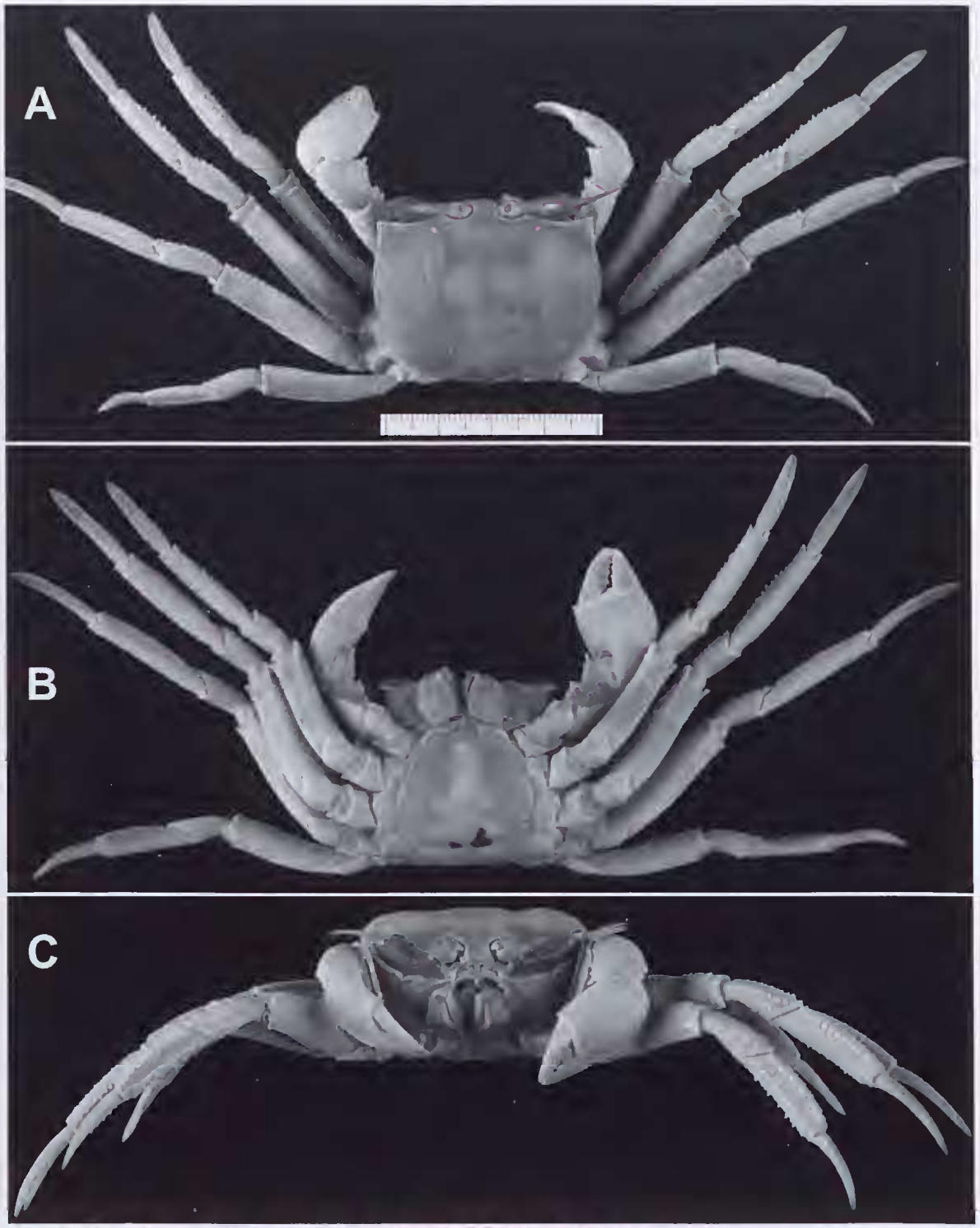

FIG. 35. *Ocypode cursor* (SMF-12165); dorsal, ventral and frontal aspects.

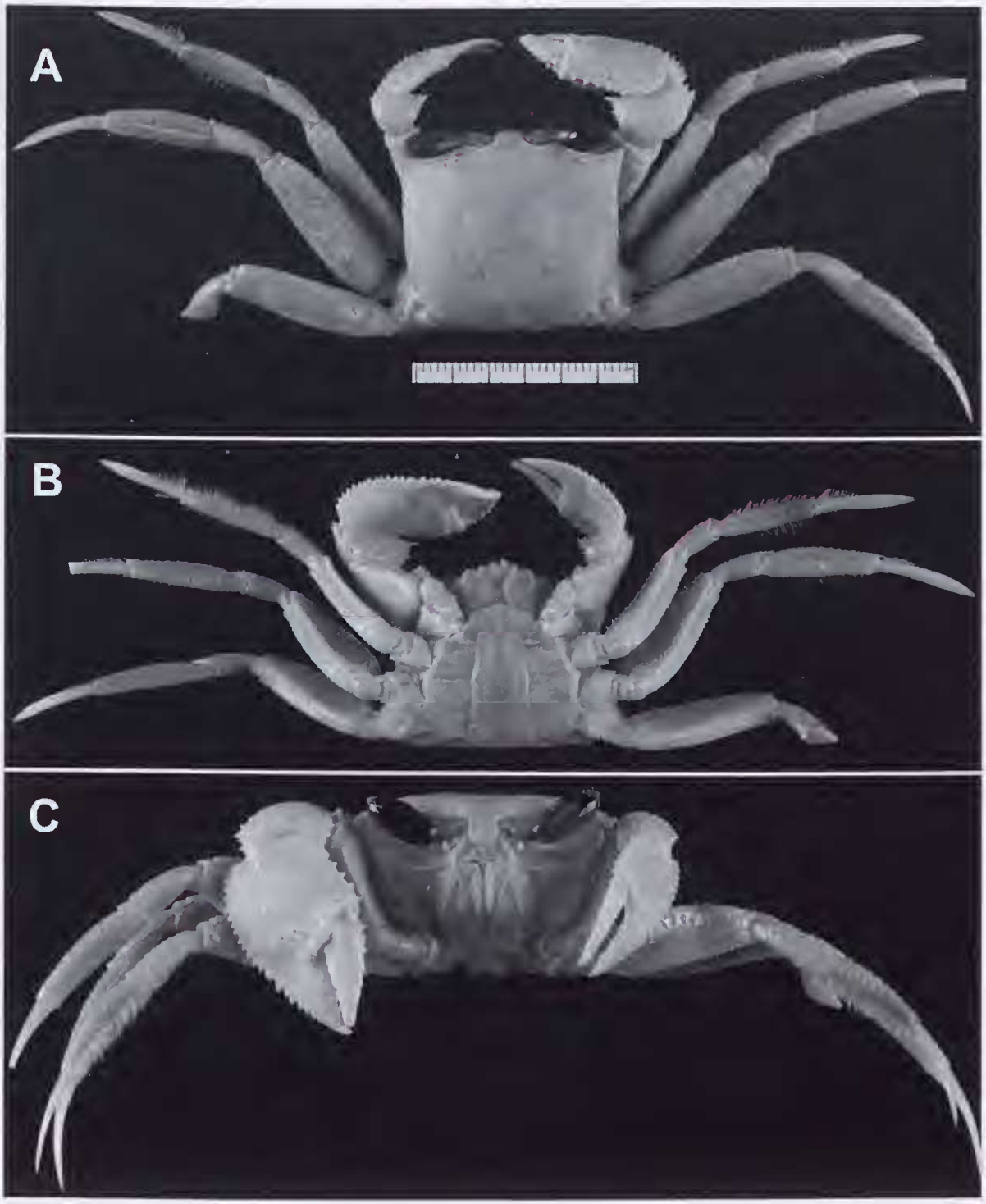

FIG. 36. *Ocypode fabricii* (SMF-10328); dorsal, ventral and frontal aspects.

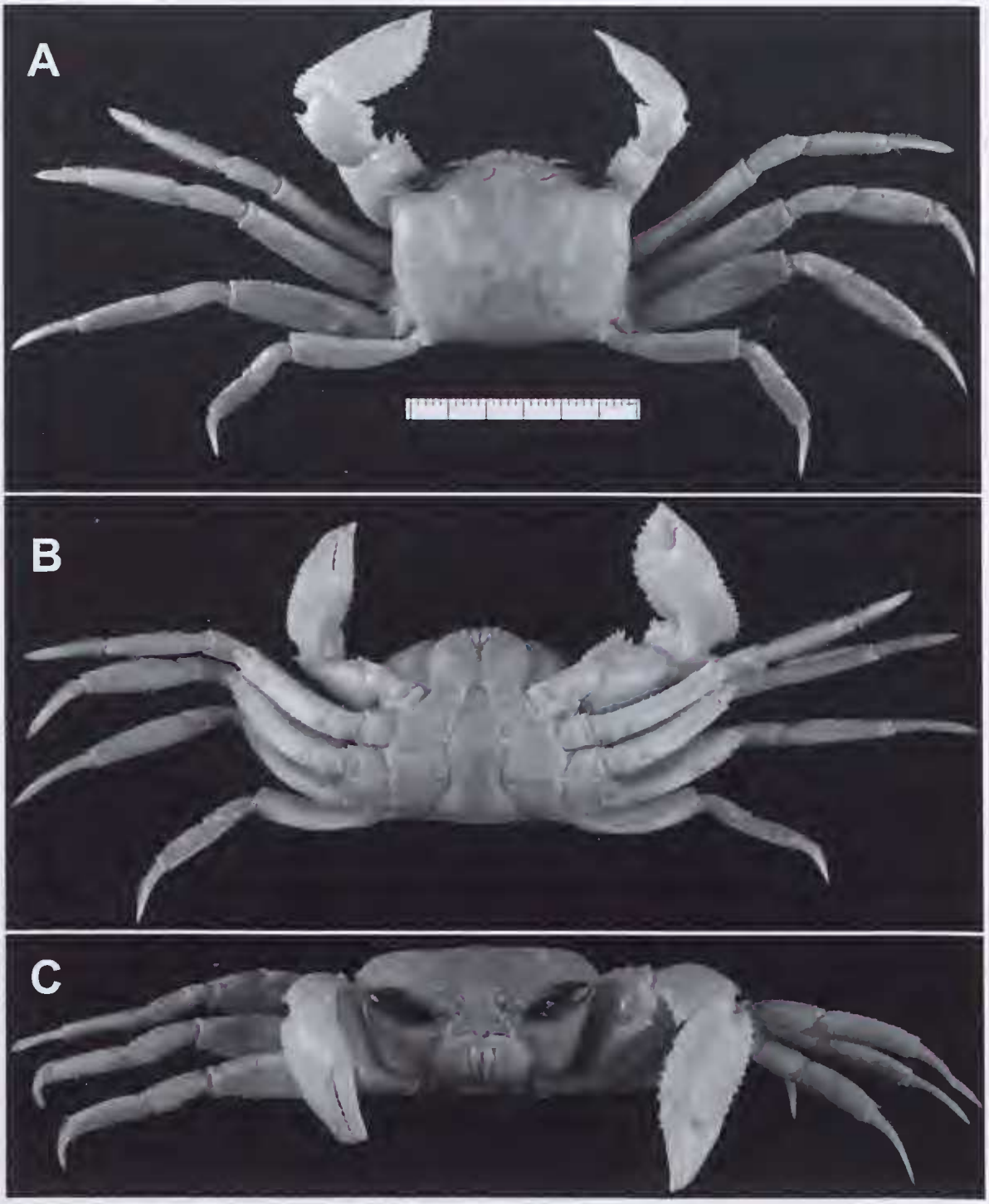

FIG. 37. *Ocypode gaudichaudii* (SMF-18684); dorsal, ventral and frontal aspects.

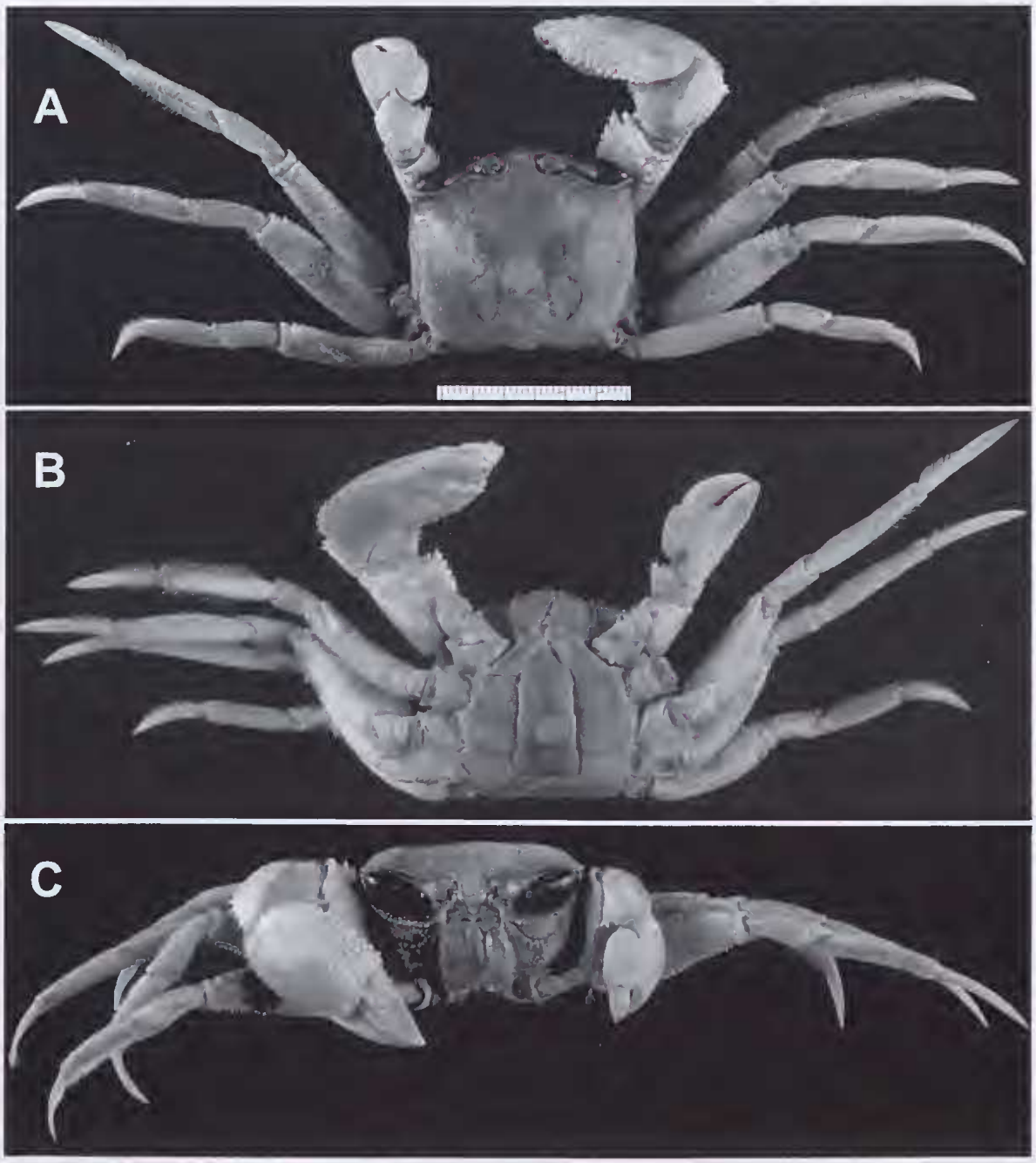

FIG. 38. *Ocypode jousseaumei* (SMF-24530); dorsal, ventral and frontal aspects.

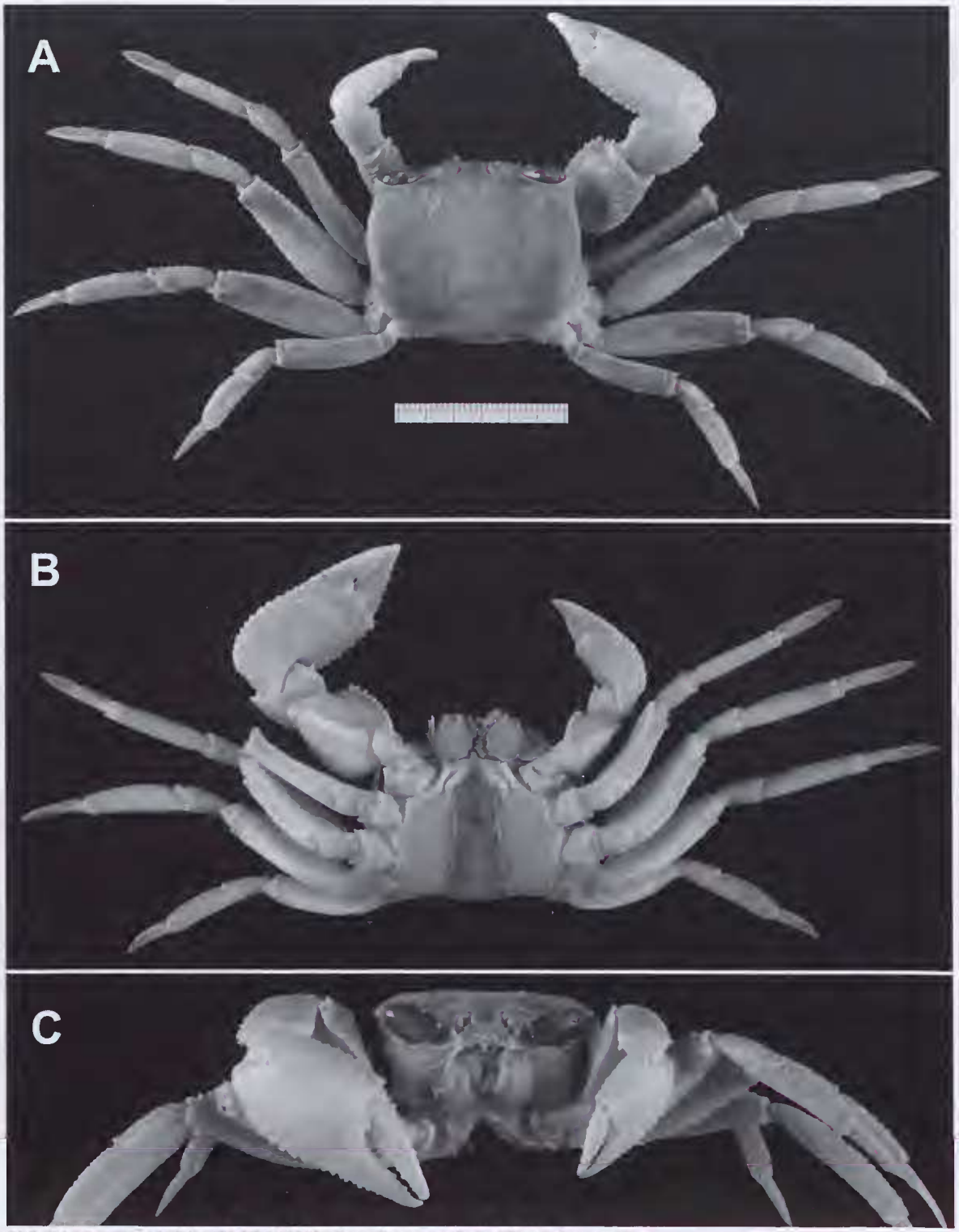

FIG. 39. *Ocypode kuhlii* (SMF-23298); dorsal, ventral and frontal aspects.

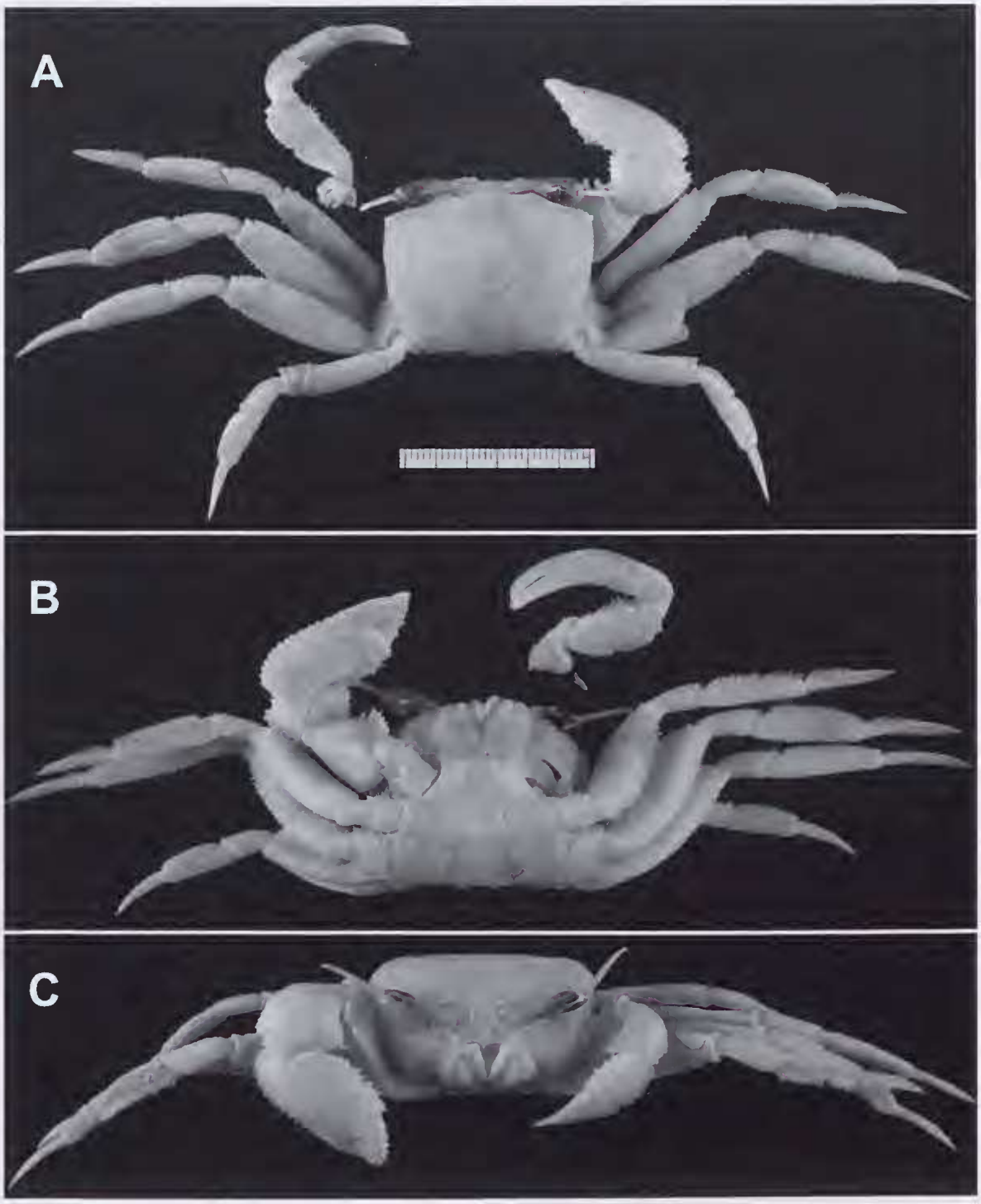

FIG. 40. *Ocypode macrocera* (SMF-6772); dorsal, ventral and frontal aspects.

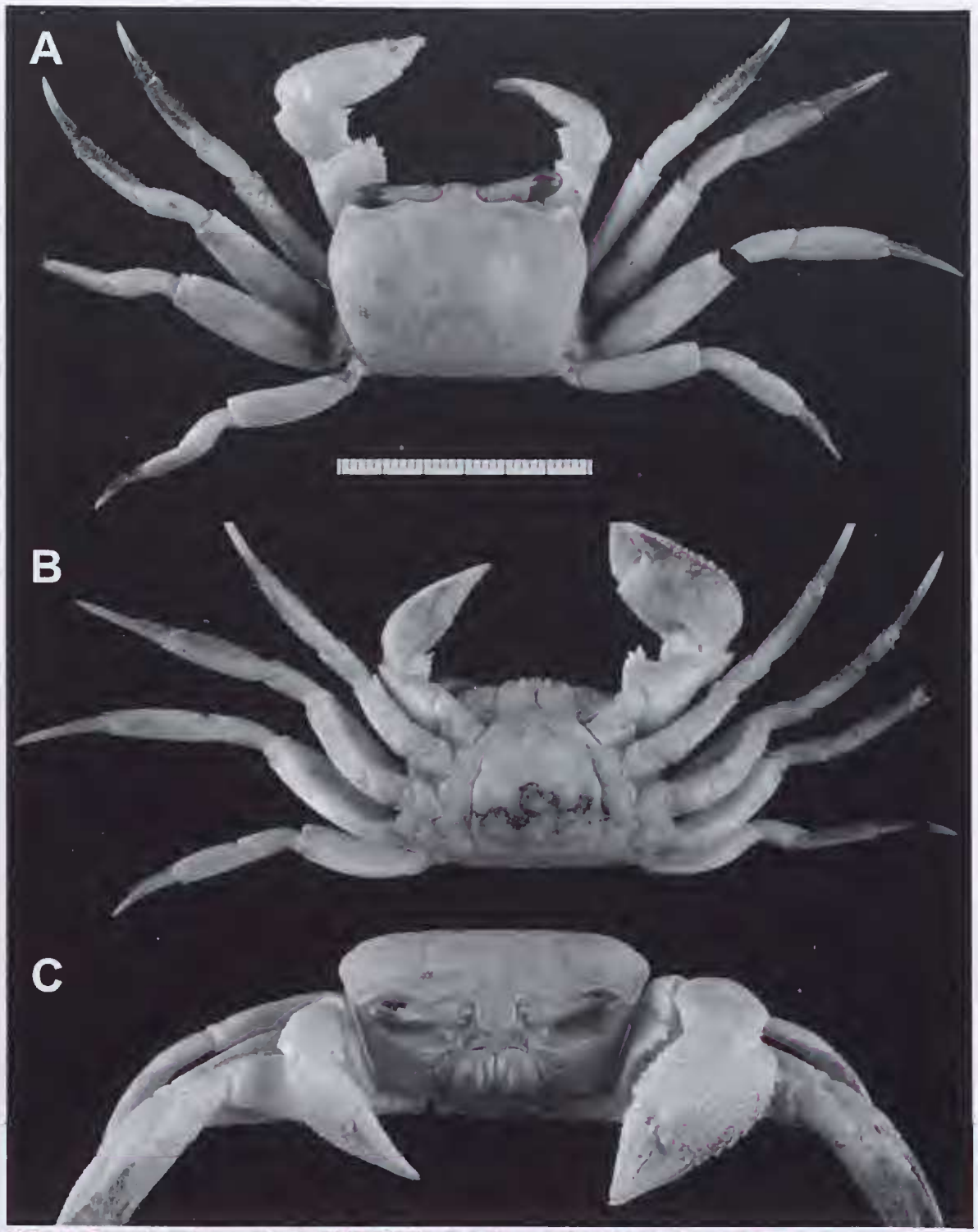

FIG. 41. *Ocypode madagascariensis* (SMF-10931); dorsal, ventral and frontal aspects.

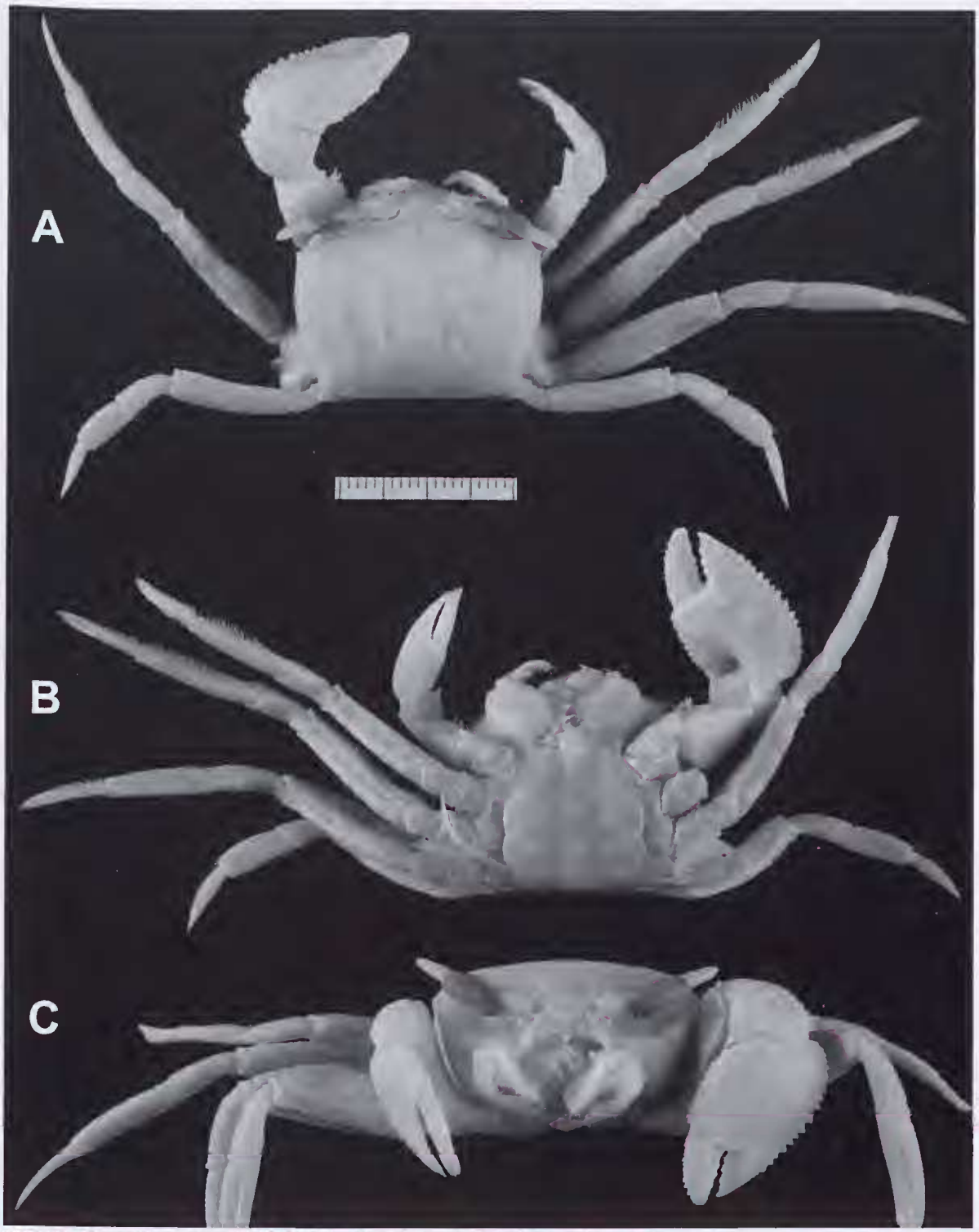

FIG. 42. *Ocypode mortoni* (SMF-36189); dorsal, ventral and frontal aspects.

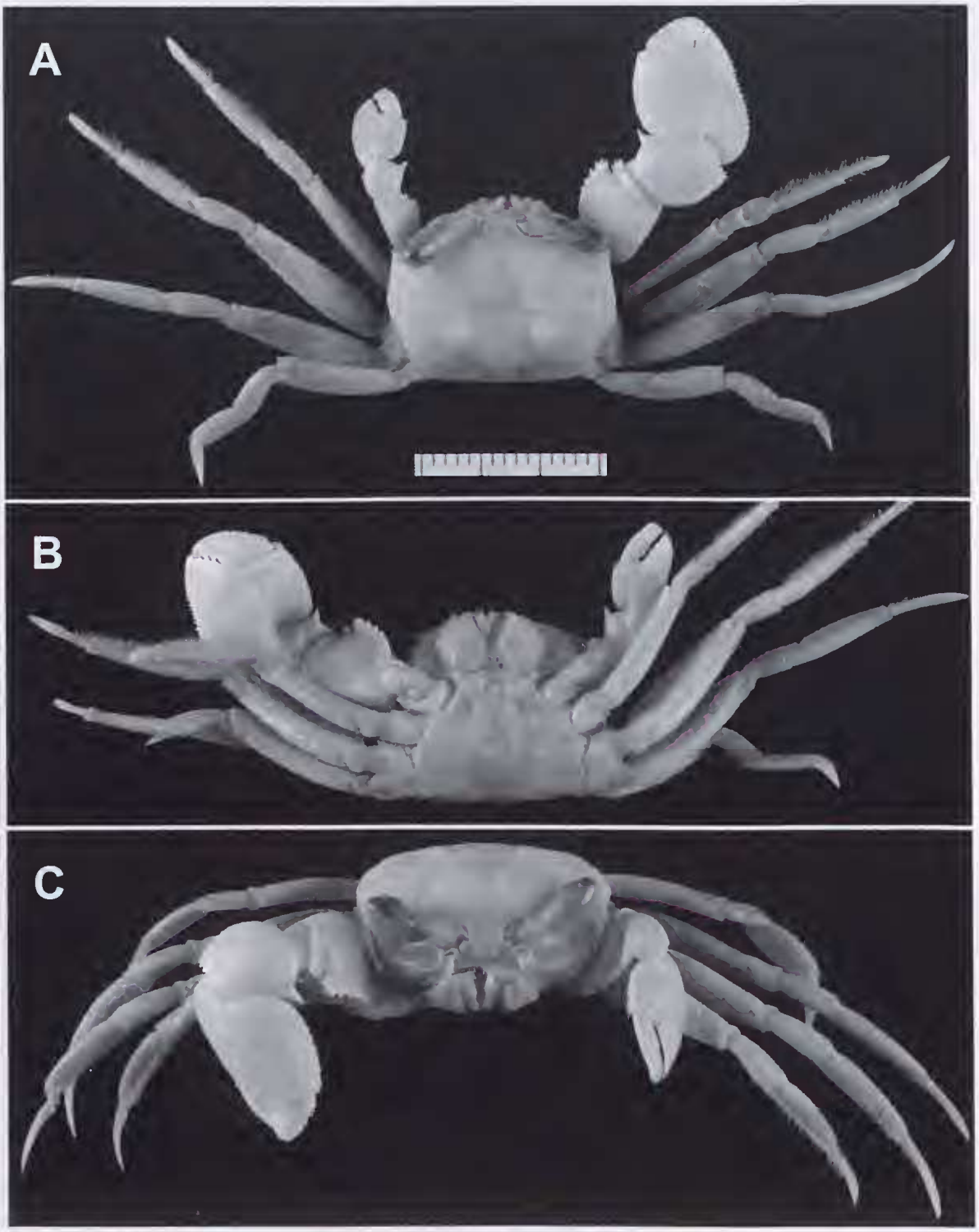

FIG. 43. *Ocypode nobilii* (SMF-7273); dorsal, ventral and frontal aspects.

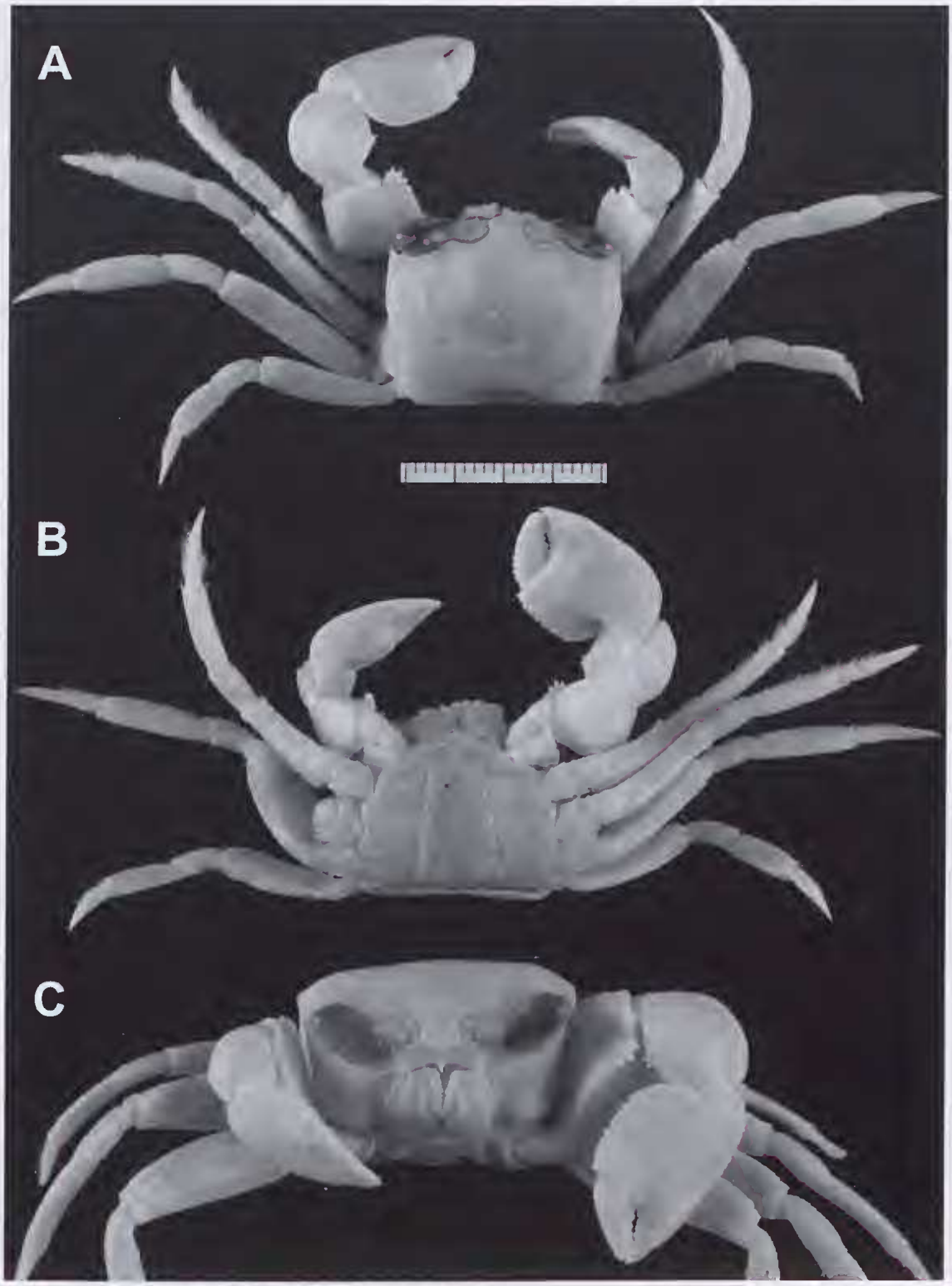

FIG. 44. *Ocypode pallidula* (SMF-6870); dorsal, ventral and frontal aspects.

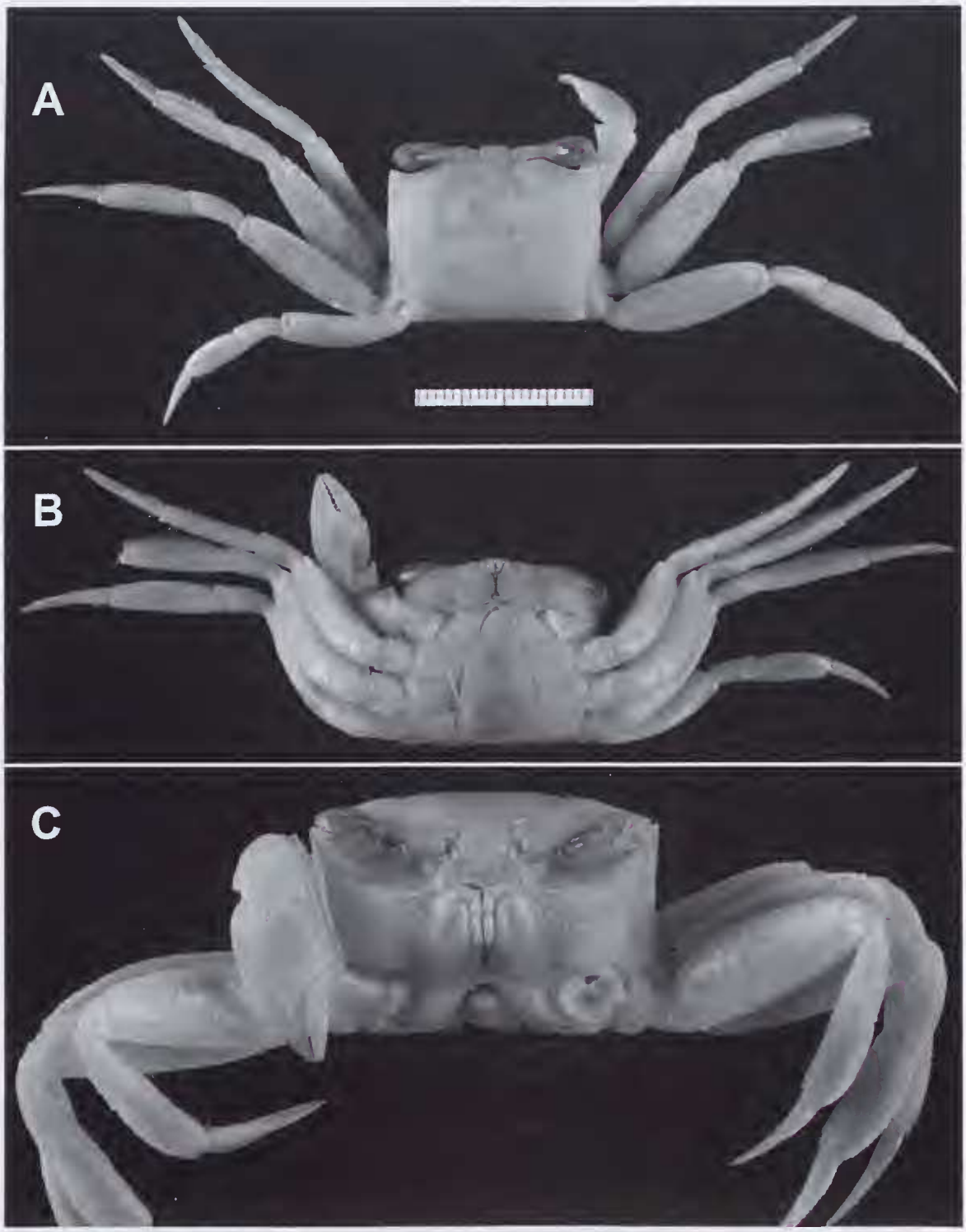

FIG. 45. *Ocypode pauliani* (SMF-1958); dorsal, ventral and frontal aspects.

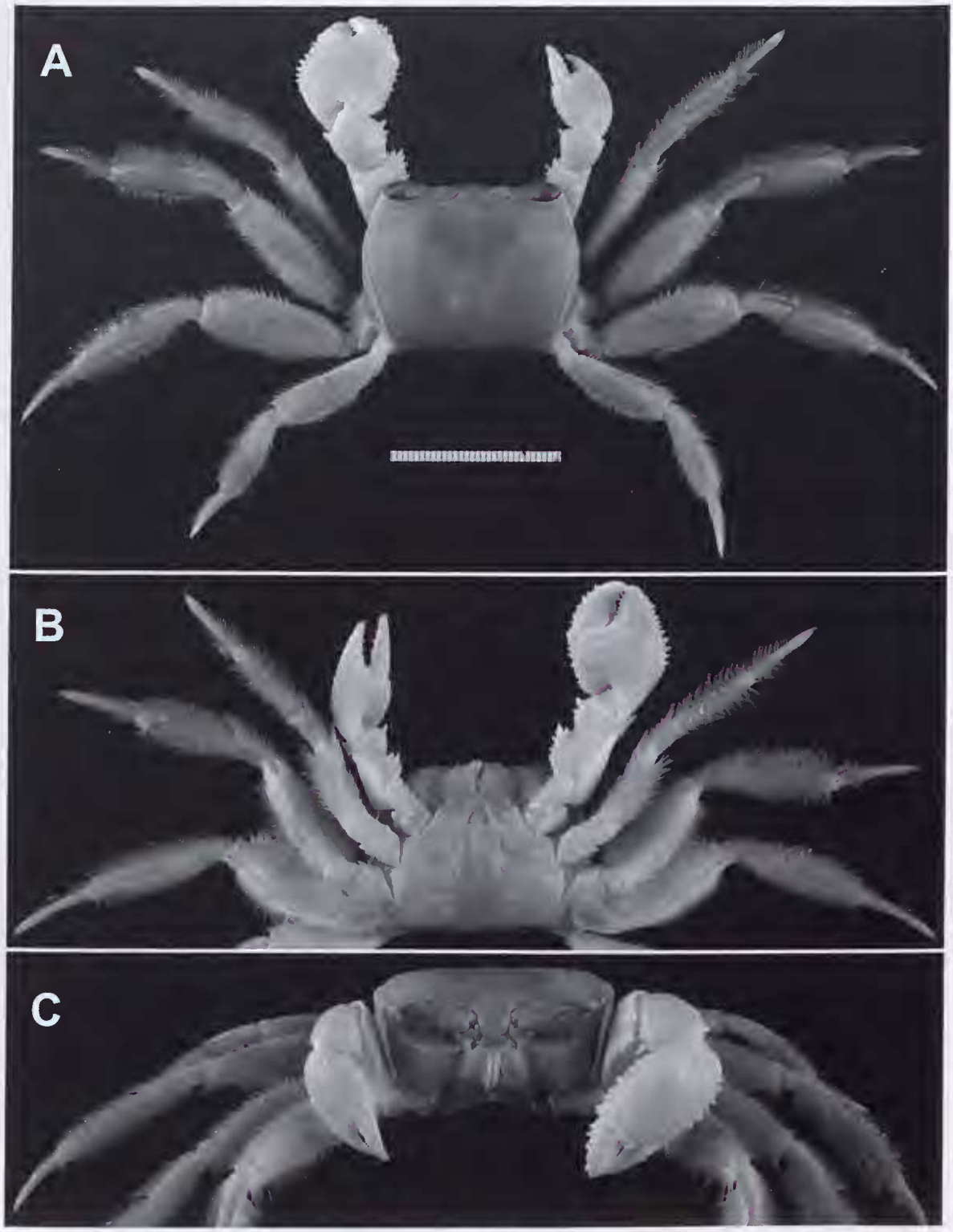

FIG. 46. *Ocypode quadrata* (SMF-6851); dorsal, ventral and frontal aspects.

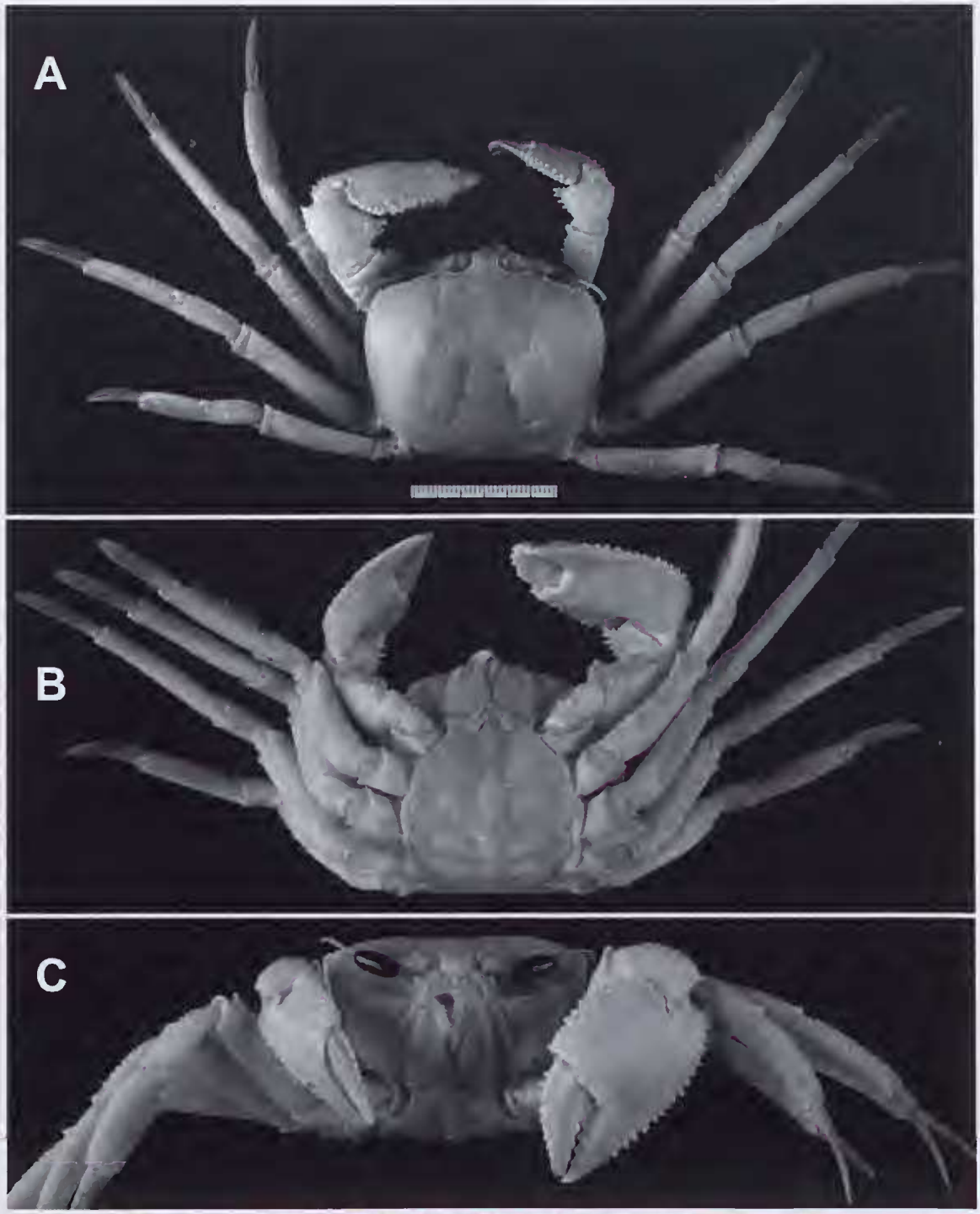

FIG. 47. *Ocypode rotundata* (SMF-23027); dorsal, ventral and frontal aspects.

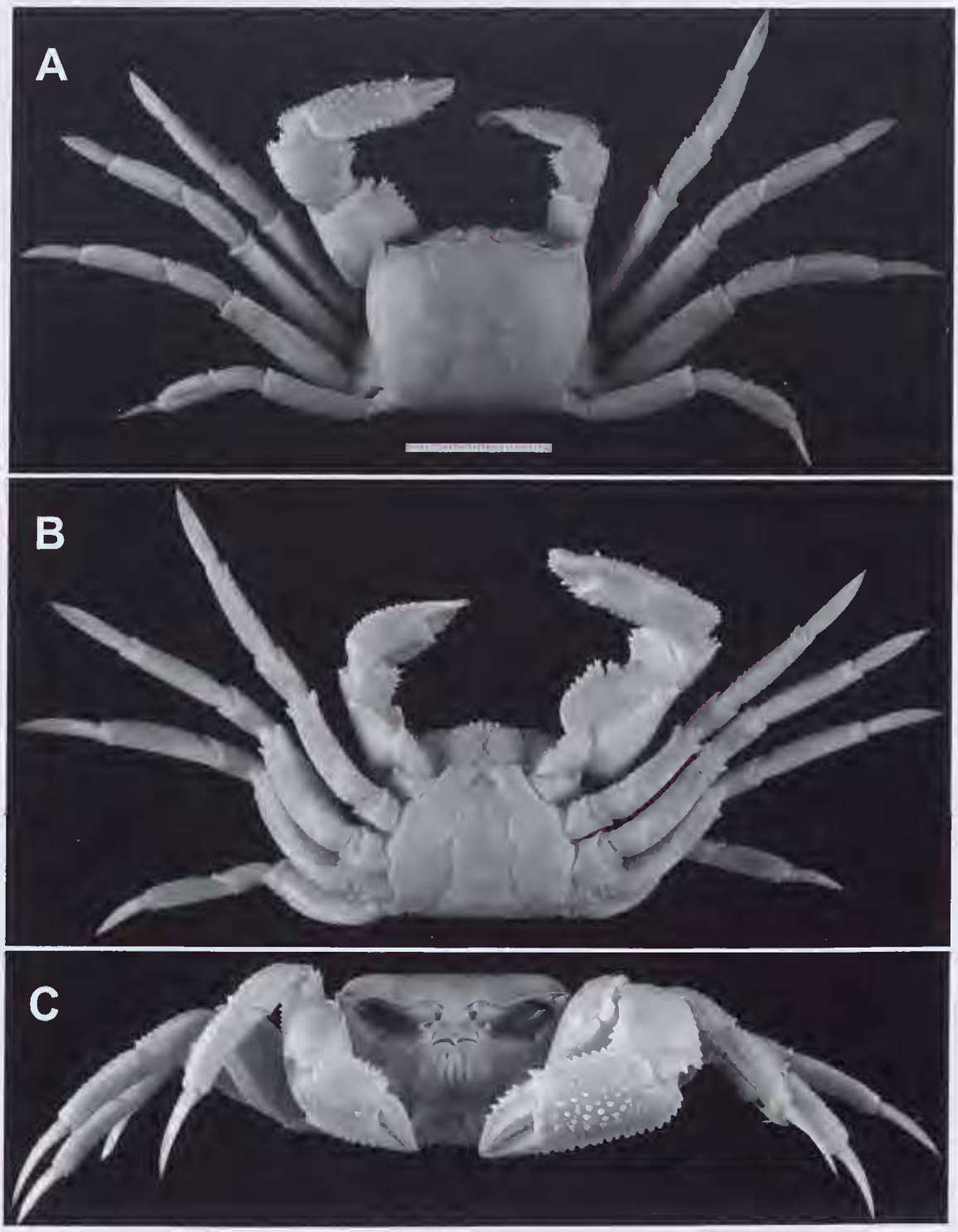

FIG. 48. *Ocypode ryderi* (SMF-10932); dorsal, ventral and frontal aspects.

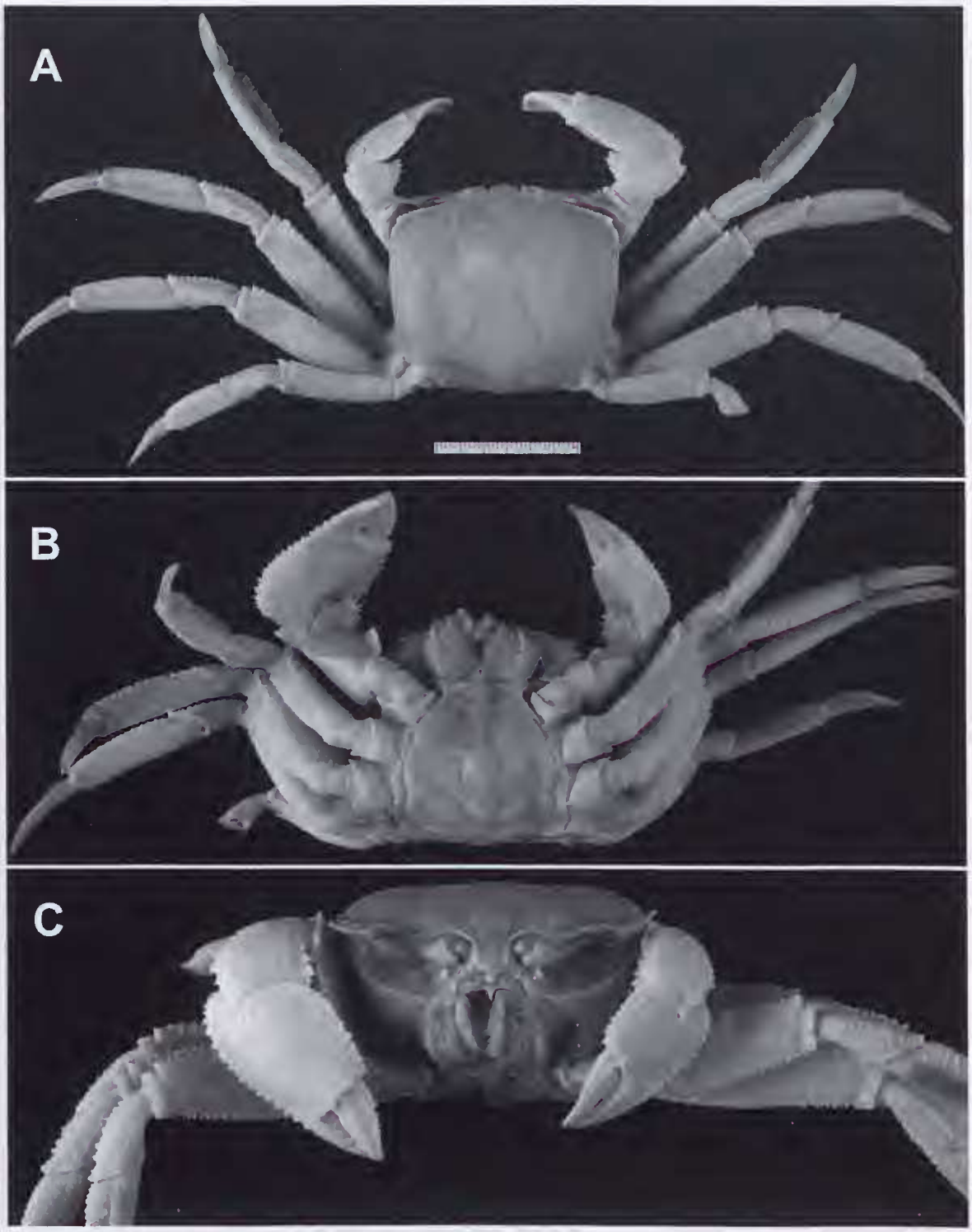

FIG. 49. *Ocypode saratan* (SMF-9711); dorsal, ventral and frontal aspects.

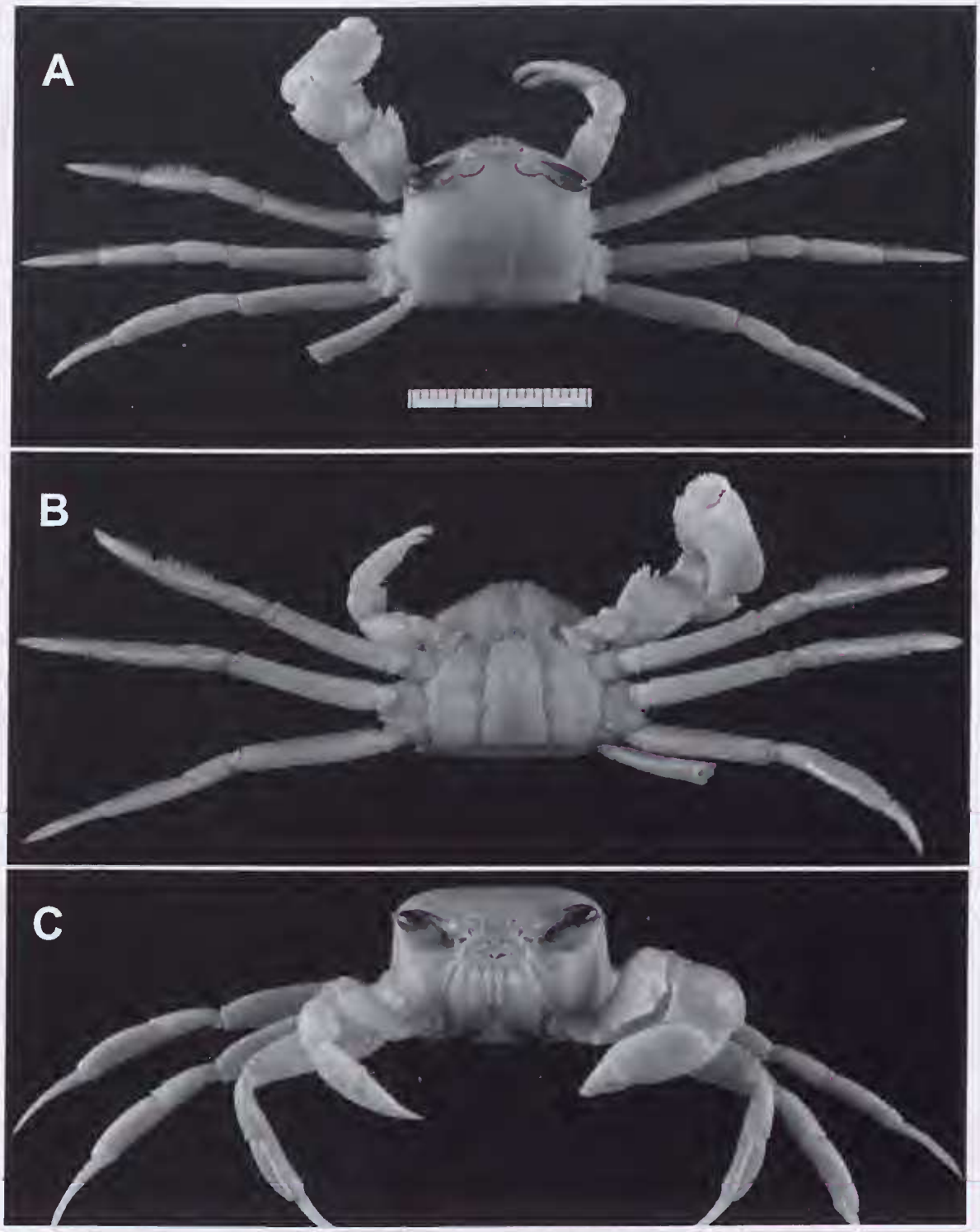

FIG. 50. *Ocypode stimpsoni* (SMF-6843); dorsal, ventral and frontal aspects.

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