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First record of the globally invasive crab, *Charybdis hellerii* (A. Milne-Edwards, 1867), in Benin, with notes on its taxonomy (Crustacea, Decapoda, Brachyura, Portunidae)

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Abstract

The Indo-Pacific portunid, *Charybdis hellerii* (A. Milne-Edwards, 1867), is a crab species native to the Indian and Western Pacific Oceans and has previously colonized the Eastern Mediterranean and the Western Atlantic. It is now recorded in the Eastern Atlantic, on the coast of Benin, where a thriving population has established. This invasive and widely distributed species exhibits morphological variations within and between populations, which are discussed in detail. Its current distribution is presented, and its future expansion along the West African coast and future impact on coastal ecosystems and local fisheries are the object of tentative forecasts. Illustrations of sexually mature specimens from different sizes and regions are presented, and their allometric, individual and geographical variations are discussed. A new synonymy and a new account on the taxonomy and the biology of the species are presented. Illustrations of the lectotype and the paralectotype of *C. hellerii* are also provided for the first time. *Charybdis spinifera* (Miers, 1884), *C. merguiensis* (De Man, 1887) and *C. vannamei* Ward, 1941 are here treated as subjective junior synonyms of *C. hellerii*. The holotype of *C. spinifera* and two syntypes of *C. merguiensis* are illustrated.

Key words: alien species, Eastern Atlantic, West Africa, systematics, type material

Introduction

The portunid crab *Charybdis hellerii* (A. Milne-Edwards, 1867), originally described based on material from New Caledonia, has a broad, natural distribution across the Indo-Pacific Ocean, ranging from the Red Sea to New Caledonia (Apel & Spiridonov 1998). It is also a very successful invasive species (Galil *et al*. 2002; Tavares 2011). In the 1920s, it entered the Eastern Mediterranean Sea, presumably via the Suez Canal (Steinitz 1929; Monod 1930), and stable populations were established in that sea (Yokes & Galil 2006; Yokes *et al.* 2007; Özcan *et al.* 2010). A single specimen of *C. hellerii* was recorded on the hull of a ship in Hawai'i prior to 1954 (Edmondson 1954; Castro 2011), and the species established a population there later on (Evans *et al.* 2018). In 1987, *C. hellerii* was recorded in the Western Atlantic (Campos & Türkay 1989; Gómez & Martínez-Iglesias 1990) and now ranges from the Atlantic coast of the USA to the south of Brazil (Tavares 2011; Negri *et al.* 2018). So far, there are very few published records of the species in the Eastern Atlantic: an accidental record from the hull of a ship in northern Spain (Cuesta *et al.* 2016), and a simple mention of its occurrence in Guinea by Fransen (2014b), which is presumably based on an unpublished record of a specimen collected in 2011 in Guinea-Bissau, 11.5342°N, 17.0770°W: (http://www.discoverlife.org/mp/20l?id=GBIF773871744 accessed 28.iii.2018). In 2017, a thriving population was detected by C.E. Dessouassi and P.A. Lalèyè on the coast of Benin.

A number of questions related to the taxonomy of *Charybdis hellerii* remain unresolved or incompletely answered. It was known that this crab included glabrous and pubescent forms (De Man 1887, as *Goniosoma*

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merguiense De Man, 1887; Chopra 1935; Leene 1938; Kathirvel & Gopalakrishnan 1974; Negri *et al*. 2018; Apel & Spiridonov 1998; Naderloo 2017). Illustrations published in literature indicate considerable variation in the shape of the frontal teeth between specimens. While part of this variation has been attributed to allometry (De Man, 1887, as *Goniosoma merguiense* De Man, 1887; Chopra 1935), it was not clear whether this was the sole factor involved. This actually raised the question whether more than one species has been confused under the name *Charybdis hellerii*, as demonstrated in other crab species which were previously considered to be variable and widely distributed (Ng & Davie 2007; Lai *et al.* 2010). It transpires that the type specimens of *Charybdis hellerii*, deposited in the Muséum national d'Histoire naturelle, Paris, have never been illustrated before. This raised doubt about the conspecificity of these types with other crabs identified as *C. hellerii*. In addition, it appeared that there are three possible names for that species: *Goniosoma hellerii* A. Milne-Edwards, 1867, *Goniosoma spiniferum* Miers, 1884 and *Goniosoma merguiense*. Evans *et al*. (2018) recently established that *C. vannamei* Ward, 1941 is a junior synonym of *C. hellerii*. Therefore, it became imperative to document the variation of all these taxa with good illustrations and to verify whether indeed more than one species has been confused under the name *C. hellerii.*

This paper consists of two parts: one on taxonomy and one on distributional and ecological data on *Charybdis hellerii* in Benin.

Material and methods

Study area. The study was carried out along Nokoué Lake in southern Benin, West Africa. The lake is directly connected to the Atlantic coast by the channel of Cotonou and communicates with Porto-Novo Lagoon via Totchè Canal (Fig. 18). The waters of Nokoué Lake are brackish, with salinity ranging 0 to 31g / L depending on hydrological seasons and measurement points (Lalèyè *et al.* 2003; Gnohossou 2006; Niyonkuru 2007). It represents a part of the RAMSAR 1018 site. Nokoué is the biggest lake or lagoon in Benin, and is located at the northern part of Cotonou, which is the biggest town of the country, occupying 150 square kilometers (Pliya 1981). The lake is 20 km long and 11 km wide (Roche International 2000) and receives fresh water from the Sô and Ouémé Rivers (Agence Béninoise pour l'Environnement 2000).

The lake's temperature generally ranges between 25.3 to 31.1°C, the pH between 6.5 and 8.2 and the dissolved oxygen between 0.5 to 9 mg/L (Lalèyè *et al.* 2003; Gnohossou 2006; Niyonkuru 2007). This lagoon experiences three seasons (Gnohossou 2006): a "dry season" from December to March when, the salinity and temperature are maximal; a "rainy season" from April to July during which the temperature is minimal, and the "flood season" when salinity and pH are minimal and dissolved oxygen are maximal. The Nokoué Lake has a total production of about 12,900 tons of fishery products, of which about 820 tons consisted of portunid crabs in 2016 (Direction Production Halieutique 2017).

Sampling methods and data collection. Nokoué Lake was divided into eight fishing sectors based on physical and chemical parameters determined from a crab inventory conducted from February 2017 to January 2018 (Fig. 18). Crabs were collected by C.E. Dessouassi and P.A. Lalèyè from artisanal and experimental fisheries in each fishing sector. A combination of several crab fishing methods (e.g. the round lift-net trap; Ghanaian crab trap) were utilized for collecting crabs monthly.

In each sector, 10 % of crab fishermen sampled systematically using each variety of crab fishing methods. The total catch of the fisherman was weighed and the sampling rates recorded in Table 1 were applied.

TABLE 1. Crabs sampling rate applied for artisanal fisheries.

	Crab traps			Others crab fishing gears
Crab total catch	0–5 kg	5–10 kg	> 10kg	All
Sampling rate (%)	50	33	25	100

After collection of artisanal fisheries, experimental fishing was organized in areas where any crab fishing gear has been deployed. Experimental fisheries were conducted using a canoe with 100 round lift-net trap for 4 hours in each fishing sector. The round lift-net traps were baited with turkey meat. They were arranged at intervals of about two meters and raised every 20 minutes or so. All catches of the experimental fishery were transported to the laboratory in a cooler then stored in a deep freezer at -18 °C for identification (Sankaré 2007; Olakolu & Fakayode 2014). The crab species were identified with standard handbooks on West African crabs (Monod 1956; Manning & Holthuis 1981). Of seven species, one species could not be identified. Ten specimens of this species were sent to the Royal Belgian Institute of Natural Sciences (RBINS), Brussels in accordance with the administrative procedures outlined in the Nagoya Protocol. This material was examined by C. d'Udekem d'Acoz and compared by him with Indo-Pacific specimens of *Charybdis hellerii* (A. Milne-Edwards, 1867) deposited in RBINS, confirming that it belonged to that species. The specimens are registered as "RBINS, INV. 150109 to 150114".

The characters of a selection of these specimens were documented in high resolution with stacked photographs. Danièle Guinot examined a selection of specimens of *Charybdis hellerii* deposited in the collections of the Muséum national d'Histoire naturelle, Paris, including the lectotype and the paralectotype of the species and requested us to publish photographs of these, which have never been previously illustrated. Photographs of the holotype of *Goniosoma spiniferum* Miers, 1884 were prepared by Harry Taylor (NHM) and photographs of the syntypes of *Goniosoma merguiense* De Man, 1887 were done by Charles Fransen (RMNH). The contrast settings of all the taxonomic photographs were adjusted by C. d'Udekem d'Acoz using Adode Photoshop CS3, and the plates were assembled using the same software. These pictures were used to characterize the type specimens of *Goniosoma hellerii*, *Goniosoma merguiense* and *Goniosoma spiniferum*, to document the variability in mature specimens of *C. hellerii* and to investigate if there is some discontinuity in this variability that would be indicative of the existence of more than one species confused under the name *C. hellerii*. Historical notes on the lectotype and the paralectotype of *C. hellerii* provided to us by Danièle Guinot (MNHN) are presented.

Measurements are provided in millimetres and reported as carapace length (cl) x carapace width (cw) respectively, taken at its maximum (including teeth). Museum collection acronyms are as follows: MNHN, Muséum national d'Histoire naturelle, Paris, France; NHM, Natural History Museum, London; RBINS, Royal Belgian Institute of Natural Sciences, Brussels, Belgium; RMNH, Naturalis (ex Rijksmuseum van Natuurlijke Historie), Leiden, The Netherlands.

A new synonymy is given for *Charybdis hellerii.* It includes most references on *Charybdis hellerii* with taxonomical information and/or illustrations, but lists neither simple records of the species (except for some important compilations and unusual records) nor ecological papers devoid of crab illustrations. A short taxonomic description and a summary on biological data are given.

Taxonomy

Infraorder Brachyura Latreille, 1802

Superfamily Portunoidea Rafinesque, 1815

Family Portunidae Rafinesque, 1815

Subfamily Thalamitinae Paulson, 1875

Genus *Charybdis* De Haan, 1833

Portunus (*Charybdis*) De Haan, 1833: 10, type species by subsequent designation (Glaessner 1929: 113): *Cancer sexdentatus* Herbst, 1783: 153, pl. 7 fig. 52 [*Cancer sexdentatus* Herbst, 1783 became an objective junior synonym of *Cancer feriatus* Linnaeus, 1758 by the designation of the same specimen as lectotype for the two taxa by Holthuis (1962: 234–235)].

Charybdis.—Alcock, 1899: 47 [precedence given over *Oceanus*, in application of the Principle of First Reviser (ICZN 1999)]; ICZN 1964: 337 (placed on official list of names in zoology).

Portunus (*Oceanus*) De Haan, 1833: 9, type species by monotypy: *Portunus crucifer* Fabricius, 1798 [= *Charybdis feriata* (Linnaeus, 1758)], name preoccupied by *Oceanus* de Montfort, 1808 [Mollusca].

Goniosoma A. Milne Edwards, 1860: 263, type speecies not specified, name preoccupied by *Goniosoma* Perty, 1833 [Arachnida].

non *Charybdis* Cocco, 1832: 207; type species *Charybdis Zanclea* Cocco, 1832 [Amphipoda], placed on the Official Index of Rejected and Invalid Generic names in Zoology by ICZN (1964: 342).

The recent phylogenetic analysis of Portunoidea by Evans (2018) recovered a monophyletic *Charybdis* lineage (excluding *Goniosupradens* Leene, 1938) with strong support, but there was no support for other proposed *Charybdis* subgenera. Therefore, we no longer use subgenera for *Charybdis hellerii* and its synonyms.

Charybdis hellerii **(A. Milne-Edwards, 1867)**

(Figs 1–17)

Talamita [sic] *sexdentata* Rüppell, 1830: 4 (in part), pl. 1 fig. 1.

Goniosoma sexdentatum.—A. Milne-Edwards 1861: 372 (fide Leene 1938, who examined the material).

Goniosoma Hellerii A. Milne-Edwards, 1867: 282; 1873: 167; Henderson 1893: 375.

Goniosoma annulatum.—De Man 1883: 151 (fide Leene 1937).

Goniosoma spiniferum Miers, 1884: 233, pl. 23 fig. C.; De Man 1887: 85 (discussion).

Goniosoma merguiense De Man, 1887 [1887–1888a]: 82, pl. 5 figs 3–4; 1888 [1887–1888b]: 335 (discussion); 1895: 560; 1897: pl. 12 fig. 9; Lenz 1905: 360; 1910: 556; Klunzinger 1913: 367.

Charybdis (*Goniosoma*) *merguiensis*.—Alcock 1899: 49, 55; Nobili 1899: 254; 1903: 31; 1906: 194, 196; Monod 1930: 140, fig. 7; Chopra 1935: 484, fig. 8; Shen 1937: 116 (key), 121, fig. 12; Leene 1937: 165; Chopra & Das 1938: 394.

Charybdis spiniferus.—Grant & McCulloch 1906: 18 (new record).

Charybdis (*Charybdis*) *hellerii*.—Leene 1938: 44–49, figs 15–17; 1940: 182 (examination of the holotype of *Goniosoma spiniferum*); Stephenson 1972b: 11 (key), 32; 1976: 14; Kathirvel & Gopalakrishnan 1974: 286; Dai & Yang 1991: 233–234, fig. 126 (1), pl. 28 (6); Wee & Ng 1995: 32–34, fig. 14a–g; Apel & Spiridonov 1998: 194–197 (synonymy), figs 13–15, 17; Davie 2002: 473 (synonymy and list of types); Galil *et al*. 2002: 110, unnumbered photograph; Padate *et al.* 2006: 587 (key); Yokes & Galil 2006: 754, fig. 2F; Yokes *et al.* 2007: 165, fig. 2d; Ng *et al*. 2008: 153 (list); Van Chung 2012: 168 (key), 174, fig. 12; Naderloo 2017: 174, figs 20.3d, 20.5, 20.7; Trivedi *et al.* 2018: 64 (list of Indian references).

Charybdis merguiensis.—Bouvier 1940: 252, fig. 162; Ward 1941: 5; Barnard 1950: 168, figs 27d, 32b; Fourmanoir 1954: 8, fig. 8; Badhra 1995: 257 (key), 258; Bhadra 1999: 410 (key), 411.

Charybdis vannamei Ward, 1941: 4, figs 5, 6; Stephenson 1972b: 32 (discussion); Santhanam 2018: 160.

Charybdis spiniferum.—Ward 1941: 5; Ng *et al*. 2001: 20 (discussion).

Charybdis (*Charybdis*) *helleri*.—Buitendijk 1947: 281; Stephenson *et al.* 1957: 492 (key), 493 (key), 497–498, figs 1a, 2i, 3j, pl. 1, fig. 4, pls 4c, 5b; Crosnier 1962: 75 (key), 77–78, figs 133–135, pl. 5 fig. 1; Apel 2001: 70.

Charybdis hellerii.—Edmondson 1954: 247–248, fig. 32a–f (Hawai'i); Campos & Türkay 1989: 119 (first published record in the Western Atlantic); Lemaitre 1995: 643–647, fig. 2; Tirmizi & Kazmi 1996: 29 (key), 45–47 (possibly in part), pl. 1, fig. B, possibly not fig. 23a–i; Tavares & Braga de Mendonça 1996: 151, 154 (key); Fransen *et al.* 1997: 179 (original material of *Talamita sexdentata* Rüppell, 1830 listed); Vannini & Innocenti 2000: 269, figs 30, 35, 93; Dineen *et al.* 2001: 778, figs 3–24 (larval and juvenile stages); Tavares & Amouroux 2003: 625, fig. 1; Alves Coelho & do Carmo Ferrão Santos 2003: 167, fig. 1; 2004: 192, fig. 5; Braga *et al.* 2005: 30, fig. 30; Sampaio & Rosa 2005: 58, fig. 1 (predation by octopus); Morán & Atencio 2006: 205; Oliveira de Almeida *et al*. 2006: 13, fig. 8; Figueiredo Frigotto & Serafim-Junior 2007: 228, fig. 1; Brockerhoff & McLay 2008: 71 (extensive data compilation); McMillen-Jackson 2008: 889, fig. 2; Lima *et al.* 2008: 37, fig. 3; Felder *et al.* 2009: 183, fig. 1b; Mizzan & Vianello 2009: 29, fig. 6; Boos *et al*. 2010: 1, fig. 1; Loebmann *et al.* 2010: 918, fig. 5; Medellín *et al.* 2001: 73, unnumbered fig.; Tavares 2011: 255, fig. 1b; Khvorov 2012: 39, unnumbered photographs; Bentes *et al.* 2013: 181, fig. 1; Cruz da Rosa 2014: 445, figs 1g–h; Elumalai *et al.* 2014: 338, fig. 1 (right, third row, *Sacculina* infestation); Watanabe *et al.* 2015: 219, fig. 3; McLay 2015: 830, fig. 71b; Abbas *et al.* 2016: 321, fig. 3; Cuesta *et al.* 2016: 622, 624, fig. 2B (Spain); da Silva Reis *et al.* 2016: 1, figs 1–3; Negri Pereira 2016: 1, figs 1, 17, 18, 19, 20b; Ng *et al*. 2017: 72 (list of Taiwan records); Ferry *et al.* 2017: 240, fig. 1; Negri & Mantelatto 2017: 282, figs 2a, 3a; Questel 2017: 1, unnumbered photographs; Santhanam 2018: 136, unnumbered fig.; Negri *et al.* 2018: 1771, figs 4–5; Evans *et al.* 2018: 641, figs 1, 2A, 4, 5 (Hawai'i).

Charybdis helleri.—Riedl 1983: 501, pl. 501, unnumbered fig.; Holthuis 1987: 350, fig. 10; Gómez & Martínez-Iglesias 1990: 70, fig. 1; Fransen 2014b: 316, fig. 31 [Guinea].

Charybdis merguiense.—Deb 1998: 144 (key).

Charybdis (*Charybdis*) *merguiensis*.—Deb 1998: 145.

Charybdis (*Charybdis*) *helleri*.—Jeyabaskaran *et al.* 2000: 52, pl. 38A; Dev Roy & Das 2000: 36, pl. 2 fig. 1, pl. 9 figs 7–8; Dev Roy & Bhadra 2011: 150 (key), 151.

Charybdis (*Charybdis*) *spinifera*.—Ng *et al*. 2008: 153 (list).

Charybdis (*Charybdis*) *vannamei*.—Ng *et al*. 2008: 153 (list).

Charybdis variegata.—Sant'Anna *et al.* 2012a: 12, fig. 2

non *Cancer sexdentatus* Herbst, 1783: 153, pl. 7 fig. 52 [= *Charybdis feriata* (Linnaeus, 1758) by lectotype designation (Holthuis 1962)].

non *Portunus annulatus* Fabricius, 1798: 364.
non *Portunus variegatus* Fabricius, 1798: 364.
non *Charybdis* (*Goniosoma*) *Hellerii*.—Nobili 1906: 194, 195 [= *Charybdis orientalis* Dana, 1852] (fide Leene 1938: 70).
non *Goniosoma Hellerii*.—Klunzinger 1913: 367 [= *Charybdis orientalis* Dana, 1852] (fide Leene 1938: 70).

Material examined (directly or after new photographs). Type material of *Goniosoma hellerii* A. Milne-Edwards, 1867. New Caledonia, no exact locality, in dry condition: lectotype male, 60.0 x 85.0 mm, New Caledonia, M. Aubry-Lecomte, MNHN-IU-2000-732 (= MNHN-B732); paralectotype male 49.0 x 72.0 mm, New Caledonia, coll. M. Jouan, MNHN-IU-2000-761 (= MNHN-B761) [photographs provided by Danièle Guinot; specimens not directly examined by the authors].

Type material of *Goniosoma merguiense* De Man, 1887. Republic of the Union of Myanmar, Mergui Archipelago, 1886: 2 male syntypes (25.0 x 40.0 mm and 21.0 x 32.0 mm), leg. J. Anderson, RMNH.CRUS.D.1310 [photographs communicated by Charles Fransen; specimens not directly examined by the authors].

Type material of *Goniosoma spiniferum* Miers, 1884. 1 male holotype, about 13 x 17 mm, Queensland, Port Molle, between tide marks, Natural History Museum, NNM 1881.31 [photographs taken by Harry Taylor, NHM photo Unit and communicated by Paul F. Clark; specimen not directly examined by the authors].

Other material. Benin, Channel of Cotonou (Ancien Pont), 4 m, cast net, 24.v.2017: 1 male (pubescent, front with teratological anomalies), 43.5 x 66.7 mm, coll. C. E. Dessouassi, RBINS, INV. 150109; Benin, Channel of Cotonou (Ancien Pont), 4 m, lift net, 24.v.2017: 2 males (not pubescent), 46.4 x 68.5 mm and 46.6 x 68.7 mm, coll. C. E. Dessouassi, RBINS, INV. 150110; Benin, Channel of Cotonou (Ancien Pont), 4 m, lift net, 19.vi.2017: 2 males (not pubescent), 49.2 x 76.0 mm and 37.0 x 56.0 mm, coll. C. E. Dessouassi, RBINS, INV. 150111; Benin, Channel of Cotonou (Ancien Pont), 4 m, lift net, 24.v.2017: 2 males (not pubescent), 38.0 x 58.0 mm and 34.5 x 52.4 mm, coll. C. E. Dessouassi, RBINS, INV. 150112; 1 ovigerous female (not pubescent), 31.3 x 48.0 mm, coll. C. E. Dessouassi, RBINS, INV. 150113; Benin, Nokoué Lake (Agbato), 5 m, lift net, 24.v.2017: 1 female (not pubescent), 34.2 x 53.0 mm, coll. C. E. Dessouassi, RBINS, INV. 150114; New Caledonia, Noumea aquarium, 20.v.1966: 1 male (not pubescent), 47.0 x 68.0 mm, leg. Fierlant, RBINS, INV. 129463; Australia, Queensland, Shoal Point, under stones, at low tide, 14.iv.1983: 3 males (two strongly pubescent; smallest one weakly pubescent) (largest 37.0 x 56.0 mm), leg. R. De Blauwe, RBINS, INV. 129466; Australia, Queensland, north of Mackay, Shoal Point, under stones, at low tide, 26.v.1983: 3 males (largest: 41.0 x 63.0 mm) and 1 immature female (30.0 x 47.0 mm) [all specimens strongly pubescent], leg. R. De Blauwe, RBINS, INV. 129467; Australia, Queensland, Brampton Island, mangrove shore, no date: 1 male (pubescent, 27.0 x 43.0 mm), leg. B. Kaspiew, 1953, RBINS, INV. 129465; Philippines, Manilla, Langsheen National Park, rocks at the coast, 4.iii.1976: 5 males (scarcely pubescent and not pubescent; largest 30.0 x 46.0 mm), leg. J. Van Goethem, RBINS, INV. 129464.

Description. *Carapace* strongly pubescent, sparsely pubescent or glabrous, with a pair of short frontal ridges (sometimes hard to see), with a pair of nearly straight anterior protogastric ridges, with a continuous nearly straight mesogastric ridge, with shorter straight metagastric ridge (continuous or with short median gap), laterally followed (after a gap) by pair of broadly curved epibranchial ridges; no ridges on posterior half of carapace. Frontal region with 8 well developed teeth separated by deep incisions (3 pairs of true frontal teeth + 1 pair of teeth forming the inner border of orbit), subequal in length (very blunt in small specimens, blunt or sharp in large specimens). Anterolateral margin with 6 sharp teeth (the 5 first ones are subequal, the sixth one is subequal to the others or a bit longer). Junction between posterior margin and posterolateral margins arched (not angular).

Basal antennal article with granular ridge.

Chelipeds: merus with 3 strong anterior spines, posterior border toothless; carpus with strong spine on distomedial corner (this spine is posteriorly followed by a ridge running all along the carpus), with 3 lateral spines, of which only the two uppermost are visible in dorsal view, and of which the uppermost and the lowermost are posteriorly followed by a long ridge; propodus with 5 spines on its upper half: one spine in proximolateral position, 2 spines on the middle of propodus (1 dorsolateral and 1 dorsomedial which is posteriorly followed by carina), 2 distal spines (1 dorsolateral that is sometimes reduced to an angular protrusion and 1 dorsomedial which is posteriorly followed by carina), with 3 lateral carinae, with 1 medial carina terminated by a granule; tip of the various cheliped spines brown (except sometimes dorsolateral distal spine of propodus, when it is obsolete).

Pereiopod 5: posterior border of merus with subdistal spine; posterior border of carpus with distal spine (better seen in ventral view) [this character is very unusual in the genus *Charybdis*]; posterior border of propodus with 5–13 denticles (sometimes up to 18 according to Negri Pereira 2016).

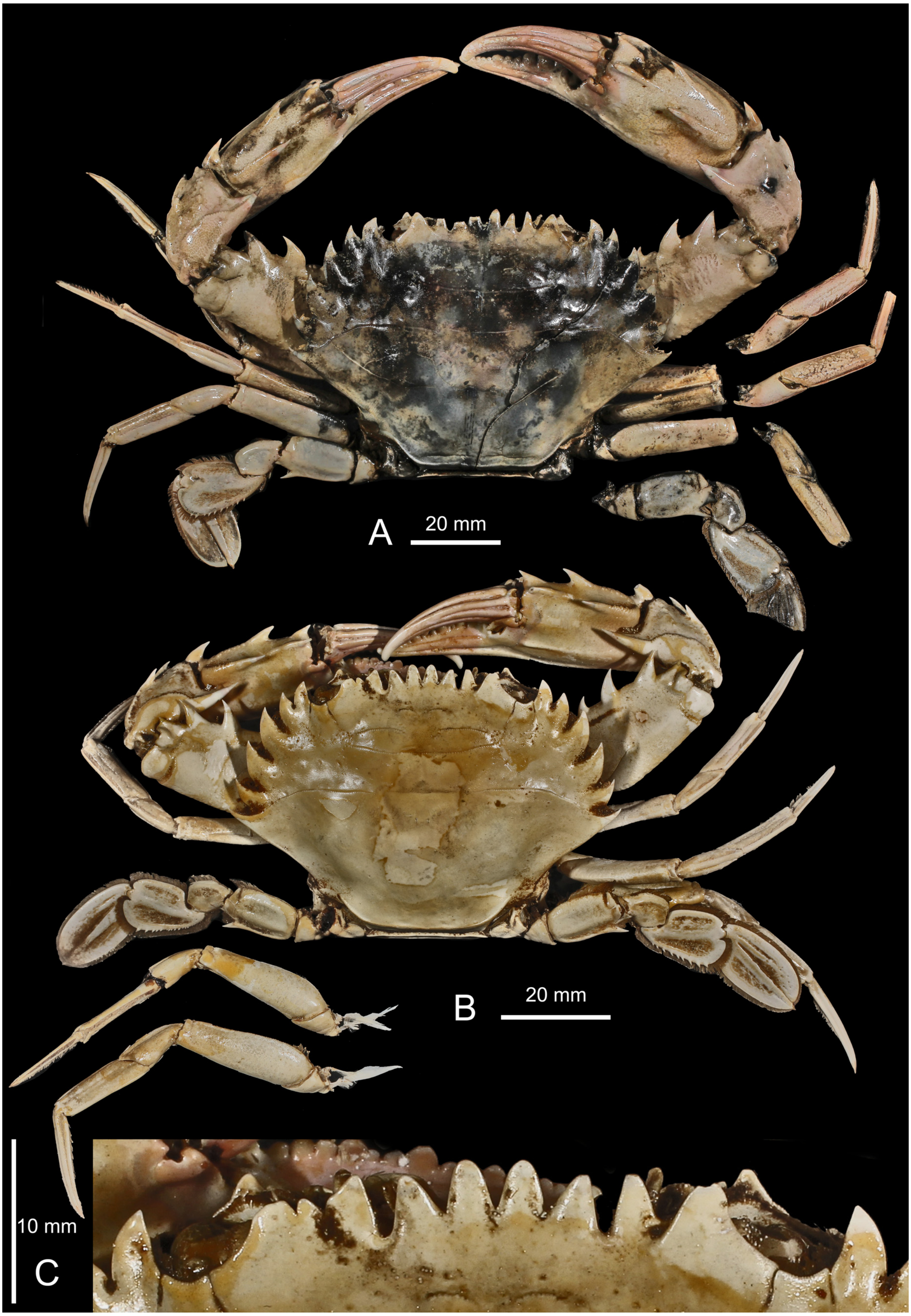


FIGURE 1. *Charybdis hellerii* (A. Milne-Edwards, 1867), New Caledonia. A. Lectotype, male, 60.0 x 85.0 mm, MNHN-IU-2000-732 (= MNHN-B732). B, C. Paralectotype, male 49.0 x 72.0 mm, MNHN-IU-2000-761 (= MNHN-B761). A, B. Dorsal habitus. C. Frontal region.

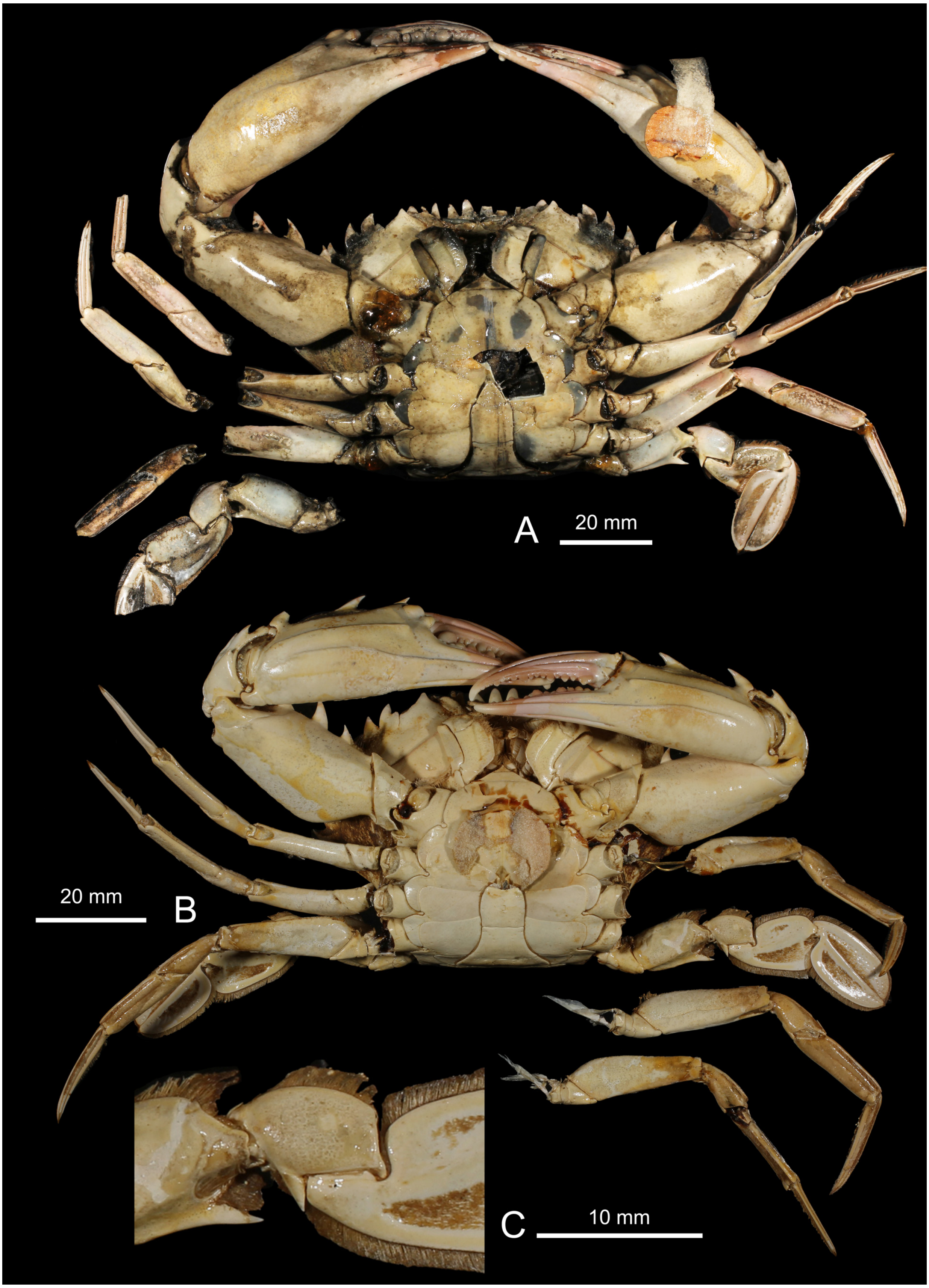


FIGURE 2. *Charybdis hellerii* (A. Milne-Edwards, 1867), New Caledonia. A. Lectotype, male, 60 x 85 mm, MNHN-IU-2000-732 (= MNHN-B732). B, C. Paralectotype, male 49.0 x 72.0 mm, MNHN-IU-2000-761 (= MNHN-B761). A, B. Ventral habitus. C. Carpus and extremity of adjacent articles of left pereiopod 5 (ventral view).

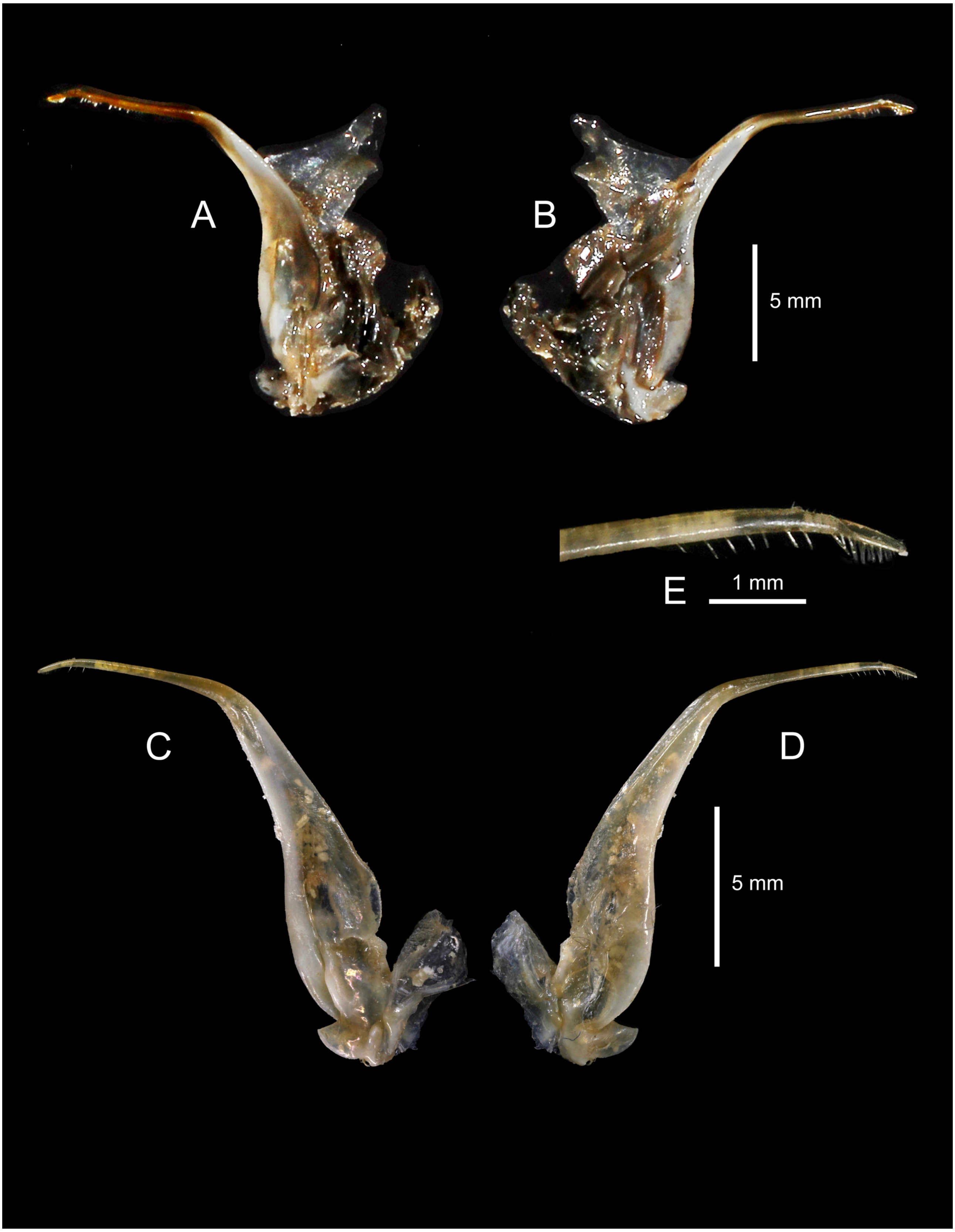


FIGURE 3. *Charybdis hellerii* (A. Milne-Edwards, 1867), males, New Caledonia, left gonopod1s (rehydrated). A, B. Lectotype, male 60.0 x 85.0 mm, MNHN-IU-2000-732 (= MNHN-B732). C, D, E. Paralectotype, male 49.0 x 72.0 mm, MNHN-IU-2000-761 (=MNHN-B761). A, C, medial view. B, D, external view. E. Tip, external view.

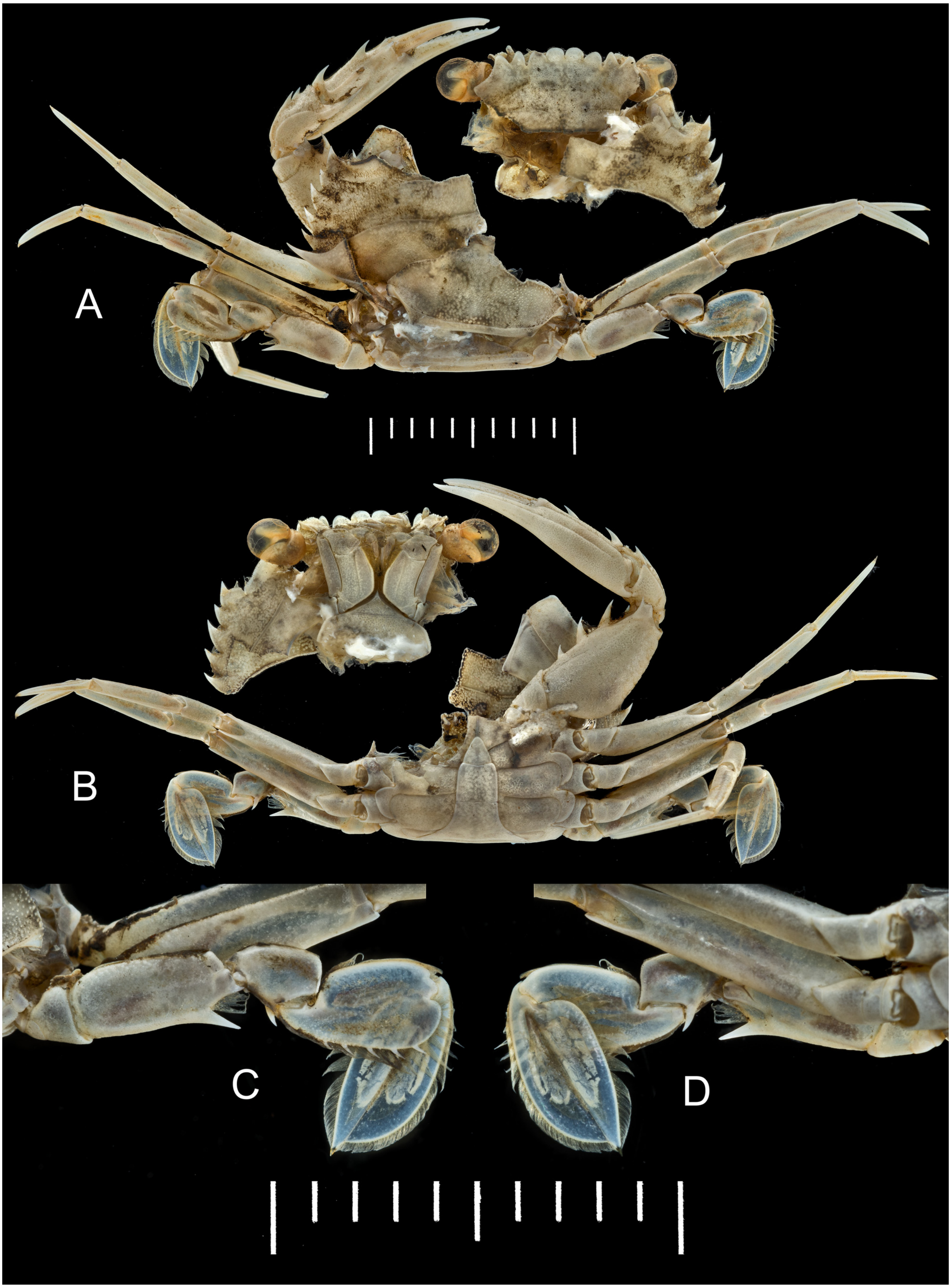


FIGURE 4. *Charybdis hellerii* (A. Milne-Edwards, 1867), male holotype of *Goniosoma spiniferum* Miers, 1884, about 13 x 17 mm, Queensland, Port Molle, NNM 1881.31. A. Dorsal habitus. B. Ventral habitus. C. Right pereiopod 5 (dorsal view). D. Right pereiopod 5 (ventral view).

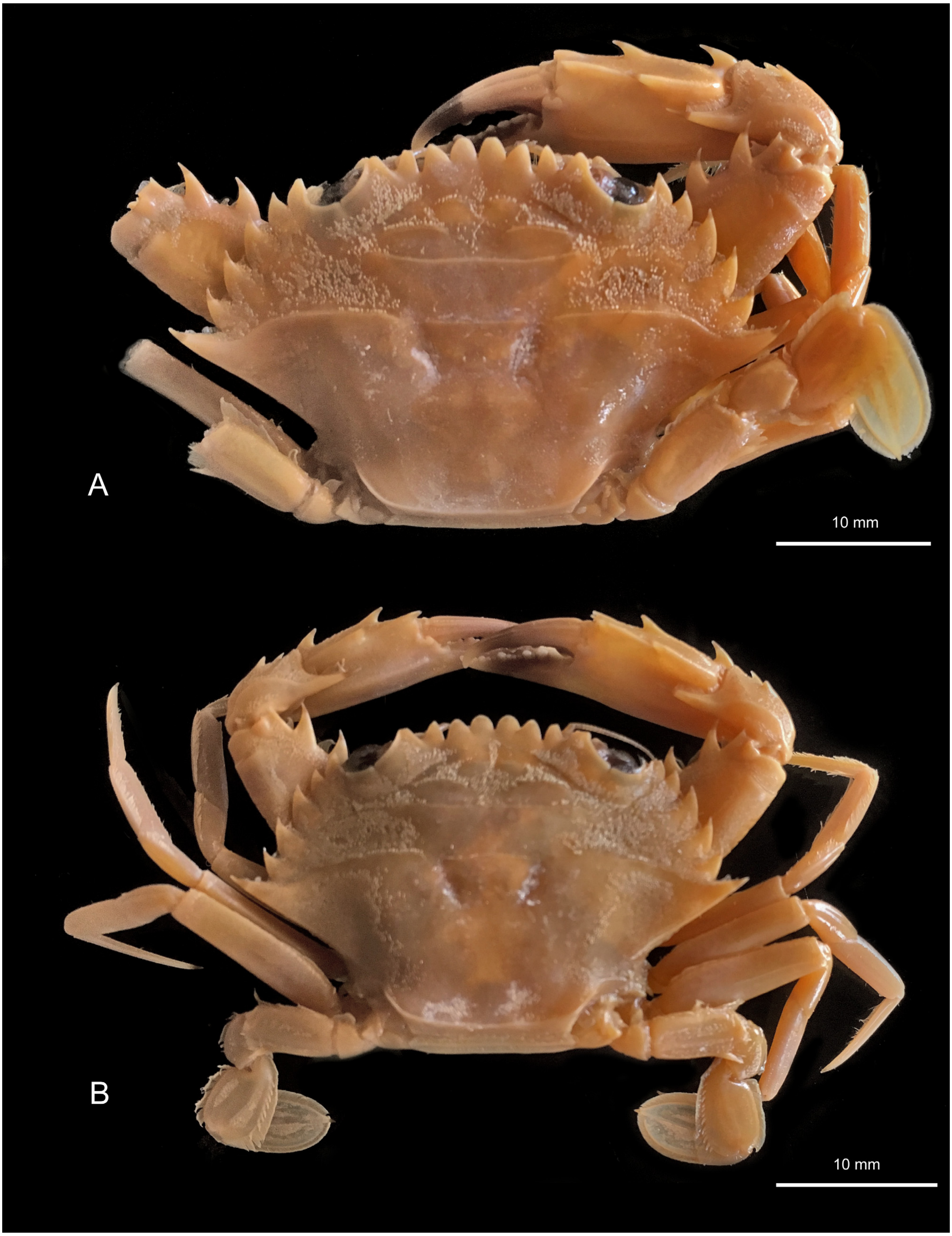


FIGURE 5. *Charybdis hellerii* (A. Milne-Edwards, 1867), males, dorsal habitus, Mergui Archipelago, syntypes of *Goniosoma merguiensis* De Man, 1887, RMNH.CRUS.D.13101886. A. 25.0 x 40.0 mm. B. 21.0 x 32.0 mm.

FIGURE 6. *Charybdis hellerii* (A. Milne-Edwards, 1867), males, Benin, Channel of Cotonou. A, B. 37 x 56 mm, RBINS, INV. 150111. C. 46.6 x 68.7 mm, RBINS, INV. 150110. A. Habitus dorsal. B, C. Frontal region.

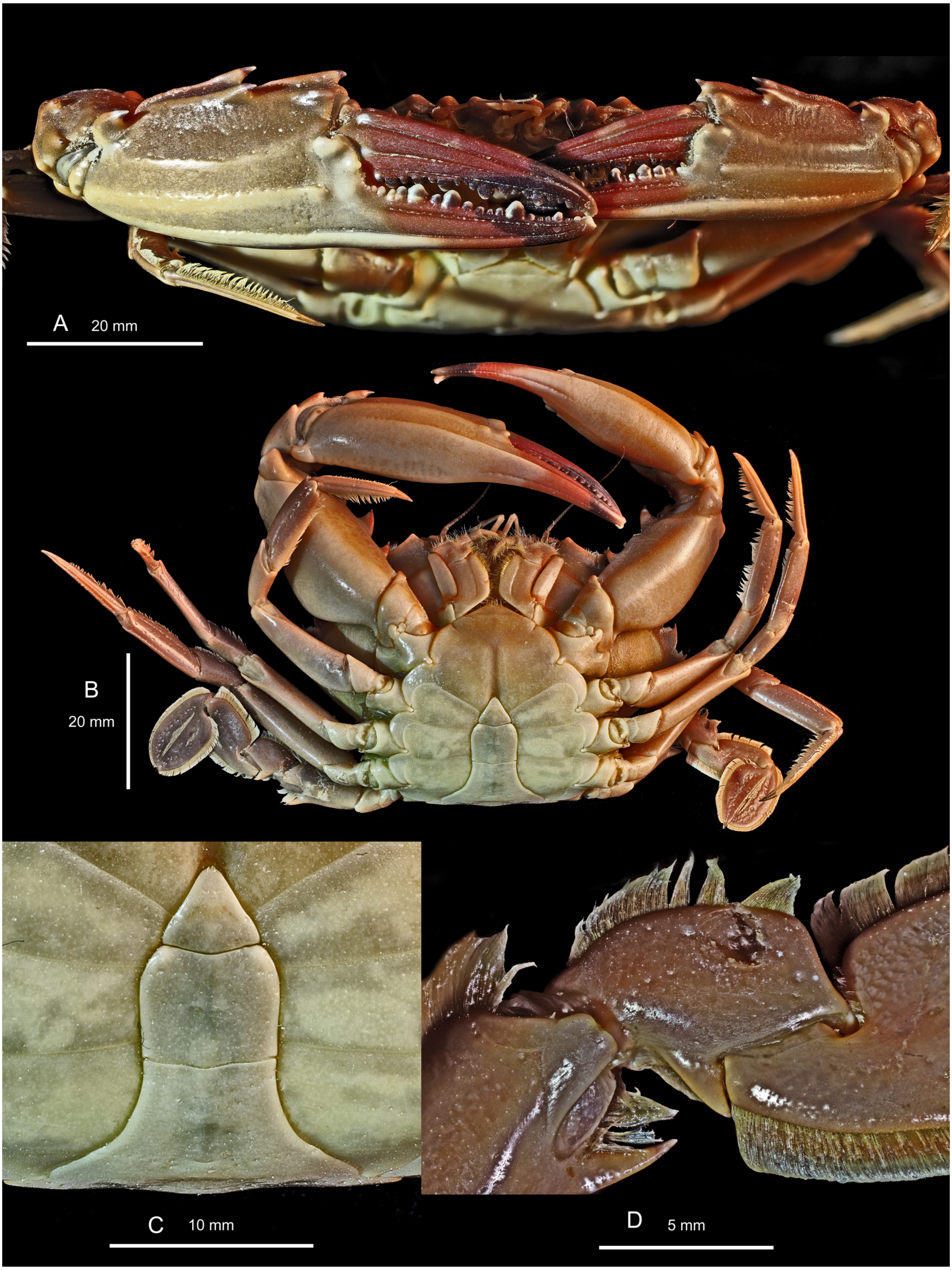


FIGURE 7. *Charybdis hellerii* (A. Milne-Edwards, 1867), male, 37.0 x 56.0 mm, Benin, Channel of Cotonou, RBINS, INV. 150111. A. Lateral view of the chelipeds. B. Ventral habitus. C. Telson. D. Carpus and extremity of adjacent articles of left pereiopod 5 (ventral view).

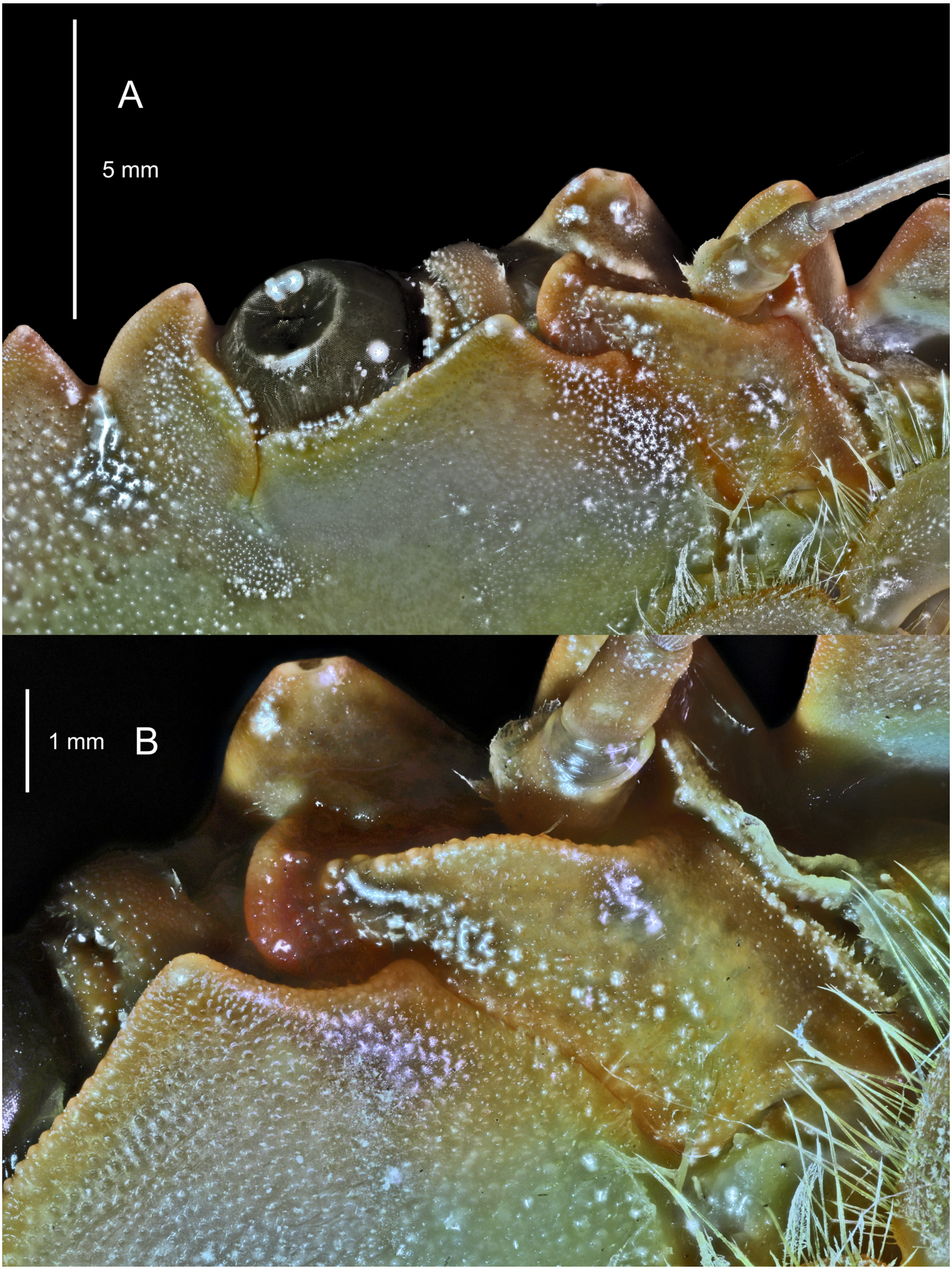


FIGURE 8. *Charybdis hellerii* (A. Milne-Edwards, 1867), male, 37.0 x 56.0 mm, Benin, Channel of Cotonou, RBINS, INV. 150111. A. Right orbital region (ventral view). B. Right basal antennal article.

FIGURE 9. *Charybdis hellerii* (A. Milne-Edwards, 1867), male, 37.0 x 56.0 mm, Benin, Channel of Cotonou, RBINS, INV. 150111. A. Gonopod 1. B. Tip of gonopod 1. The colour have been enhanced to increase the contrasts.

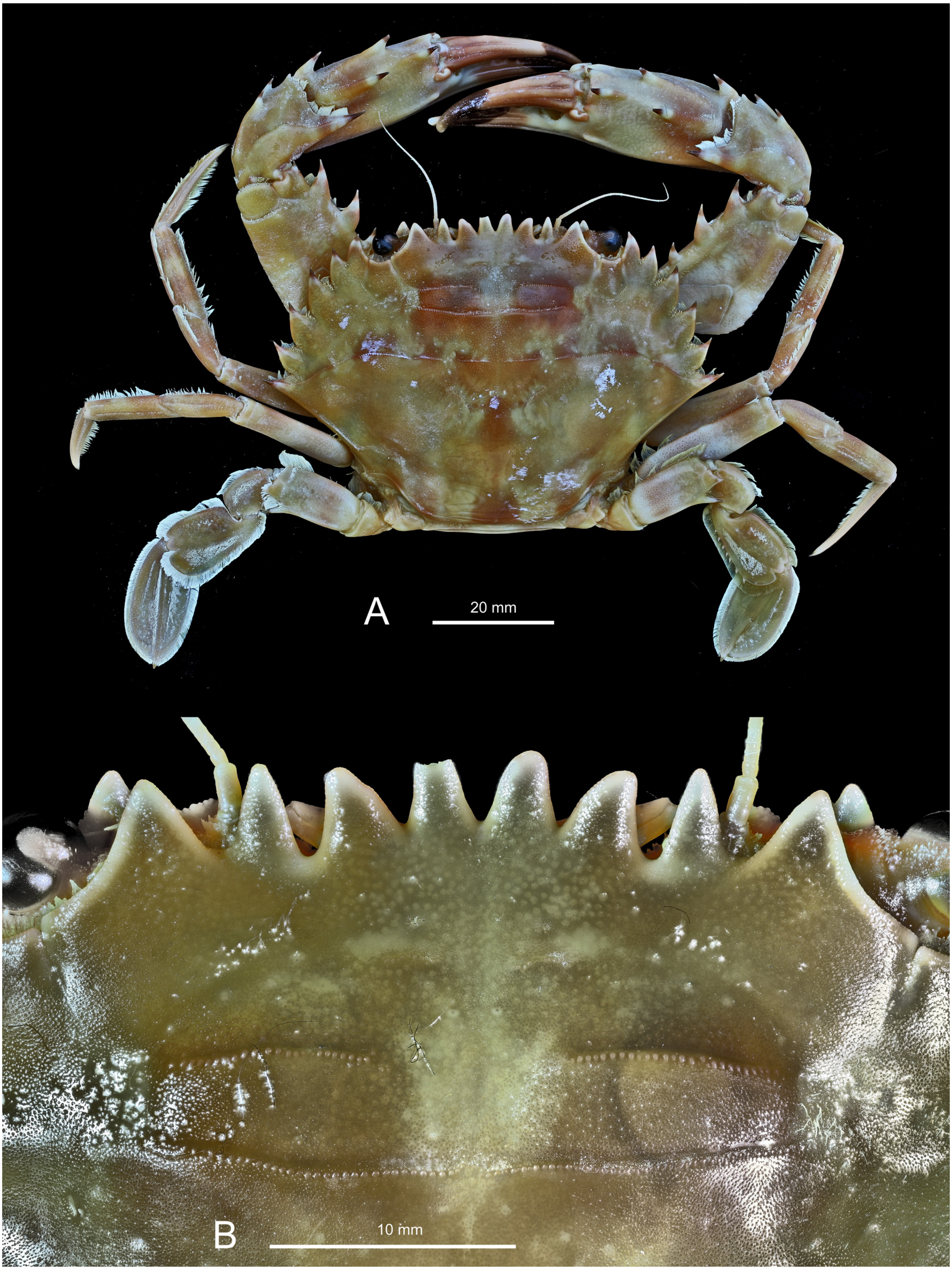


FIGURE 10. *Charybdis hellerii* (A. Milne-Edwards, 1867), male, 47.0 x 68.0 mm, New Caledonia, RBINS, INV. 129463. A. Dorsal habitus. B. Frontal region.

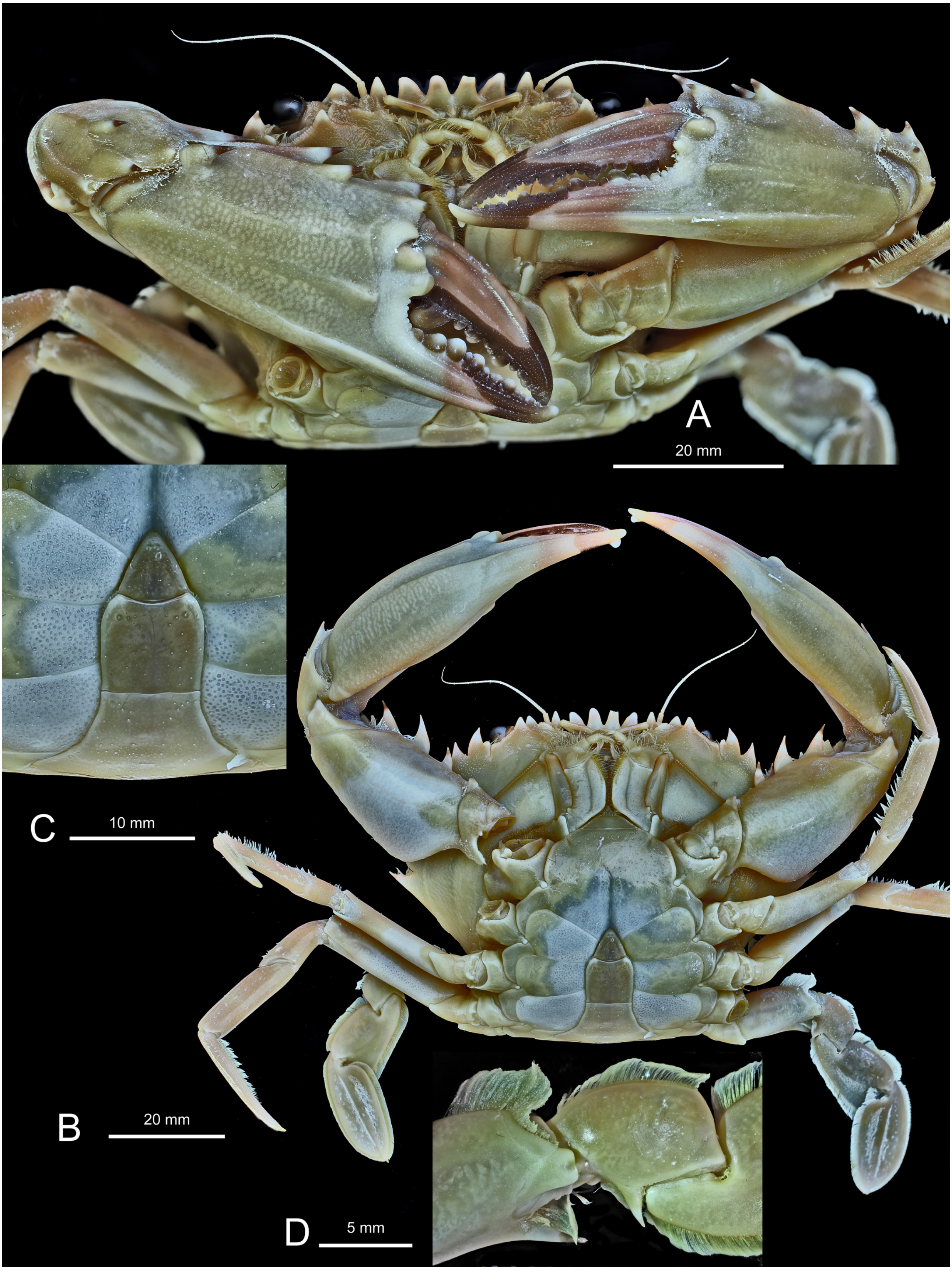


FIGURE 11. *Charybdis hellerii* (A. Milne-Edwards, 1867), male, 47.0 x 68.0 mm, New Caledonia, RBINS, INV. 129463. A. Lateral view of chelipeds. B. Ventral habitus. C. Telson. D. Carpus and extremity of adjacent articles of left P5, ventral view). The colour have been enhanced to increase the contrasts.

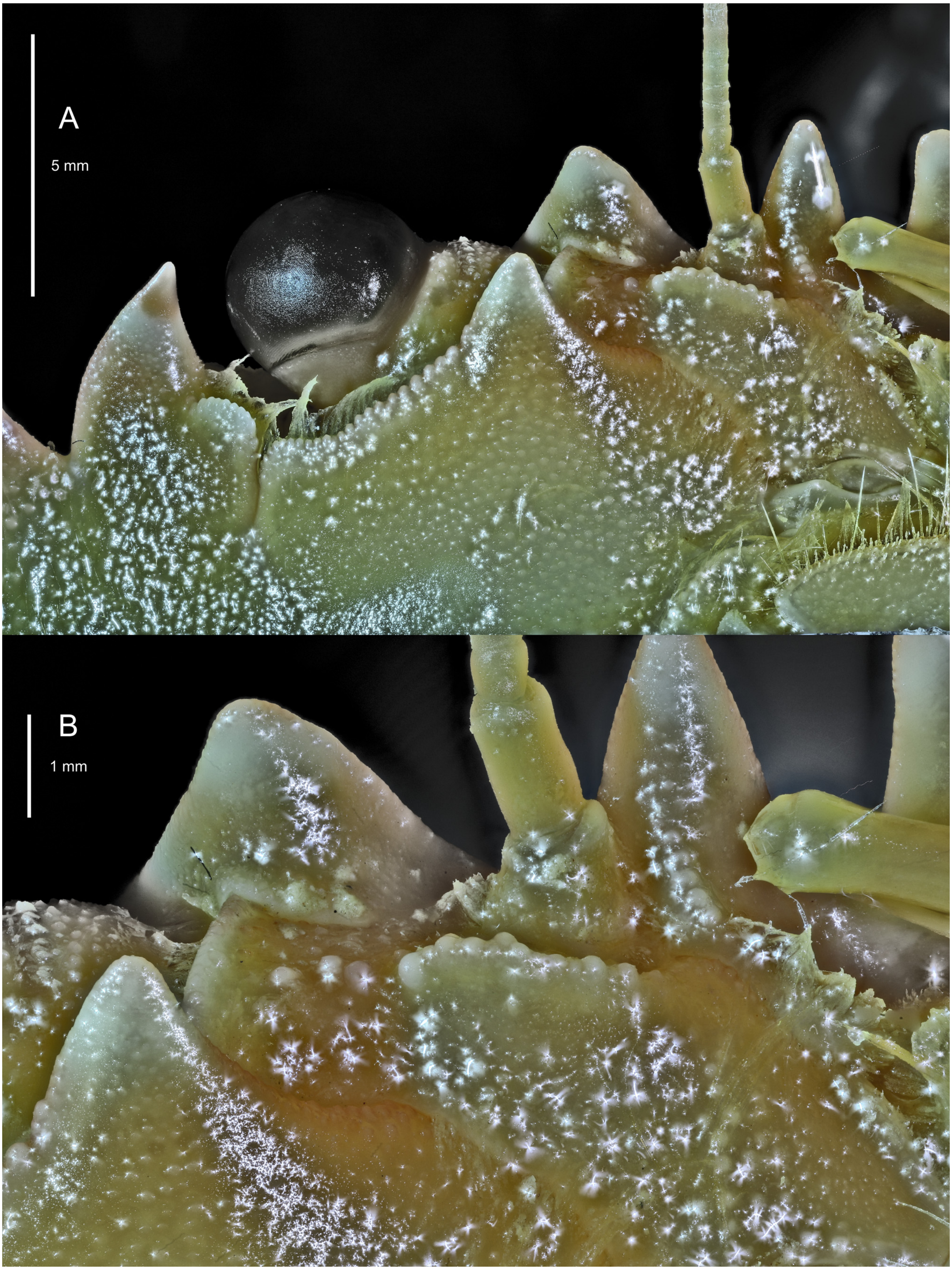


FIGURE 12. *Charybdis hellerii* (A. Milne-Edwards, 1867), male, 47.0 x 68.0 mm, New Caledonia, RBINS, INV. 129463. A. Right orbital region (ventral view). B. Right basal antennal article.

FIGURE 13. *Charybdis hellerii* (A. Milne-Edwards, 1867), male, 47.0 x 68.0 mm, New Caledonia, RBINS, INV. 129463. A. Right gonopod 1. B. Tip of right gonopod 1. The colour have been enhanced to increase the contrasts.

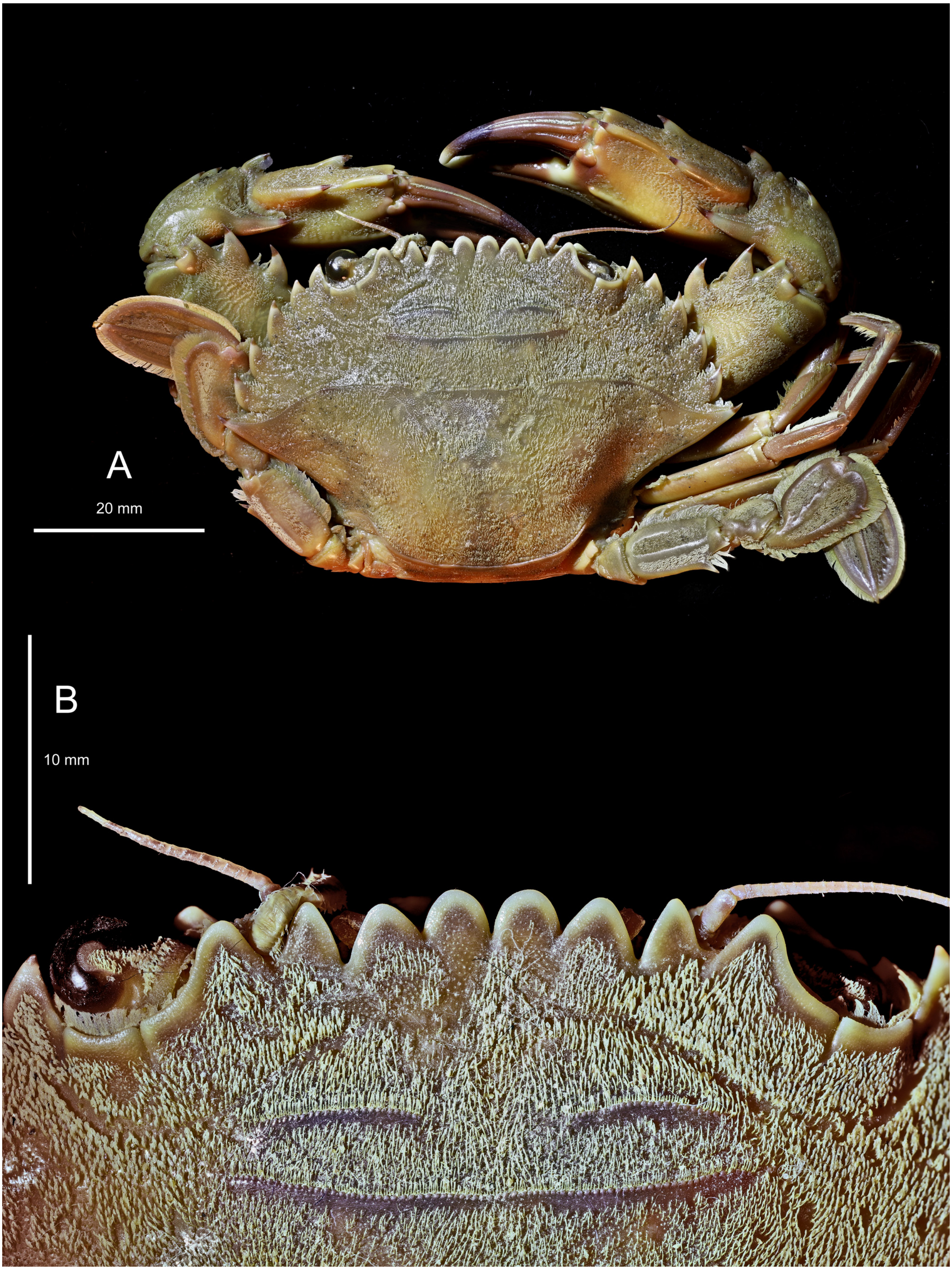


FIGURE 14. *Charybdis hellerii* (A. Milne-Edwards, 1867), male, 37.0 x 56.0 mm, Queensland, RBINS, INV. 129466. A. Dorsal habitus. B. Frontal region.

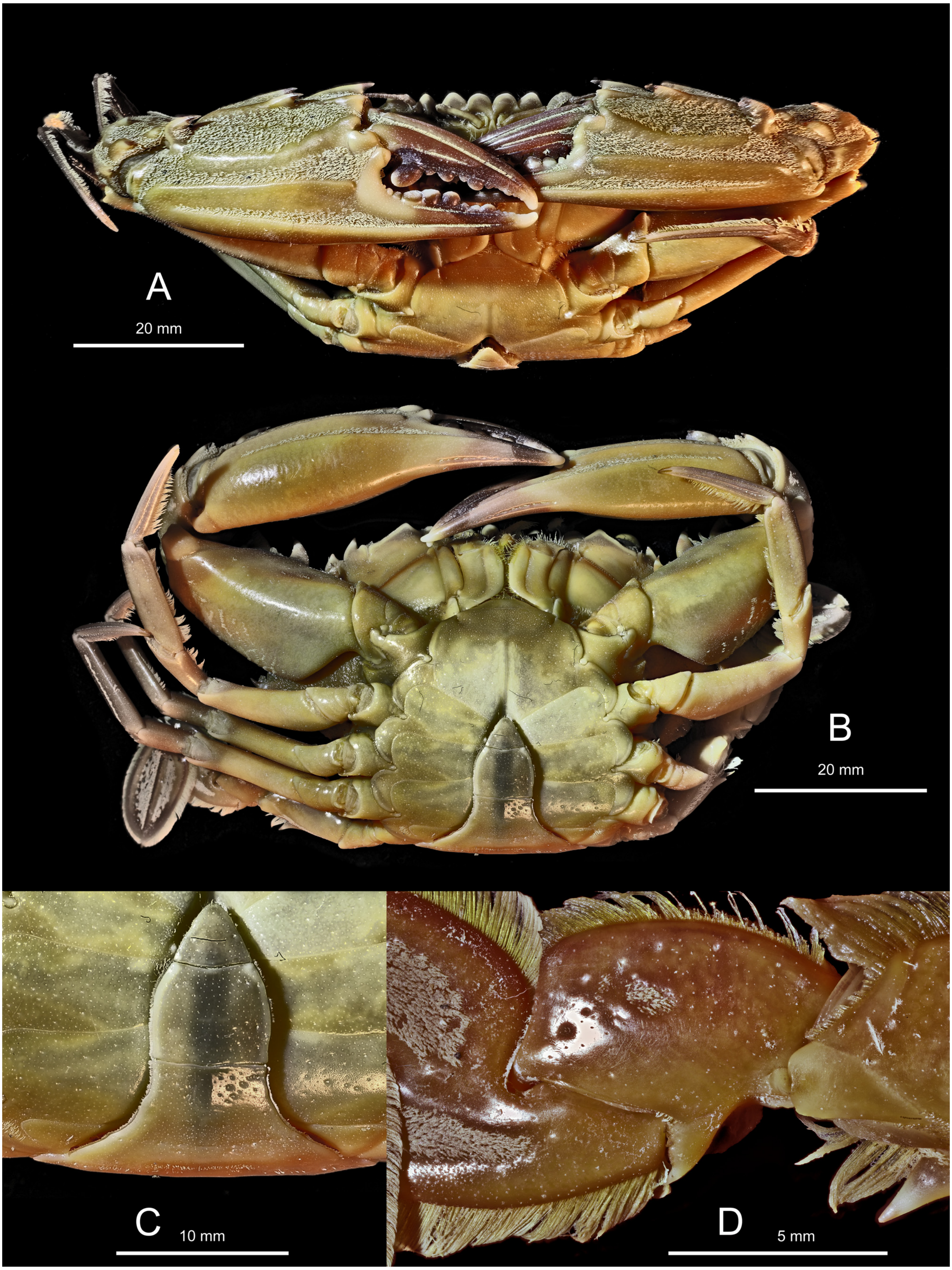


FIGURE 15. *Charybdis hellerii* (A. Milne-Edwards, 1867), male, 37.0 x 56.0 mm, Queensland, RBINS, INV. 129466. A. Lateral view of the chelipeds. B. Ventral habitus. C. Telson. D. Carpus and extremity of adjacent articles of right pereiopod 5 (ventral view). The colour have been enhanced to increase the contrasts.

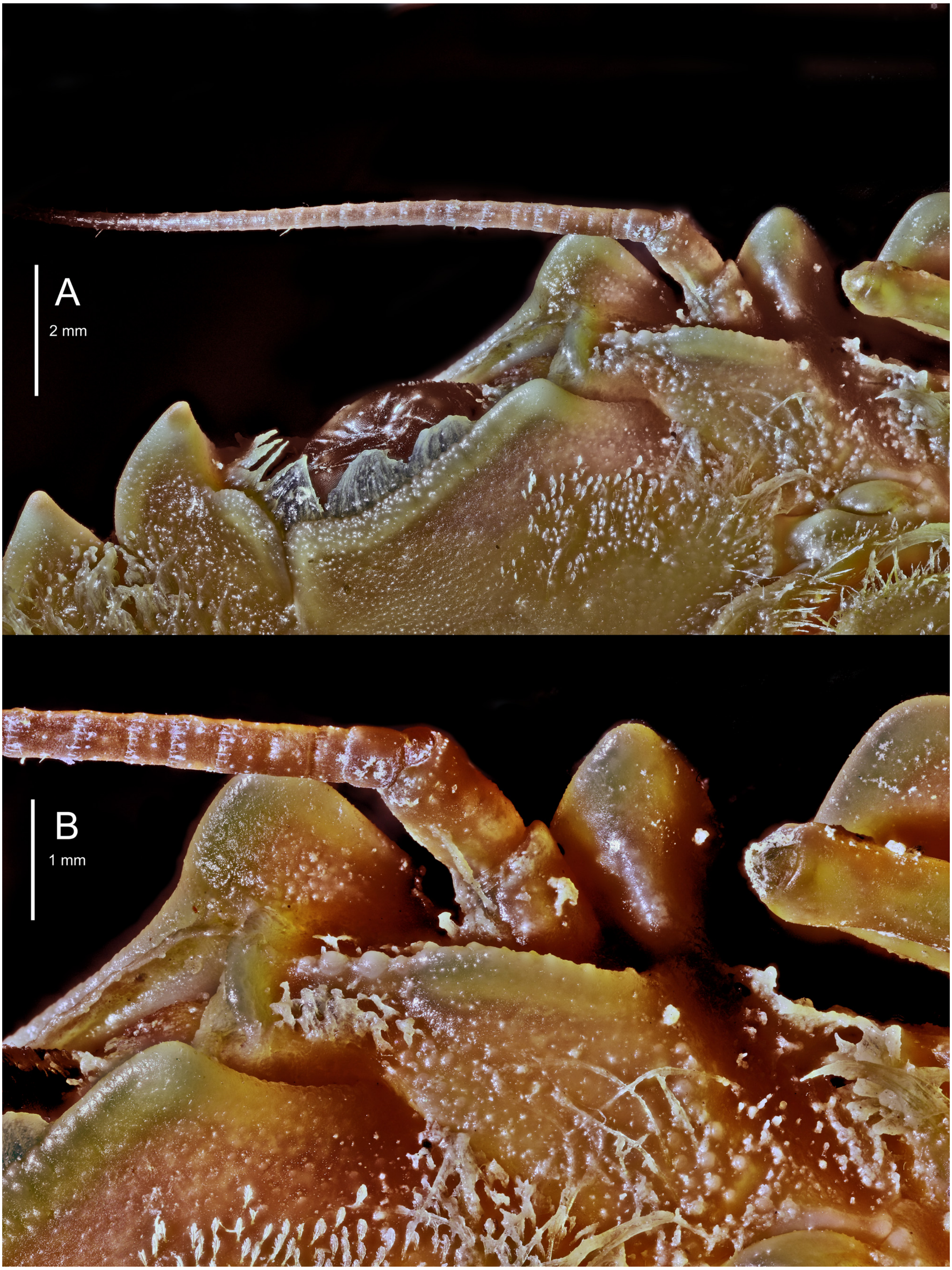


FIGURE 16. *Charybdis hellerii* (A. Milne-Edwards, 1867), male, 37.0 x 56.0 mm, Queensland, RBINS, INV. 129466. A. Right orbital region (ventral view). B. Right basal antennal article. The colour have been enhanced to increase the contrasts.

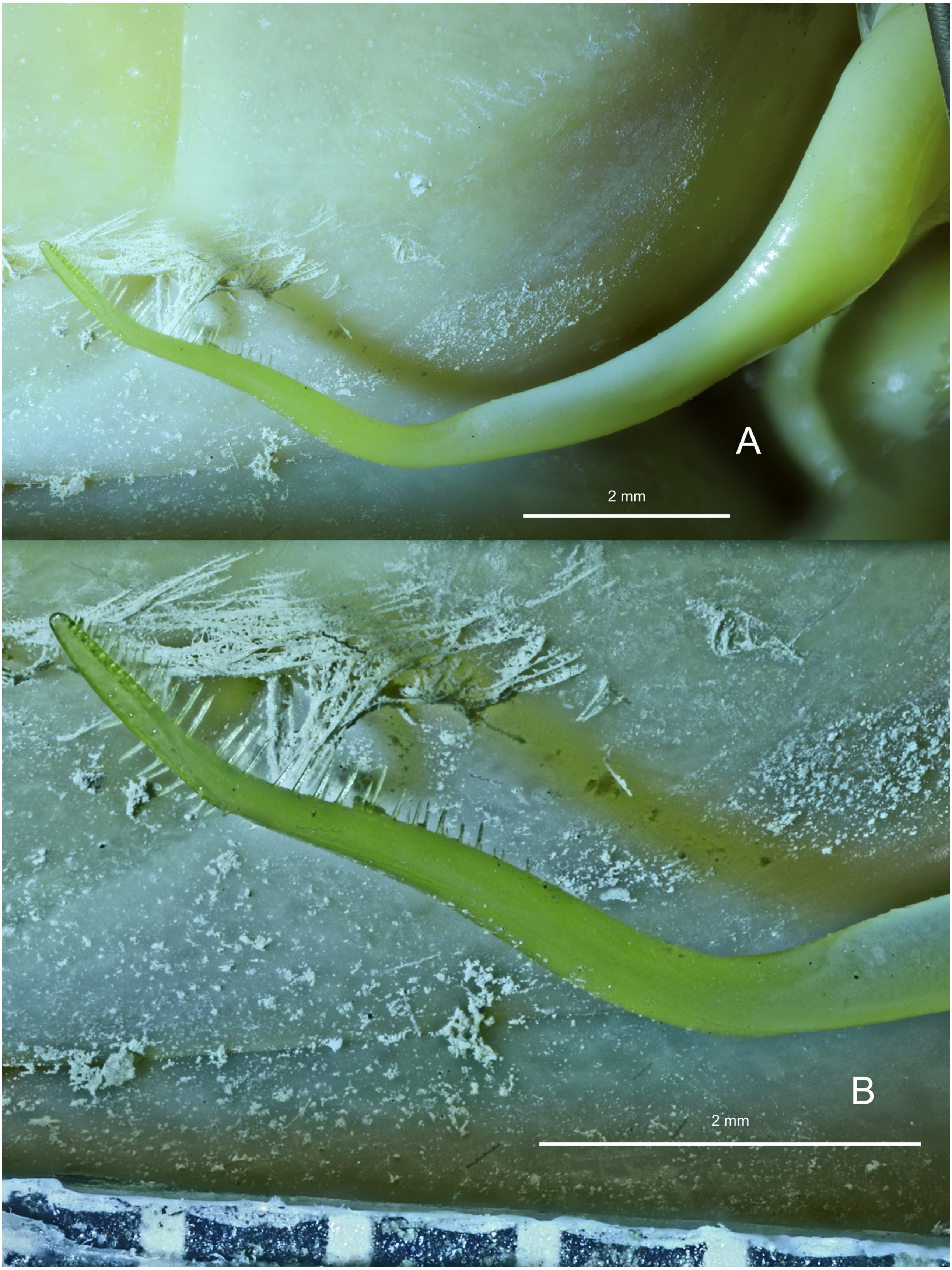


FIGURE 17. *Charybdis hellerii* (A. Milne-Edwards, 1867), male, 37.0 x 56.0 mm, Queensland, RBINS, INV. 129466. A. Left gonopod 1 B. Tip of gonopod 1.

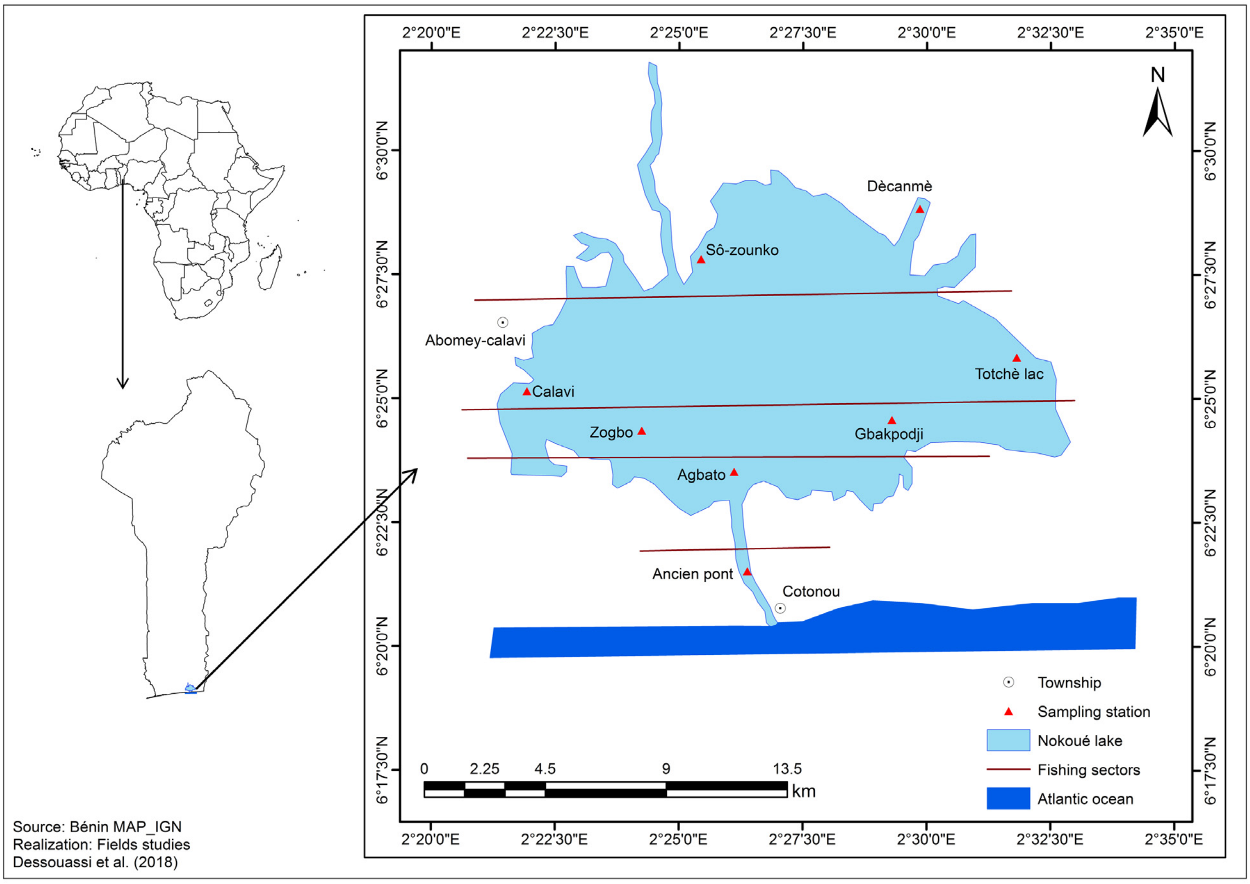


FIGURE 18. Location of the study area, showing fishing sectors.

Telson of mature males: segment 6 about as long as wide, with borders convex on their distal 0.2. Gonopods as illustrated.

Size. Up to 85 x 60 mm (A. Milne-Edwards, 1867). The lectotype of *Charybdis hellerii* is apparently the largest specimen of the species ever recorded.

Habitat and biology. Intertidal to 47 m, substrates rocky/cobble, sandy, muddy bottoms, mangroves and coral reefs (Stephenson *et al.* 1957; Crosnier 1962; Wee & Ng 1995; Apel & Spiridonov 1998; Özcan et al. 2010; Dineen *et al.* 2001; Naderloo 2017). Exceptionally found as deep as 86 m (Stephenson 1972a). Dineen *et al.* (2001) stated that *Charybdis hellerii* appeared to be closely associated with habitat structure of both hard substrates and some plant structures and presents a secretive and cryptic behaviour during daytime. The same authors reported that they collected it only at salinities > 28 ppt and Trento Occhi (2016) demonstrated that it cannot survive in low salinity brackish water, with 100% mortality after two days at 20 ppt. This crab reaches sexual maturity within about one year (Dineen *et al.* 2001). Its lifespan is estimated to 2–3 years and it reproduces continuously during the year (Bolaños *et al.* 2012), but ovigerous females are less abundant during the warmest months (Mantelatto & Garcia 2001). The smallest ovigerous female recorded was 34.6 mm carapace width (Mantelatto & Garcia 2001) and the largest still immature females recorded by Oshiro & da Conceição (2001) were about 45 mm cw. The diameter of the eggs ranges from 0.224 to 0.266 mm in Turkish populations (Özcan *et al*. 2010). Fecundity in *C. hellerii* is high and ranges from 22,550 eggs to 3,200,000 eggs per brood depending on size of the female (for review see Dineen *et al*. 2001). It can store sperm to produce multiple broods (up to 6 broods per year in captive condition) and its larval development (through 6 zoeas and one megalopa stages) requires about 44 days at 24°C and 32-ppt salinity (Dineen *et al*. 2001). *C. hellerii* is an opportunistic feeder. Excluding organic matter, the most abundant food items found in its stomach by Sant'Anna *et al.* (2015) were crustaceans (25%), molluscs (21%) and macrophytes (13%). It is documented that *C. hellerii* is itself consumed by octopuses (Sampaio & Rosa 2005). Parasitism by *Sacculina* has been reported in Australian populations [1.3% of infection] (Stephenson *et al.* 1957) and India (Elumalai *et al.* 2014) but not yet in invasive populations.

Distribution. Native: South Africa, East Africa, Madagascar, Red Sea, Gulf of Aden, Socotra, southern Oman, Persian Gulf, Gulf of Oman, Pakistan, India, Sri Lanka, Mergui-Archipelago, Andaman Sea, Thailand, Malaysia, Philippines, Indonesia, Singapore, Australia, New Caledonia (Naderloo 2017). Invasive: Mediterranean (Steinitz 1929; Monod 1930; Galil *et al*. 2002; Yokes & Galil 2006; Yokes *et al.* 2007); Hawai'i (Edmondson 1954: isolated record; Evans *et al.* 2018: population); south Pacific: sea-chest of a fishing vessel in New Zealand (Dodgshun & Coutts 2003); western Atlantic from the Atlantic coast of the USA to the south of Brazil (for review see Negri Pereira 2016; Negri *et al*. 2018); tropical eastern Atlantic: Guinea-Bissau [11.5342°N, 17.0770°W: (http://www.discoverlife.org/mp/20l?id=GBIF773871744 accessed 28.iii.2018)] and Benin (present material). An accidental isolated record on the hull of a ship in northwest Spain has been reported by Cuesta *et al*. (2016). The Mediterranean populations arrived from the Red Sea via the Suez Canal (Galil *et al.* 2002; Negri *et al.* 2018). It seems that the sources of invasive Western Atlantic populations are manyfold, consisting both of specimens from the western Indian Ocean and Mediterranean Sea group (major source) and from the Eastern Indian + western Pacific group (minor source, southern Brazil only) (Negri Pereira 2016; Negri *et al.* 2018).

Taxonomic discussion

Variation in the material examined. *Charybdis hellerii* exhibits considerable variation in pubescence and in the sharpness of its frontal teeth. It is common to find both pubescent and glabrous specimens in the same population (Negri & Pereira 2016; Negri *et al.* 2018; Naderloo 2017), but according to our observations, the proportion of pubescent and glabrous specimens is very variable from population to population. For example, in the samples examined by us, pubescent specimens predominated in the specimens from Queensland (Fig. 14) and glabrous specimens were largely dominant in those of Benin (Fig. 6). Intermediate forms with pubescence limited to some part of the carapace were frequently observed, e.g. the syntypes of *Goniosoma merguiense* conserved in Naturalis (Fig. 5). Variation in pubescence was observed by one of the authors (C. d'Udekem d'Acoz) in other portunoid crabs like *Liocarcinus navigator* (Herbst, 1794) and *L. vernalis* (Risso, 1827) and we conclude that this character is of limited value in portunids in general, and not significant in the present case.

More intriguing is the variation in the sharpness of the frontal teeth. In 1887, De Man (1887 [1887–1888a] as *Goniosoma merguiensis*) examined juveniles and small to medium-sized mature specimens, and indicated that these teeth increased in sharpness with the size of the specimens. Our own observations, which are largely based on small to large-sized mature specimens, confirm these allometric changes in this character after the puberty moult. However, this only explains part of the observed variation. Some individual variation is also observed within all populations, between specimens of the same size, but also between populations. In the first instance (before the publication of the paper of Negri *et al*. (2018)), we interpreted these differences as a possible indication that several species were confused under the name *Charybdis hellerii* and that the invasive species was possibly not *C. hellerii*. This led us to examine specimens from different origins and to carry out a thorough review of literature. Our morphological study indicated that some available topotypical specimens from New Caledonia (the type specimens from the MNHN discussed more extensively in the historical section, and a specimen from the collections of Royal Belgian Institute of Natural Sciences) had sharper frontal teeth than in other specimens examined. The fairly small syntypes from the Mergui Archipelago, Queensland and the Philippines and the large specimens from Benin have relatively broader frontal teeth. Finally, according to Negri Pereira (2016) and Negri *et al.* (2018), individual variation in the sharpness of frontal teeth is high in West Atlantic specimens and there is no correlation between the different phenotypes and genotypes studied by them. Illustrations of a selection of specimens examined is presented herein (Figs 1–19).

The *Charybdis* specimen illustrated with line drawings by Tirmizi & Kazmi (1996: fig. 23) as *C. hellerii* presents short ridges on the posterior half of its carapace. This raises questions about its real identity because *C. hellerii* is not supposed to have posterior ridges.

Presumed absence of cryptic species. Recently, Negri *et al.* (2018) published a global-scale genetic study on *C. hellerii*. Only one species, with only minor genetic differences between populations, was present in their material—which included specimens from numerous localities from the Indo-Pacific Ocean (including New Caledonia, which is the type locality), the Mediterranean Sea and the West Atlantic Ocean. Although genetic data are not yet available for the population from Benin, it presumably belongs to that same widespread species.

Note on the type specimens of *Goniosoma hellerii* A. Milne-Edwards, 1867. Alphonse Milne-Edwards (1867: 182–183) based the original description of *Goniosoma hellerii* (now in *Charybdis*) by reference to *Goniosoma orientale* of Heller (1865: 29, pl. 3, fig. 3), from the Nicobar Islands, which in turn was judged different from *G. orientale* of Dana, 1852 (p. 85). A. Milne-Edwards (1867) mentions a specimen measuring cl 60.0 mm, cw 85.0 mm, without any figures, and quotes two origins—"Inde archipélagique", which refers to the species of Heller, and New Caledonia, which is the actual type locality. The MNHN contains in its historical collection a dry specimen labelled "*Charybdis helleri* A. Edw., M. Aubry Lecomte, Nlle Calédonie" (MNHN-IU-2000-732 = MNHN-B732), a male with measurements similar to those cited in the original publication. As most often at this period, there was no indication of "type". However, as the size of the crab matches with the account of A. Milne-Edwards (1867) and as it was collected by Aubry-Lecomte who was working in Oceania after 1854 and before 1859, this sample can be considered to have been examined by A. Milne-Edwards (1867) for the establishment of *Charybdis hellerii.* According to Danièle Guinot (pers. com.), Charles Eugène Aubry-Lecomte (1821–1898) was a French colonial administrator, responsible for creating a permanent collection of objects from the French colonies, and was well known for donating material to the MNHN; material which was then subsequently used by the Muséum scientists in their studies. For this reason, on request of Michael Apel in 1998, Danièle Guinot proposed that he selects this male specimen as the lectotype. In their revision of the Portunidae from the Arabian Gulf, Apel & Spiridonov (1998: 195, 196) implemented this lectotype designation (without examining the specimen) but erroneously indicated "MNHN-B.761 S" as its registration number. As indicated earlier in the present paper, the correct registration number of the specimen (lectotype) collected in New Caledonia by Aubry-Lecomte is MNHN-IU-2000-732 (= MNHN-B732). Apel & Spiridonov (1998: 196) may have inadvertently interchanged the registration numbers of two different specimens. They indicated "MNHN-B.732 S" as the registration number of another old dry specimen, a smaller male 50.00 x 72.40 mm labelled "*Charybdis helleri*, M. Jouan, Nlle Calédonie", whilst its correct registration number is MNHN-IU-2000-761 (= MNHN-B761). Jouan's specimen was originally a syntype, and became a paralectotype as a consequence of the designation of Aubry-Lecomte's specimen as lectotype by Apel & Spiridonov (1998). "M. Jouan" refers to the French navigator, geographer, naturalist and ethnologist Henri Jouan (1821–1907) who captained the *Bonite* (December 1859) bound for New Caledonia, explored the island and left in March 1863 with an important collection of animals that he donated to the MNHN. The "Catalogue des Animaux articulés : Crustacés, Arachnides, Insectes, reçus, donnés, échangés ou achetés", recording the entry of the material in the MNHN, mentions five crabs "collected on the Neocaledonian coasts by M. Jouan, Commander of the *Bonite*". "Jouan reef" located about 7 km northwest of the island of Lifou in the Loyalty Islands was dedicated to him.

In the lectotype collected by Aubry-Lecomte (Figs 1A, 2A, 3A–B), the carapace is glabrous and shows a bluish colour. Its left frontal teeth are broken (the inter-dental cavity of all teeth is well visible), whereas the right ones are sharp and pointed. The antero-lateral marginal teeth on the carapace and chelipeds are in good condition (Guinot, pers. com.). The left gonopod 1 has been rehydrated and is now preserved in ethanol. In the paralectotype collected by Jouan (Figs. 1B–C, 2B–C, 3C–E), the front is not damaged, all teeth are complete: the two median ones are blunt and narrow, the lateral ones are triangular and more acute. The left gonopod 1, which has been rehydrated and is now preserved in ethanol, is figured, as for the lectotype.

Alphonse Milne-Edwards (1867: 232, as *Goniosoma hellerii*) chiefly compared the species to '*Goniosoma orientale*' of Heller (1865) and did not describe his new species at length but did mention that the carapace was devoid of setae. Later on, A. Milne-Edwards (1873: 167, as *Goniosoma hellerii*) wrote that the species can reach a quite considerable size, is found among the rocks, and the colour is greenish, the legs with shades of violet, this colour turning red on the chelipeds, the tips of fingers being black.

It must be noted that the *Goniosoma orientale* of Heller, 1865 [not *Charybdis orientalis* Dana, 1852] is in fact *Charybdis* (*Charybdis*) *annulata* (Fabricius, 1798) (fide De Man (1888 [1887–1888b]: 83, footnote; Leene 1938: 69, 70).

Leene (1938) made enigmatic statements about the type material of *C. hellerii*: she stated (p. 45) "In the Paris Museum I examined a large male of *Goniosoma hellerii* A. M. Edw. from New Caledonia, which very probably is the type-specimen". But on page 46, she gave a figure of a specimen captioned as "*Charybdis hellerii* (A. M. Edw.), ♀ type specimen (x 9/10), drawn by Miss Millon." The specimen has three pereiopods missing (left P5 and right P2 and P3). Its frontal teeth are very narrow, as in the lectotype and paralectotype of *G. hellerii* but the carapace seems pubescent, so the hypothesis that it could represent the paralectotype examined is unlikely. It cannot be ruled out that the crab illustrated in Leene (1938) was an additional specimen from the type series, which is now lost or stored at an unknown location. This, however, seems rather unlikely.

Finally, in the "list of specimens of *Charybdis hellerii* used for morphological analysis" by Negri *et al*. (2018), there is a crab from New Caledonia indicated as "MNHN-B761S [lectotype], specific site and collection date not given". This is a repetition of the incorrect registration number given by Apel & Spiridonov (1998). It must be changed to MNHN-IU-2000-732 (= MNHN-B732).

Synonyms and nomenclatural issues. Examination of photographs of the (juvenile) holotype of *Goniosoma spiniferum* Miers, 1884 collected in Queensland and deposited in the Natural History Museum, London (published herein as Fig. 4) indicated that it also falls within the range of variation of *C. hellerii* and confirms that this taxon is a junior synonym of the later. This was previously stated by Leene (1940), who re-examined the holotype (without illustrating it), but not always accepted in more recent literature.

Examination of photographs of two syntypes of *Goniosoma merguiense* De Man, 1887 collected in the Mergui Archipelago and deposited in Naturalis, Leiden (published herein as Fig. 5) reveals no differences with other *Charybdis* specimens examined and confirms that this taxon is a junior synonym of *C. hellerii*, as usually assumed (Leene 1938; Wee & Ng 1995; Apel & Spiridonov 1998). According to Apel & Spiridonov (1998), another syntype exists in the Berlin Museum für Naturkunde. Other syntypes are presumably deposited in the Zoological Survey of India. There are no syntypes in the Natural History Museum, London (P.F. Clark, pers. comm.).

Evans *et al.* (2018), who re-examined the type material of *Charybdis vannamei* Ward, 1941, that was collected in the Philippines, confirmed that this taxon is also identical with *C. hellerii*.

There is an issue concerning *Talamita sexdentata* Rüppell, 1830. Rüppell (1830) described *Talamita sexdentata* Rüppell, 1830 [misspelling for *Thalamita sexdentata* Rüppell, 1830], apparently considering it as a new species. Indeed, he added "Mihi" (old disused term technically equivalent to sp. nov. or n. sp.) after the species name. However, at the same time he placed *Cancer sexdentatus* Herbst, 1783, in the synonymy of his *Talamita sexdentata*. It is not ruled out that "Mihi" was printed by mistake, after *Talamita sexdentata*, in place of "Herbst". We cannot be certain. If one accepts that Rüppell (1830) really intended to create a new species, the specimens studied by him have to be considered as syntypes. According to Fransen *et al*. (1997: 179–180), this material consists of two specimens of *Charybdis hellerii* (A. Milne-Edwards, 1867) and two specimens of *Charybdis japonica* (A. Milne-Edwards, 1861). As *Cancer sexdentatus* Herbst, 1783, has precedence over *Talamita sexdentata* Rüppell, 1830, and as all the type material of these two taxa belong to the genus *Charybdis*, the name introduced by Rüppell (1830) is not available and not a threat to the stability of nomenclature.

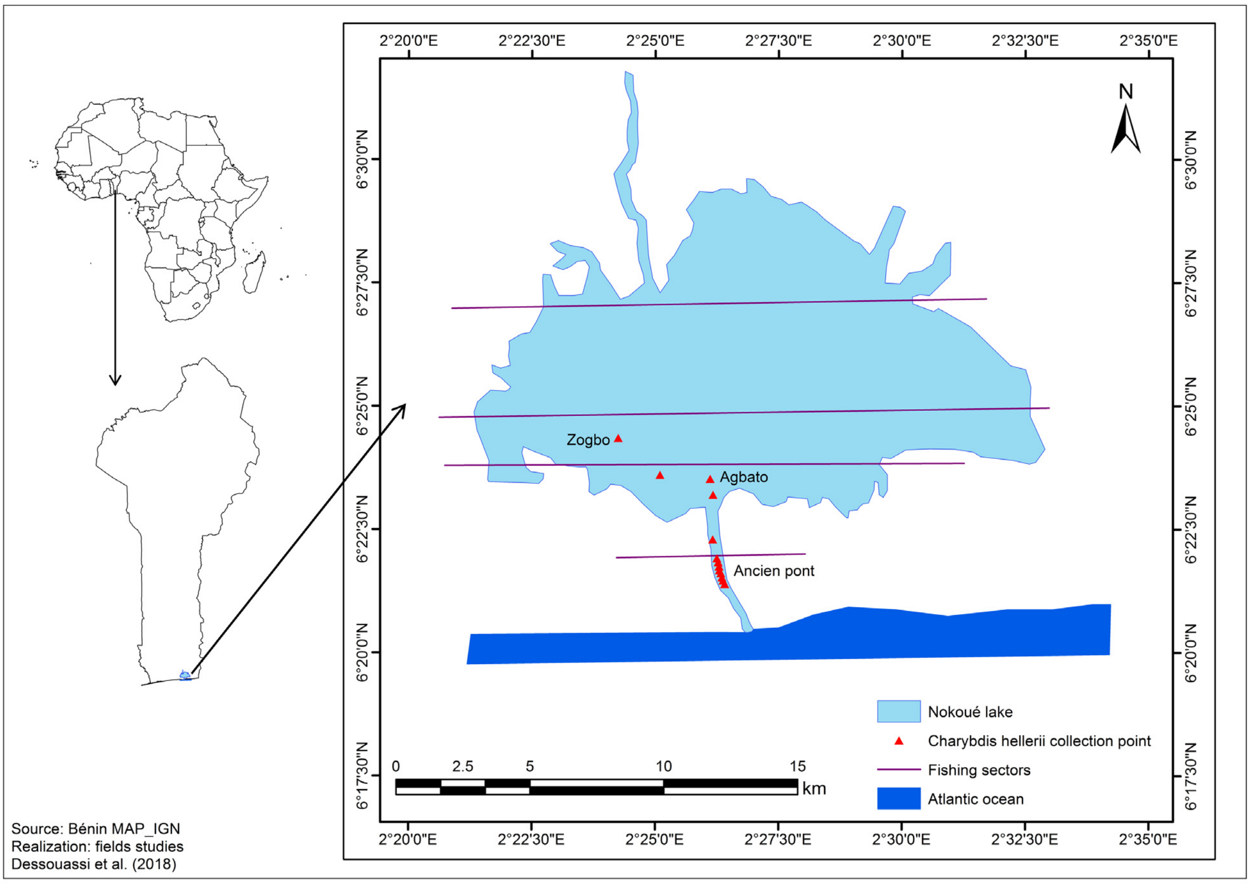
Finally, it must be noted that *Cancer sexdentatus* Herbst, 1783, is an objective junior synonym of *Cancer feriatus* Linnaeus, 1758 [currently *Charybdis feriata* (Linnaeus, 1758)] by the designation of the same specimen as lectotype for the two taxa by Holthuis (1962).

Distributional and ecological data on *Charybdis hellerii* (A. Milne-Edwards, 1867) in Benin

Observations. Seven crab species belonging to two families and five genera were inventoried in Benin from February 2017 to January 2018. The relative abundance of the different species is presented in Table 2.

Charybdis hellerii was recorded at 13 sampling sites, including in three fishing sectors out of eight on Nokoué Lake (actually a lagoon) from February to June (Fig. 19). The highest occurrence is noticed in the 'Ancien Pont' fishing sector, which is located on the channel of Cotonou, and which connects the lake to the Atlantic (Fig. 19). The abundance of these crabs decreases upstream (Table 3). According to some experienced fishermen working at 'Ancien Pont' fishing sector, *C. hellerii* first appeared in their catches in 2012. The species is sold at the local market together with other portunid crabs. As suspected, the species observed in the lake came from the sea, we showed some preserved *C. hellerii* specimens to the marine fishermen at Cotonou Fishing Port located about 2 kilometers from the 'Ancien Pont' fishing sector. They informed the first author that the species is also found among rocks on the Atlantic coast of Benin. The details of the *C. hellerii* collection sites and occurrence data are presented in Table 3 and Fig. 20.

Origin and long-term consequences of introduction of *C. hellerii* on the Western African coast. A number of factors associated with human activities such as the presence of living organisms in ship ballasts, and the increase and acceleration of maritime transport are promoting the dispersal of species far beyond their natural range (Carlton 1996, 2011; Ojaveer *et al.* 2018). This alarming problem, which irreversibly homogenises the world's marine ecosystems, is steadily increasing, and invasive marine species have become a global issue with immense ecological and often economic impacts (Boudouresque 2008). In this respect, a number of decapod crustaceans have proved to be very successful, conspicuous invaders (Galil *et al*. 2011; McLay 2015). Some species have strong predispositions for invading new territories (Boudouresque 2008) and species, which have already invaded new territories, have a high potential for succeeding in secondary invasions (Daehler & Strong 1993; Ricciardi & Rasmussen 1998). *C. hellerii* corresponds perfectly to this profile. Dineen *et al.* (2001) noted five biological traits likely responsible for the invasive success of this crab species, namely (1) a relatively long larval life (44 days), which facilitates dispersal; (2) a rapid growth and maturation (within about one year), contributing to a short generation time, which then promotes rapid population growth; (3) the ability to store sperm and to produce multiple broods of high fecundity in rapid succession, which favours rapid expansion of founder populations; and (4) a generalized carnivorous diet, which allows opportunistic exploitation of a variety of food resources; (5) the ability to use a diversity of structured habitats, which enables it to exploit a range of habitats.



Source: Bénin MAP_IGN
Realization: fields studies
Dessouassi et al. (2018)

FIGURE 19. Distribution of *C. hellerii* by fishing sectors on Nokoué Lake.

Charybdis hellerii first colonized the Mediterranean Sea, presumably via the Suez Canal (Steinitz 1929; Monod 1930). So far, its Mediterranean distribution remains confined to its eastern basin, where it has become locally common (Yokes *et al.* 2007). However, it never became as abundant as another invasive *Charybdis* species originating from the Red Sea, *C. longicollis* Leene, 1938, which has become a dominant component of the East Mediterranean benthos (Innocenti & Galil 2007). In 1987, *C. hellerii* was recorded for the first time in the Western Atlantic, in Colombian and Cuban waters (Campos & Türkay 1989; Gómez & Martínez-Iglesias 1990). In the coming years, it was recorded in the whole Gulf of Mexico, on the Atlantic coast of Florida (Lemaitre 1995), and all along the warm Atlantic coasts of Latin America (Tavares & Braga de Mendonça 1996). It is currently reaching the south of Brazil (Negri Perreira 2016; Negri *et al.* 2018). Locally, *C. hellerii* became extremely abundant in the West Atlantic, and Sant'Anna *et al.* (2012b) reported that in the estuary-bay complex of São Vicente, State of São Paulo, Brazil, it has become the second most abundant crab species on rocky shores. Genetic data suggested a double origin for West Atlantic populations. While the largest source of introduction would be the Mediterranean Sea, population from southern Brazil would have originated, at least partly, from the eastern Indian or Pacific Oceans (Negri *et al.* 2018). In Brazil, *C. hellerii* is not consumed by the local population and, as a result, only the native portunids are the object of fishery pressure (Tavares 2011).

FIGURE 20. Collecting sites. A, B. "Ancien Pont". C, D. Behind the "Berlin".

The point and the time of arrival of *C. hellerii* in the Eastern Atlantic are not known. However, the crab was observed in 2011 in Guinea-Bissau, 11.5342°N, 17.0770°W: (http://www.discoverlife.org/mp/20l?id=GBIF773871744 accessed 28.iii.2018) and in 2012 in Benin (present data), i.e. in localities separated by 2000 km. This suggests that it arrived in West Africa around 2010 or before. Actually, it might have already colonized considerable territories, maybe far north of Guinea-Bissau and far south of Benin. As investigations on the inshore and estuarine decapod fauna along the West African mainland have been scarce in the early years of the 21st century, the current distributional range of *C. hellerii* along the Atlantic coast of Africa remains unknown.

However, considering the invasion pattern observed for the Western Atlantic, it can be predicted that this tropical and subtropical crab might spread as far south as Angola (and perhaps beyond) and as far north as the Western Sahara (and perhaps as far north as the southern tip of the Iberian Peninsula). Considering its pattern of invasion in the Western Atlantic (Tavares & Braga de Mendonça 1996; Negri *et al.* 2018), this process is expected to be rapid.

The vector of invasion to West Africa cannot be established. However, it is most likely maritime transports, either ballast water or hull fouling, which have been of major importance for the dispersal of invasive species (e.g. Galil *et al.* 2014; Ojaveer *et al.* 2018). The first records of *C. hellerii* in Hawai'i (Edmondson 1954) and north Spain (Cuesta *et al.* 2016) were based on specimens found on the hull of ships.

TABLE 2. Relative abundance of Benin crab species in fishery catches

Species	Relative abundance of crab species (% of specimens) in fishery catches												
	February 2017	March 2017	April 2017	May 2017	June 2017	July 2017	August 2017	September 2017	October 2017	November 2017	December 2017	January 2018	Total per species
Callinectes amnicola (Rochebrune, 1883)	99.03	95.68	80.36	74.28	84.53	77.70	96.99	100.00	99.19	100.00	83.51	64.03	86.24
Callinectes marginatus (A. Milne-Edwards, 1861)	0.00	0.00	0.36	1.85	0.30	1.28	0.41	0.00	0.00	0.00	0.00	0.00	0.47
Callinectes pallidus (Rochebrune, 1883)	0.00	3.60	18.32	20.30	13.20	21.02	2.46	0.00	0.00	0.00	16.49	35.97	12.29
***Charybdis hellerii* (A. Milne-Edwards, 1867)**	**0.97**	**0.00**	**0.60**	**2.31**	**1.28**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.57**
Cronius ruber (Lamarck, 1818)	0.00	0.36	0.24	1.27	0.30	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.25
Panopeus africanus A. Milne-Edwards, 1867	0.00	0.36	0.00	0.00	0.39	0.00	0.14	0.00	0.81	0.00	0.00	0.00	0.16
Sanquerus validus (Herklots, 1851)	0.00	0.00	0.12	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01
Total crab number per month	103	278	835	867	1015	547	731	648	620	314	376	467	6801

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TABLE 3. Habitat characteristics and spatio-temporal distribution of *C. hellerii* on Nokoué lake.

Code	Fishing Sectors	Sampling Point Coordinates		Altitude (m)	Depth (m)	Habitat Characteristic	Month				Total
		Longitude	Latitude				February 2017	April 2017	May 2017	June 2017	
	ANCIEN PONT						**0**	**4**	**12**	**6**	**22**
1.1	Ancien pont	2°26'19.6"E	6°21'23.3"N	4	4.35	Sandy bottom			1		1
1.2	Embarcadère DPH	2°26'15.2"E	6°21'35.7"N	1	1.25	Sandy bottom			2		2
1.3	Zone Police Fluviale	2°26'17.0"E	6°21'32.1"N	4	4.55	Sandy and muddy bottom		1	1		2
1.4	Derrière HOMEL	2°26'14.8"E	6°21'40.4"N	2	3.4	Sandy and Hard (block) bottom			2	1	3
1.5	Derrière marché Missèbo	2°26'13.8"E	6°21'45.5"N	3	7.5	Sandy and muddy bottom			2		2
1.6	Derrière Ecole Primaire Missèbo	2°26'12.2"E	6°21'50.2"N	4	3.8	muddy bottom		1			1
1.7	Entre Ancien Pont et 3$^{\text{ème}}$ Pont	2°26'18.3"E	6°21'27.1"N	4	4.35	Sandy and muddy bottom		2	4	4	10
1.8	Derrière le Berlin	2°26'21.7"E	6°21'19.1"N	5	4.25	Sandy bottom				1	1
	AGBATO						**1**	**1**	**8**	**6**	**16**
2.1	Agbato	2°26'3.9"E	6°23'26.9"N	6	5.15	Sandy bottom	1	1	2	3	7
2.2	Nouveau Pont (Tokpa)	2°26'7.1"E	6°22'13.3"N	3	3.7	Sandy bottom			2	3	5
2.3	Zone Hôtel Houzanpi	2°26'7.5"E	6°23'7.5"N	6	3	Sandy bottom			2		2
2.4	Awansori	2°25'3.0"E	6°23'31.7"N	5	1.18	Sandy bottom			2		2
	ZOGBO									**1**	**1**
3.1	Zogbo	2°24'12.0"E	6°24'16.6"N	4	1.5	Muddy bottom				1	1
	TOTAL						**1**	**5**	**20**	**13**	**39**

The origin of West African population is currently unknown. They might be derived from the invasive populations of the Mediterranean Sea or the Western Atlantic, or come directly from the Indo-Pacific Ocean.

Charybdis hellerii is a medium to large crab species, and in Brazil, it has been reported to be an aggressive predator, presumably able to outcompete the morphologically similar native *Cronius ruber* (Lamarck, 1818) on hard bottom substrates (Sant'Anna *et al.* 2012b). The same authors suspected that it would be less competitive against portunid crabs with a preference for softer substrates, like *Callinectes* spp. *Charybdis hellerii* is now present along the coast of West Africa, where it interacts with three endemic species of *Callinectes* Stimpson, 1860 (Manning & Holthuis 1981) and *Cronius ruber* (or at least a form extremely close to it (Mantelatto *et al*. 2009)). It would be important to document the pattern of interaction and competition between *C. hellerii* and these species. It is not known whether *C. hellerii* will be able to colonize habitats not occupied by native portunids or to use additional trophic resources. If this is the case, it might negatively impact other organisms and cause major disturbance to the structure of coastal and estuarine ecosystems of West African countries.

After the penaeid shrimp *Penaeus monodon* (Fabricius, 1997) (Clotilde-Ba *et al.* 1997), the palaemonid shrimps *Macrobrachium equidens* (Dana, 1852) (Powell 1986; Fransen 2014a) and *M. rosenbergii* (De Man, 1879) (Fransen 2014a), the palinurid lobster *Panulirus argus* (Latreille, 1804) (Freitas & Castro 2005) and possibly the pilumnid crab *Pilumnus minutus* De Haan, 1835 (De Estavão Neves 2016 as *Pilumnus hirsutus* Stimpson, 1858; González 2018), the portunid crab *C. hellerii* would be the sixth known marine/estuarine invasive decapod recorded from West Africa. This is a low number in comparison with many other regions of the world (Galil *et al*. 2002; Brockerhoff & McLay 2011; Galil 2011; Tavares 2011; McLay 2015). For example, Galil (2011) recorded 69 exotic decapod species in the Mediterranean Sea, a number which is already outdated. However, it is likely that in the future, more exotic marine and brackish-water decapods will colonize the Atlantic coasts of Africa. Indeed, the merging of biogeographical borders resulting from increasing human activities is an accelerating global phenomenon (Boudouresque 2008; Ojaveer *et al.* 2018).

If *C. hellerii* outcompetes the native African *Callinectes* species, it might have a negative impact on local fisheries and human food resources, because it is a smaller crab requiring more time for the extraction of the same amount of meat. Finally, Tavares & Braga de Mendonça (2004) and Tavares (2011) consider it to be a possible vector of the White Spot Syndrome Virus (WSSV), which could decimate penaeid shrimps from wild populations and aquaculture facilities.

Conclusion

Charybdis hellerii exhibits substantial morphological variability, especially in the presence/absence, density of pubescence, and in the sharpness of its frontal teeth. Pubescent and glabrous specimens co-occur in most (if not all) populations, but the proportions of these two forms considerably varies from population to population. The sharpness of frontal teeth is partly allometry-dependent, the sharpest teeth being observed in the largest specimens. However, in similar-sized specimens, moderate variation is observed in the same population and between populations. For example, large specimens from Benin usually have broader teeth than similar-sized specimens from New Caledonia. Morphological observations of specimens from distant localities carried out during this study could not establish the existence of pseudocryptic species within *Charybdis hellerii* and a recent genetic study (Negri Pereira 2016; Negri *et al.* 2018) confirmed that the species is genetically quite homogeneous, despite its very broad natural geographical distribution. It is concluded that *Charybdis spinifera* (Miers, 1884), *C. merguiensis* (De Man, 1887) and *C. vannamei* Ward, 1941 are junior synonyms of *C. hellerii* (A. Milne-Edwards, 1867).

Charybdis hellerii has established a thriving invasive population in Benin, tropical Eastern Atlantic and it is possible that it has already colonized a wide stretch along the West African coast, as there is also an isolated record from Guinea-Bissau. Data are missing for most countries of the Gulf of Guinea. In the absence of genetic data, the origin of the West African populations is currently impossible to establish. It might come from other invasive populations: Eastern Mediterranean Sea or Western Atlantic or it might be an independent colonization event from an Indo-Pacific population. Further research should be carried out to address this question.

It is hoped that the present paper will stimulate the attention of biologists working on the marine and estuarine fauna of West Africa and help to document the ongoing patterns of invasion.

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