

ON THE IDENTITIES OF THE RAFTING CRABS
CANCER DEPRESSUS FABRICIUS, 1775, *CANCER SQUAMOSUS* HERBST, 1790,
PLAGUSIA IMMACULATA LAMARCK, 1818, AND
PLAGUSIA TUBERCULATA LAMARCK, 1818
(CRUSTACEA: DECAPODA: BRACHYURA: PLAGUSIIDAE)

Christoph D. Schubart

Department of Biological Sciences, National University of Singapore, 10 Kent Ridge Crescent, Singapore 119260,
Republic of Singapore. Present address: Biologie I, Universität Regensburg, D-93040 Regensburg, Germany
Email: cd_schubart@yahoo.com

and

Peter K. L. Ng

Department of Biological Sciences, National University of Singapore, 10 Kent Ridge Crescent, Singapore 119260,
Republic of Singapore. Email: dhsngkl@nus.edu.sg

ABSTRACT. - The identities of the common Indo-West Pacific and Atlantic rafting crabs which have been identified with *Plagusia depressa* and *P. tuberculata* are clarified. The type series of *Cancer depressus* Fabricius, 1775, is mixed, and includes specimens of *Plagusia immaculata* Lamarck, 1818. A lectotype is selected to maintain its current use. The lectotype of *Cancer squamosus* Herbst, 1790, agrees very well with what is currently known as *Plagusia tuberculata* Lamarck, 1818, and the two names are clearly synonymous. The lectotype of *Cancer squamosus* Herbst, 1790, is here designated as the neotype of *Plagusia tuberculata* Lamarck, 1818. The types of *Plagusia orientalis* Stimpson, 1858, were examined and the name is also a junior synonym of *P. squamosa*. The identity of *Plagusia immaculata* Lamarck, 1818, a species very close to and often confused with *P. tuberculata*, is clarified and a neotype designated.

INTRODUCTION

In the modern scientific literature, three names are being used to refer to morphologically very similar species (or subspecies) of rafting crabs belonging to the genus *Plagusia*: *P. depressa* (Fabricius, 1775), *P. immaculata* Lamarck, 1818, and *P. tuberculata* Lamarck, 1818. There seems to be a general consensus on the use of these names and the distribution of the corresponding species (see Dawson, 1987). In the late 1800s and early 1900s, however, their status had been more uncertain, with their morphological differences, distributions and the correct synonymies in some doubt and confusion. In appraising the taxonomy of several plagusiid species in connection with other larval and systematic studies, we discovered that the taxonomy of these species is far from certain; and the currently used names are in fact either imprecise or incorrect. In the present paper, we show that the type series of *Cancer depressus* Fabricius, 1775, is mixed and a lectotype is

selected to maintain its current usage; *Cancer squamosus* Herbst, 1790, is a senior synonym of *Plagusia tuberculata* Lamarck, 1818, and *Plagusia orientalis* Stimpson, 1858; and a neotype is selected for *Plagusia immaculata* Lamarck, 1818, to stabilise its taxonomy.

HISTORY

The genus *Plagusia* was first used by Latreille (1804: 125) for only one species, *Cancer depressus* Fabricius, 1775. As such, it becomes the type species by monotypy. Latreille (1806: 34) subsequently used *Plagusia* for four species, *P. clavimana* Latreille, 1806 (validating a nomenclaturally invalid Seba name) (from "Oceano Indiae Orientalis, Australiasiam versus"), *P. depressa* (Fabricius, 1775) (Mediterranean), *P. semicylindrica* (Fabricius, 1798) (from Indian Seas), and *P. squamosa* (Herbst, 1790) (from East Indies).

Plagusia clavimana is now generally regarded as a junior synonym of *Cancer planissimus* Herbst, 1804, and placed in the genus *Percnon* Gistel, 1848. The identity of *Cancer semicylindricus* Fabricius, 1798, has been the matter of some debate, with some authors thinking it is a pinnotherid, but the name is currently an incerta sedis (see Schmitt et al., 1975: 138). The second author has examined the holotype male specimen in the Copenhagen Museum. *Cancer semicylindricus* Fabricius, 1798, is actually a species of *Xenophthalmodes* Richters, 1880 (Pilumnidae), a genus currently with four other species. As for the remaining two species, Latreille (1806: 34) distinguished *P. depressa* from *P. squamosa* in having "tuberculis dorsalibus nudis" (naked dorsal tubercles) versus "tuberculis dorsalibus ciliato-squamosis" (squamiform and setose dorsal tubercles, *P. squamosa*).

In 1818, Lamarck described three more species of *Plagusia*: *P. immaculata* (from "la Méditerranée? Je la crois de l'Océan Indien"), *P. serripes* (based on a nomenclaturally invalid Seba name) (from "les mers australes") and *P. tuberculata* (from "mers de l'Île-de-France", present day Mauritius). While *Plagusia serripes* is now regarded as a junior subjective synonym of *Percnon planissimum*, *Plagusia immaculata* and *P. tuberculata* appear to be morphologically similar to *P. depressa* and *P. squamosa* and their validities were questioned from early on. Lamarck (1818: 247) himself says of *P. tuberculata*: "...voisine de la plagusie écaillée [i.e. *P. squamosa*], mais distincte" (near to the squamiform *Plagusia* [i.e. *P. squamosa*], but distinct). Latreille (1825: 145) believed that *P. immaculata* was identical to *P. depressa*, commenting that "le même individu décoloré" (the same form, but uncolored), but accepted the validity of *P. tuberculata*. Latreille's specimen(s) of *P. squamosa* was from the Atlantic and he again describes *P. depressa* as with "tuberculis glabris" (naked tubercles) (p. 145).

Henri Milne Edwards (1837, 1853) followed Latreille's synonymy of *P. immaculata* with *P. depressa*, and recognized *P. depressa* and *P. squamosa* as valid taxa. Of *P. tuberculata*, he stated (1837: 94) "... ne me paraît être autre chose qu'un individu de l'espèce précédente [i.e. *P. squamosa*] dont on aurait enlevé les poils en la brossant" (does not appear to me to be different from the previous [i.e. *P. squamosa*], which has its setae brush-like elevated). Like Lamarck (1806, 1825), he describes the dorsal tubercles of *P. depressa* as "déprimés et complètement dépourvue de

poils" (flattened and completely devoid of setae) (H. Milne Edwards, 1837: 93).

Stimpson (1858, 1860) noted that Indo-Pacific material of *Plagusia*, to which H. Milne Edwards and others have referred to as *P. squamosa* "... is not the true *Cancer squamosus* of Herbst, as may be seen from his figure. It [the Indo-Pacific material] is distinguished from the Atlantic species by the non-dentate superior lobe of the ischium-joint in the ambulatory feet and by the septem-dentate margin of the epistome" (Stimpson, 1860: 231). This was the first time that differences in the shape of the coxae of the walking legs were noticed and thus the existence of at least two forms with setose tubercles, one from the Atlantic and the other from the Indo-Pacific, was recognized. Stimpson (1858) consequently introduced a new name for the Indo-Pacific form, *P. orientalis*.

In his revision of the Plagusiinae, Miers (1878) followed Stimpson (1860) in considering that Herbst's drawing of *P. squamosa* (see Herbst, 1790: pl. 20, fig. 113) represents the Atlantic form. He therefore synonymized *P. squamosa* under the Atlantic *P. depressa* and Stimpson's *P. orientalis* under the older available name for the Indo-Pacific, *P. tuberculata*. Miers (1878) recognized an Atlantic and a Indo-Pacific form and in addition to Stimpson's (1860) morphological criteria for separation, he suggested that the male telson of *P. depressa* is "... narrower with the sides more distinctly convergent to the distal extremity" (p. 149). Nevertheless, his action of synonymizing *P. squamosa* under *P. depressa* implied an almost worldwide distribution of *P. depressa* considering that the type locality of *P. squamosa* is the East Indies and that of *P. depressa* is the Mediterranean. Miers (1878) furthermore revalidated *P. immaculata* as a full species, considering that "... in this species the carapace is more convex than in either of the preceding [i.e. *P. tuberculata* and *P. depressa*], the tubercles much depressed, quite naked, often almost obsolete upon the gastric and cardiac regions" (p. 150). He concluded that the specimens with naked tubercles to which Latreille (1825), H. Milne Edwards (1837, 1853), Dana (1852) and Stimpson (1858) had referred to *P. depressa* actually belonged to *P. immaculata* instead.

Hilgendorf (1882) admitted that the drawing of *P. squamosa* by Herbst (1790) shows multi-dentate ambulatory coxae. However, his comparison of the drawing with the type material in Berlin suggested that the type corroborates Herbst's (1790: 260-261)

description: "einen spitzigen Zahn" (one pointed tooth) and thus differs from the original drawing, which is rather schematic and not very accurate in any case. The type material of *Cancer squamosus* Herbst, 1790, therefore can be attributed to the Indo-Pacific form, which is in agreement with Herbst's information on the type locality, "Ostindien" (East Indies). It is thus very possible that Herbst's original material (not all of which now exists) had representatives of at least two species, with his drawing belonging to the Atlantic *P. depressa*, a species that was also listed in his study (Herbst, 1790). Hilgendorf therefore concludes that the name *P. squamosa* can be used for what he calls the "eastern form".

De Man (1883) questioned the validity of the distinguishing characters introduced by Stimpson (1860) and Miers (1878) to separate the species, noting that a female *Plagusia* specimen from Ambon (Indonesia) "... wholly [original emphasis] agrees with the individuals from the West-Coast of Africa" (p. 168) and that "the other characters, quoted by Mr. Miers, by which these two forms can be distinguished, are of no importance, for al(l)most all our [i.e. Leiden collection] specimens of the West-African *depressa* Say [sic, should be Fabricius] have the lobe above the bases of the second and third ambulatory legs not dentated, and the terminal segment of the postabdomen in the male of a Liberia specimen is broadly semioval..." (p. 169). This suggests that their distributional patterns are not concordant with their accepted taxonomy. Nevertheless, de Man (1883, 1887) followed Miers (1878) in using the name *P. tuberculata* for most of his Pacific specimens.

Alcock (1900: 437) synonymized *P. tuberculata*, *P. immaculata*, and *P. orientalis* under *P. depressa* var. *squamosa* without any additional remarks. Laurie (1906: 429) disagreed with Alcock's synonymy of *P. tuberculata* and *P. immaculata* and suggested that three subspecies (as varieties) of *P. depressa* could be recognised: var. *depressa* (carapace tubercles squamiform and bordered by a fringe of short stiff hairs; ambulatory coxal processes dentate), var. *tuberculata* (tubercles as in var. *depressa*; ambulatory coxal processes entire), and var. *immaculata* (tubercles depressed and obsolescent on gastric region; ambulatory coxal processes entire). However, he also notes "that the above distinctions are average, not absolute" (p. 430) and refers to exceptions among Miers' and de Man's material. He concludes "I retain for the varieties the names used by Miers, entirely avoiding *squamosa*. If used, the latter should apply to the *tuberculata* series only, but it has the grave

disadvantage of having been used by Herbst to denote in the text a form with entire coxal process and in his figure one with coxal process dentate".

Rathbun's (1918: 332-335) classification is clearly based on Miers (1878) and Laurie's (1906) taxonomy. She subdivided *P. depressa* into two subspecies: *P. depressa depressa* from the Atlantic Ocean (including Ambon, as de Man, 1883) and *P. depressa tuberculata* from the Indo-Pacific. For her, the only consistent morphological difference between the two subspecies is the shape of the ambulatory coxal joints of the legs (dentate in *P. depressa* and rounded in *P. tuberculata*) (Rathbun, 1918: fig. 154). Rathbun also considers *P. squamosa* to be a junior synonym of *P. depressa depressa* by referring to the original drawing by Herbst (1790). However, she admits that she never saw the type of *Cancer squamosus* ("I searched for the type, but could not find it", p. 332). Like Miers (1878), Rathbun considers *P. immaculata* to be a distinct species.

Rathbun's taxonomy (1918) has since been adopted by most carcinologists of the 20th century (see Dawson, 1987) with the exception of a few carcinologists from India who still follow Alcock's (1900) nomenclature by referring to *P. depressa squamosa* (e.g. Rajabai, 1961). The only disagreement in modern taxonomy seems to be whether *P. depressa* and *P. tuberculata* should be considered full species (e.g. Ng, 1998) or subspecies as suggested by Laurie (1906) and Rathbun (1918). Recently, Schubart et al. (in press) showed that larval morphology and molecular differences justify separation of these allopatric taxa at the species level.

TYPE STATUS AND DESIGNATIONS

Recently, the second author had an opportunity to examine the type specimens of *Cancer depressus* Fabricius, 1775, in the Copenhagen Museum (ZMUC). Zimsen (1964: 643) noted that in the Fabricius material of this species in ZMUC, there were two specimens originally from Kiel and another two from originally from Copenhagen. All were regarded as syntypes of *Cancer depressus* Fabricius, 1775, and are labelled as such. Three of them (ZMUC Cru 10-1 to 10-3) are labeled as being from the Mediterranean and thus agree with Fabricius' locality description, "in mare mediterraneo" (p. 406). All three can be considered to be syntypes. A fourth immature animal (male, 11.2 by 10.1 mm, ZMUC Cru 10-4) is from Tranquebar (India) and was not originally mentioned by Fabricius (1775) and as such, it is clearly not part of the type series; this

specimen is actually what is now called *P. tuberculata*. Study of the type material in Copenhagen showed that the actual syntype series of *Cancer depressus* actually contains two different species, *P. depressa* s. str. (1 male, 34.6 mm by 33.5 mm, ZMUC Cru 10-3, from the original Copenhagen material of Fabricius) (Fig. 1) and *P. immaculata* (1 male, 34.2 by 33.2 mm, ZMUC Cru 10-2, 1 female, 32.5 by 31.3 mm, ZMUC Cru 10-1, both from the original Kiel material of Fabricius). Since *P. immaculata* is not yet known from the Atlantic Ocean and Mediterranean, the type localities for ZMUC Cru 10-1 and 10-2 are probably erroneous. This could also be the case for the single specimen of

P. depressa (ZMUC Cru 10-3), which although known from Morocco in the Atlantic, has yet to be formally recorded from the Mediterranean (d'Udekem d'Acoz, 1999). To ensure stability, the male specimen (ZMUC Cru 10-3; 34.6 by 33.5 mm) (Fig. 1) is here selected as the lectotype of *Cancer depressus* Fabricius, 1775. Although this specimen is not in a very good condition and the carapace is detached from the rest of the body (Fig. 1), it clearly shows the expected carapace features and dentate ambulatory coxal lobes, and is representative of the Atlantic *P. depressa* as presently recognised.

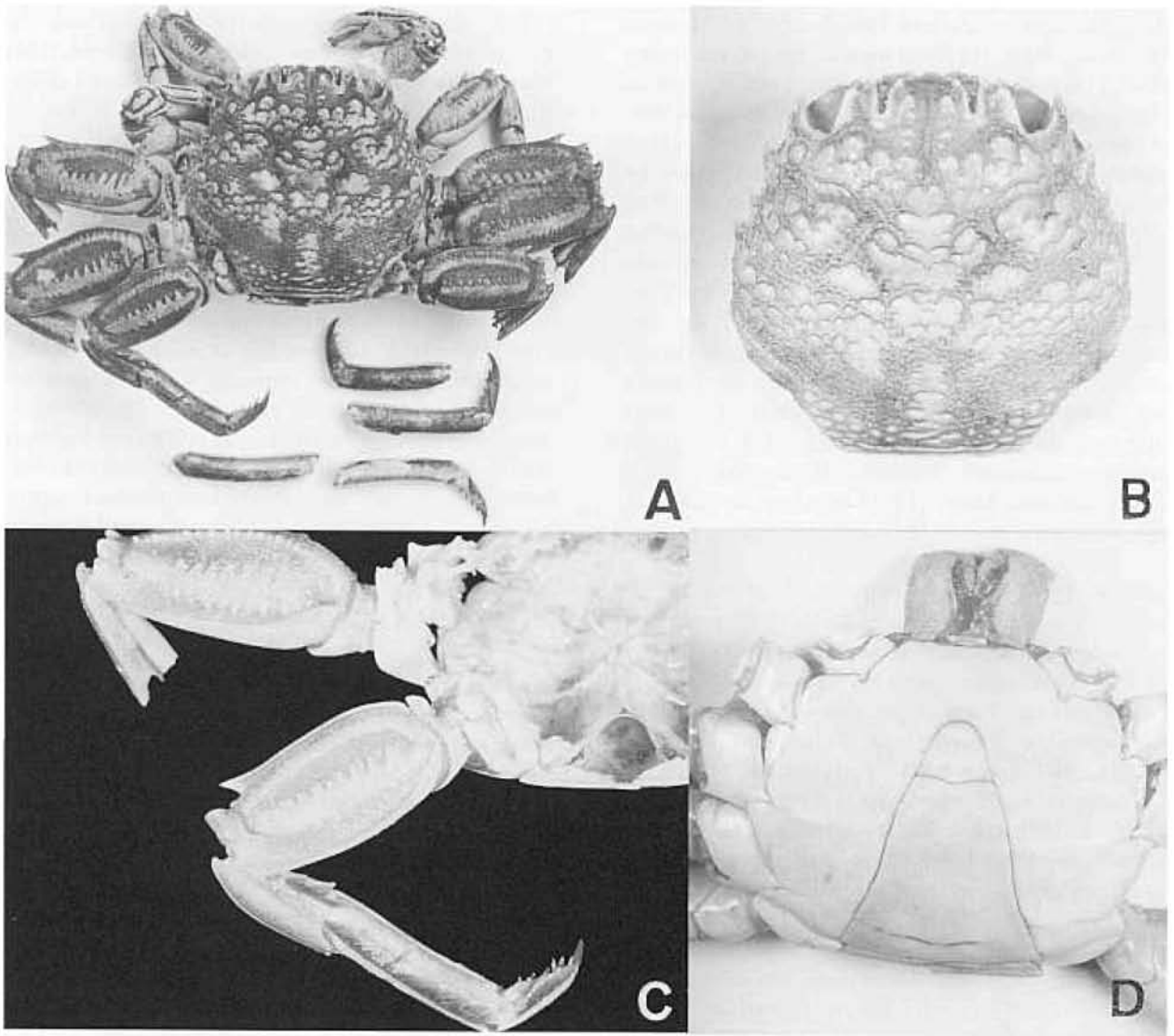


Fig. 1. Lectotype of *Cancer depressus* Fabricius, 1775, male, ZMUC Cru 10-3, 34.6 by 33.5 mm. A, original dried mounted specimen; B, dorsal view of carapace; C, left fourth and fifth ambulatory; D, ventral view showing abdomen.

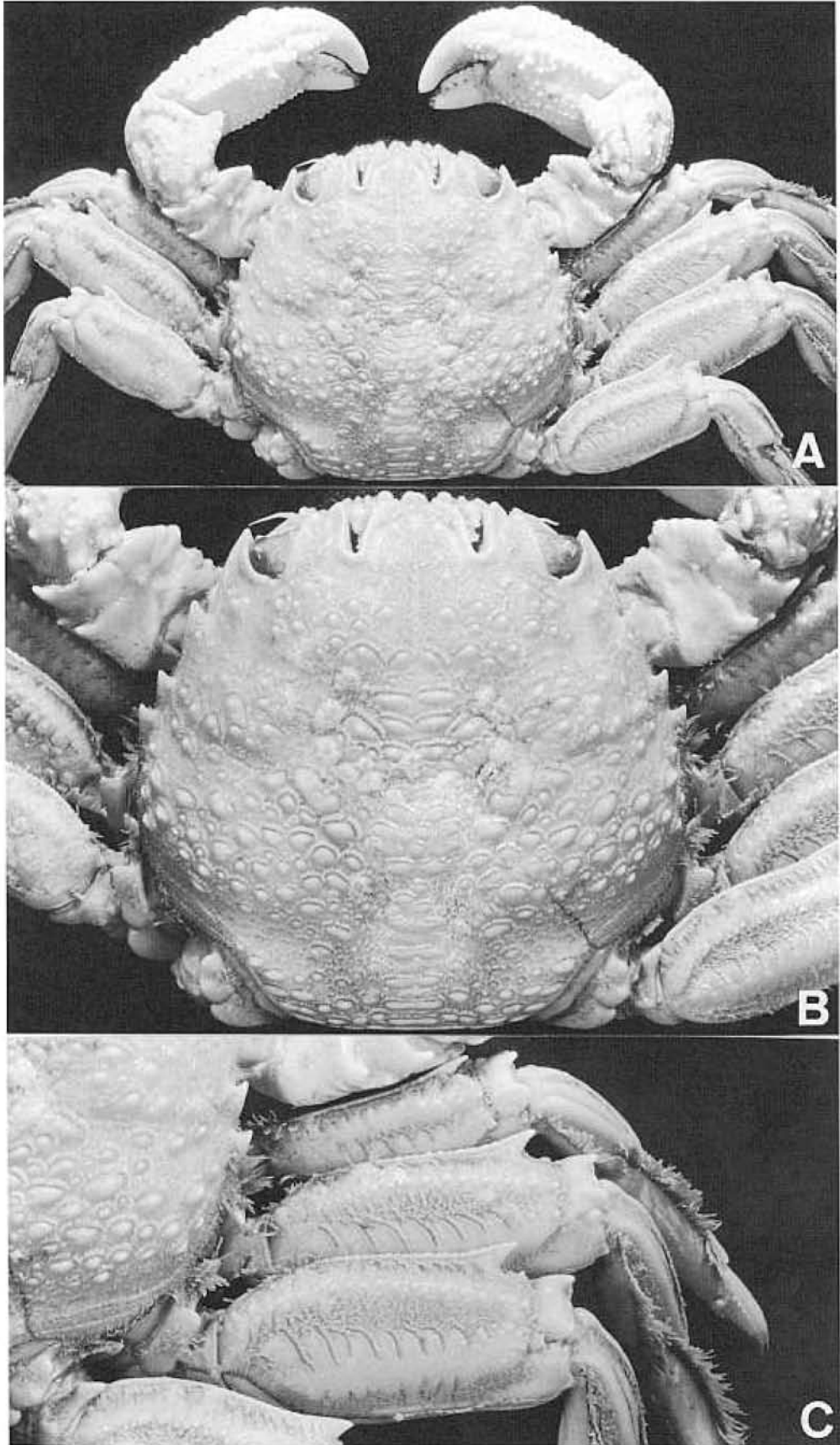


Fig. 2. *Plagusia orientalis* Stimpson, 1858, lectotype male, 49.2 by 48.2 mm, USNM 2012a. A, overall view; B, carapace; C, right ambulatory legs.

The situation with *Cancer squamosus* and *Plagusia tuberculata* is also problematic. Sakai (1999) reported on the Herbst collection in Berlin, providing a good photograph of the "holotype" of *Cancer squamosus* Herbst, 1790, a dried male specimen 36.5 by 32.0 mm (ZMB 498) (Sakai, 1999: pl. 21c). Since Herbst did not designate a holotype, all of his material must be regarded as syntypes, and the designation by Sakai (1999: 39) is a de facto lectotype designation and is regarded as such here. The more rounded ambulatory coxa is easily discerned from this figure and confirms Hilgendorf's (1882) observations and the Indo-Pacific origin of Herbst's material. We have also examined the original and other slides taken of this specimen and another paralectotype in the Berlin Museum and they confirm the above observations (Fig. 3). It matters not that Herbst may have had more material of other species at his disposal since a valid lectotype designation has been made by Sakai (1999). All other

specimens of *Cancer squamosus* in the Berlin Museum are thus paralectotypes (1 dried female, 30.5 by 29.5 mm, ZMB 479; 1 male, 37.6 by 36.0 mm, ZMB 499; 1 female, 44.5 by 42.0 mm, ZMB 2165). Since *Cancer squamosus* Herbst, 1790, was described earlier than *P. tuberculata* Lamarck, 1818, Herbst's name clearly has precedence over Lamarck's. Unfortunately, the type(s) of *P. tuberculata* Lamarck, 1818, from Mauritius is no longer extant (D. Guinot, pers. comm.). We have examined the type specimens of *P. orientalis* Stimpson, 1858 (two syntype males, 49.2 by 48.2 mm, 35.3 by 33.8 mm [possibly with parasite on left posterior cardiac region], USNM 2012, Hong Kong, China, coll. W. Stimpson, North Pacific Exploration Expedition) and it is clearly a subjective junior subjective synonym of *P. squamosa* as presently defined. The larger and more intact male specimen measuring 49.2 by 48.2 mm (Fig. 2) is here designated as the lectotype of *Plagusia orientalis* Stimpson, 1858.

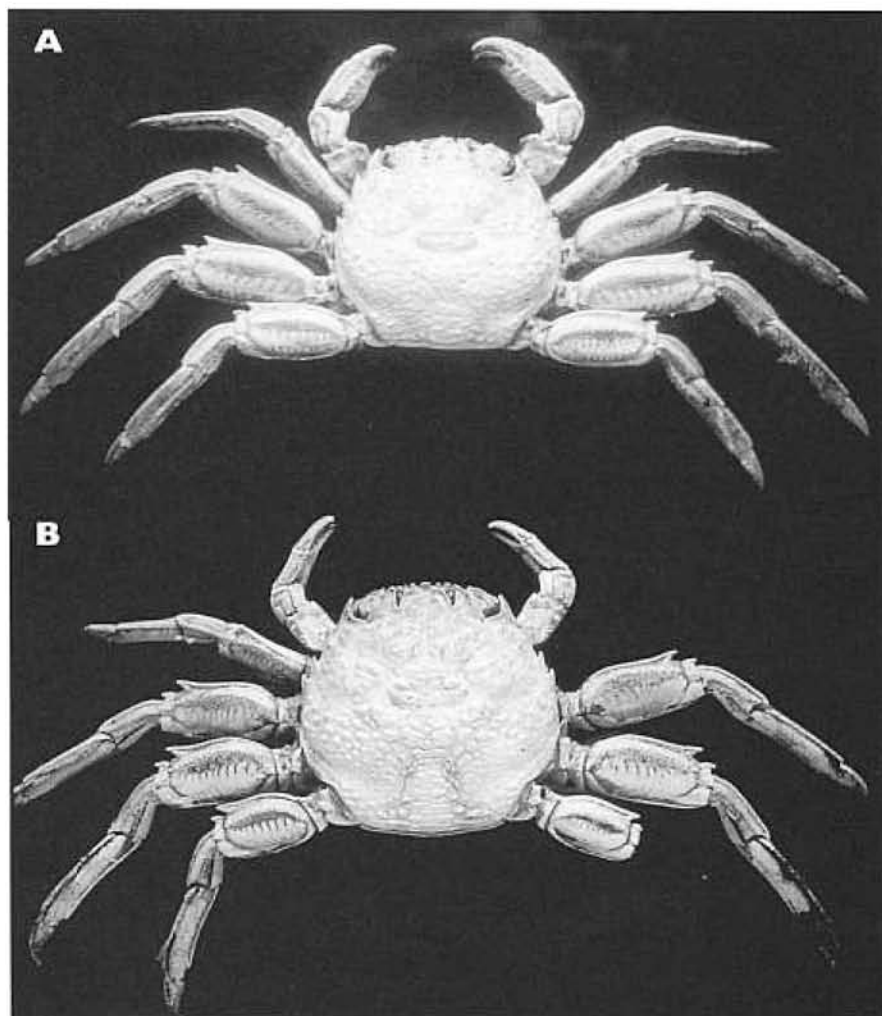


Fig. 3. *Plagusia squamosa* (Herbst, 1790). A, dried lectotype male of *Cancer squamosus* Herbst, 1790, 36.5 by 32.0 mm, ZMB 0498, East Indies, simultaneously neotype of *Plagusia tuberculata* Lamarck, 1818; B, paralectotype of *Cancer squamosus*, female, 44.5 by 42.0 mm, ZMB 2165, East Indies.

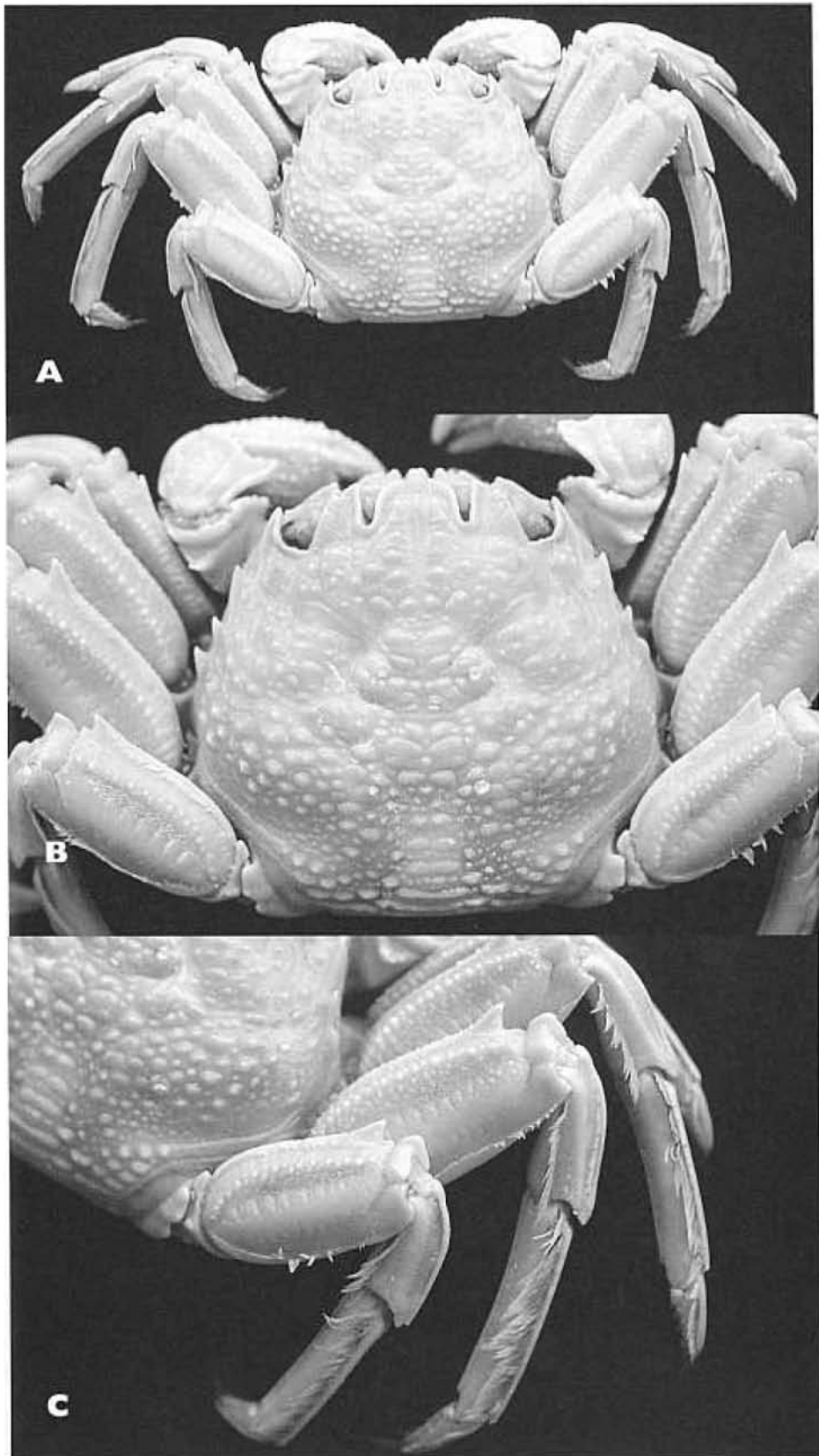


Fig. 4. Neotype of *Plagusia immaculata* Lamarck, 1818, male, 40.7 by 38.6 mm, Cocos-Keeling Islands, Indian Ocean, ZRC 1965.1965.7.27.120. A, overall view; B, carapace; C, ambulatory legs.

The fact that type series for *Cancer depressus* Fabricius, 1775, includes two specimens belonging to *P. immaculata* explains part of the confusion around the identity and validity of some species of *Plagusia*. To compound matters further, the types of *P. immaculata* are also lost (D. Guinot, pers. comm.). The absence of types for two key species (*Plagusia tuberculata* Lamarck, 1818, and *P. immaculata* Lamarck, 1818), the long history of uncertainty and confusion between *C. depressus* Fabricius, 1775, *C. squamosus* Herbst, 1790, *P. tuberculata* Lamarck, 1818, and *P. immaculata* Lamarck, 1818, and the fact that some of these species closely resemble each other and may even be sympatric in distribution with very similar habits, seriously compounds the problems. This is clearly unsatisfactory for a group of common crabs, some of which have commercial value (Ng, 1998). There is thus a need to stabilise the nomenclature of the above mentioned species by fixing neotypes for *Plagusia tuberculata* Lamarck, 1818, and *P. immaculata* Lamarck, 1818.

We hereby designate the dried lectotype male of *Cancer squamosus* Herbst, 1790, measuring 36.5 by 32.0 mm, collected from somewhere in the East Indies, and now in the Berlin Museum (ZMB 0498) (Fig. 3A) as the neotype of *Plagusia tuberculata* Lamarck, 1818. This will make both names objective synonyms with *Cancer squamosus* having priority. With regards to *Plagusia immaculata*, as there are no reliable records of this species from the Mediterranean, we follow Lamarck's belief that his type material was actually from the Indian Ocean. We hereby choose a male specimen measuring 40.7 by 38.6 mm (Fig. 4), collected from the Cocos-Keeling Islands in the Indian Ocean by C. A. Gibson-Hill in 1934 and now in the Zoological Reference Collection (ZRC 1965.1965.7.27.120) of the National University of Singapore, as the neotype of *Plagusia immaculata* Lamarck, 1818.

Plagusia squamosa (Herbst, 1790), and *P. immaculata* Lamarck, 1818, are both superficially very similar and can easily be confused. They can, however, be separated by a dense row of setae surrounding the anterior margins of the flattened granules on the carapace of *P. squamosa*, giving the carapace a rather "scalloped" look when viewed from a distance. In *P. immaculata*, the setae surrounding the granules are distinctly sparser and/or shorter, with the carapace appearing much smoother. Overall, *P. squamosa* appears to carry longer and more prominent setae. This is also the case on the anterior border of the merus of the walking legs and along the dorsal grooves of all

pereiopods. The dorsal surface of the carpus of the cheliped has a prominent oblique row of short, stiff black setae. Also the longitudinal grooves on the dorsal and subdorsal surfaces of the carpus and propodus of walking legs as well as on the manus and dactylar finger of the chelipeds each has a well developed row of short, stiff black setae. In *P. immaculata*, these setae are sparse, few, hardly organised into rows or absent. This is most obvious in adult males but can be discerned even in females and juveniles. However, there are apparently no other morphological characters which are very reliable, with male gonopods and abdomen being very similar. In any case, the setal characters described above seem very effective for the moment. As both taxa are known to be sympatric at least in the areas studied, it seems best to regard them as separate species for the moment rather than as subspecies. Because of their close similarity, we also believe that most older records previously referred to

Table 1. List of recognised *Plagusia* species and synonyms

- Plagusia* Latreille, 1804 (type species *Cancer depressus* Fabricius, 1775, by monotypy; gender feminine)
- Plagusia chabrus* (Linnaeus, 1758) [*Cancer*]
 = *Cancer velutinus* Linnaeus, 1764
 = *Grapsus (Plagusia) capensis* de Haan, 1835
 = *Plagusia tomentosus* H. Milne Edwards, 1837
 = *Plagusia spinosa* Macleay, 1838
 = *Plagusia gaimardii* H. Milne Edwards, 1853
- Plagusia dentipes* (de Haan, 1835) [*Grapsus (Plagusia)*]
- Plagusia depressa* (Fabricius, 1775) [*Cancer*]
 = *Plagusia sayi* de Kay, 1844
 = *Plagusia gracilis* de Saussure, 1858
- Plagusia glabra* Dana, 1852
- Plagusia immaculata* Lamarck, 1818
- Plagusia integripes* Garth, 1973
- Plagusia speciosa* Dana, 1852
- Plagusia squamosa* (Herbst, 1790) [*Cancer*]
 = *Plagusia tuberculata* Lamarck, 1818
 = *Plagusia orientalis* Stimpson, 1858

(Original genus in square parenthesis)

"*P. tuberculata*" should be rechecked before a better idea of each species distribution can be determined. Many lots in the ZRC were, in fact, mixed or wrongly identified. Overall, the genus *Plagusia* now contains eight species (Table 1) distributed in all the temperate and tropical oceans of the world. We follow Schubart et al. (2000) in regarding the Plagusiidae as a distinct family.

COMPARATIVE MATERIAL EXAMINED

Plagusia squamosa: 1 female (ZRC 1988.2251), Singapore, no other data; 1 male (ZRC 1999.419), Pulau Hantu, Singapore, coll. N. Goh, 15 Apr. 1997; 1 male, 3 females (ZRC 1965.7.27.115-118), Horsburgh Lighthouse, Singapore, coll. Apr. 1934; 1 female (ZRC 1965.7.27.123-124), Horsburgh Lighthouse, Singapore, coll. C. A. Gibson-Hill, 1934; 1 female (ZRC 1999.418), Raffles Lighthouse, Singapore, coll. S. Teo, 11 Apr. 1997; 1 male, 1 female, 1 juvenile (ZRC 1965.7.27.125-127), Christmas Island, coll. C. A. Gibson-Hill, 1940; 2 males, 1 female (ZRC 1999.988), Keelung, Taiwan, coll. N. K. Ng & Y. Cai, 27 Nov. 1997; 1 male (ZRC 2000.452), Waikiki, Oahu, Hawaii, coll. D. Takaoka, 27 Jan. 2000; 3 males, 2 females (ZRC 2000.412), Kewalo, Waikiki, Oahu, Hawaii, coll. P. Ng & S. H. Tan, 22 Jan. 2000; 1 male (ZRC), Ritidian Point, Guam, coll. G. Paulay, 19 January 1997. *P. immaculata*: 1 female (ZRC 1999.982), bunds along Labrador, Singapore, coll. P. Ng, 1990; 1 female (ZRC 1965.7.27.119), Horsburgh Lighthouse, Singapore, coll. C. A. Gibson-Hill; 1 male (ZRC 1989.3426), Southern Islands, Singapore, coll. J. B. Sigurdsson, 1986; 1 male (ZRC 1993.259), West Coast Park, Singapore, coll. P. Y. Aow, 20 Jun. 1987; 1 male (1999.609), 1 female (ZRC 1999.616), Pulau Redang, Peninsular Malaysia, coll. P. Ng, Jun. 1992; 1 male (ZRC 1985.1568), Pulau Sri Buat, near Pulau Tioman, Peninsular Malaysia, coll. P. Ng, 2 May 1983; 2 males, 1 female (ZRC 1987.593-595), Pulau Tiga, Sabah, Malaysia, coll. L. Nyanti; 2 juveniles (ZRC 1965.1965.7.27.121-122), Cocos-Keeling Islands, coll. C. A. Gibson-Hill, 1934; 1 male, 1 female (ZRC 1999.1413), Keelung, Taiwan, coll. N. K. Ng & Y. Cai, 27 Nov. 1997; 1 female (ZRC 2000.589), Orote Peninsula, Guam, coll. G. Paulay, Apr. 2000.

ACKNOWLEDGEMENTS

The authors are grateful to Danile Guinot for her help in checking the specimens in the Paris Museum and

general advice. Katsushi Sakai kindly provided information and slides of the types of *P. squamosa*. Torben Wolff kindly helped sort out the problems with Fabricius specimens. Tan Swee Hee helped to check and photograph the types of *P. orientalis*. Odin Futterer kindly helped translate some of the Latin texts. The study has been partially supported by a long-term research fellowship to the first author from Raffles Museum, and a research grant to the second author from the National University of Singapore.

LITERATURE CITED

- Dana, J. D., 1852. Crustacea, Part 1. In: *United States Exploring Expedition during the years 1838, 1839, 1840, 1841, 1842, under the command of Charles Wilkes, U.S.N.* 13: 1-685. Atlas (1855): 1-27, pls 1-96. C. Sherman, Philadelphia.
- Dawson, E. W., 1987. A key to the world species of *Plagusia* (Crustacea: Brachyura), with a new record of *P. depressa tuberculata* Lamarck from New Zealand. *Nam. Mus. New Zealand Rec.*, 3(4): 37-45.
- Fabricius, J. C., 1775. *Sistema entomologiae, sistens insectorum, classes, ordines, genera, species, adiectis synonymis, locis, descriptionibus, observationibus.* Flensburgi et Lipsiae, 832 pp.
- Herbst, J. F. W., 1782-1790. *Versuch einer Naturgeschichte der Krabben und Krebse nebst einer systematischen Beschreibung ihrer verschiedenen Arten.* 1. 274 pp., 21 pls. (1782: 1-86, pl. 1; 1783: 87-182, pls. 2-9; 1785: 183-206, pls. 10-13; 1788: 207-238, pls. 14-17; 1790: 239-274, pls. 18-21).
- Hilgendorf, F., 1882. Einige carcinologische Mittheilungen. *Sitzungsber. Ges. Naturforsch. Freunde Berlin*, 1882: 22-25.
- Lamarck, M. de, 1818. Homobranches Brachyures. In: *Les caractères généraux et particuliers de ces animaux, leur distribution, leurs classes, leurs familles, leurs genres, et la citation des principales espèces qui s'y rapportent.* Tome 5. Deuxième section., pp. 226-273.
- Latreille, P. A., 1804. Tableau méthodique des Crustacés. In: *Nouveau dictionnaire d'histoire naturelle appliqué aux Arts, principalement à l'agriculture et à l'économie rurale et domestique: par une Société de naturalistes et d'Agriculteurs: avec des figures tirées des trois règnes de la nature.* Paris, 24: 125-127.
- Latreille, P. A., 1806. *Genera crustaceorum et insectorum secundum ordinem naturalem in familias disposita, iconibus exemplisque plurimis*

- explicata*. I. Amand Koenig, 302 pp., pl. 1.
- Latreille, P. A., 1825. Plagusie, Plagusia. *Encycl. méthod. Hist. Nat. Ins.*, **10**: 145-148.
- Laurie, R. D., 1906. Report on the Brachyura collected by Professor Herdman, at Ceylon, in 1902. In: *Rep. Pearl Oyster Fish. Ceylon*, **5**: 249-432. pls. 1-2.
- Man, J. G. de, 1883. Carcinological studies in the Leyden Museum. No. 3. *Notes Leyden Mus.*, **5**(15): 150-169.
- Man, J. G. de, 1887. Bericht über die von Herrn Dr. J. Brock im indischen Archipel gesammelten Decapoden und Stomatopoden. *Arch. Naturgesch.*, **53**: 215-600, pls. 7-22.
- Miers, E. J., 1878. Revision of the Plagusiinae. *Ann. Mag. Nat. Hist.*, ser. **5**(1): 147-154.
- Milne Edwards, H., 1837. *Histoire naturelle des Crustacés, comprenant l'anatomie, la physiologie et la classification de ces animaux*. Vol. 2. 532 pp. Atlas 32 pp. Librairie Encyclopédique de Roret, Paris.
- Milne Edwards, H., 1853. Mémorial sur la famille des Ocypodiens, suite. *Ann. Sci. Nat.*, ser. 3: Zool., **20**: 163-228, pl. 6-11.
- Ng, P. K. L., 1998. Crabs. In: K. E. Carpenter & V. H. Niem (Eds.), *FAO Species identification guide for fishery purposes. The living marine resources of the Western Central Pacific. Volume 2. Cephalopods, crustaceans, holothurians and sharks*. Food & Agriculture Organisation, Rome. Pp. 1045-1155.
- Rajabai, K. G., 1961. Studies on the larval development of Brachyura. VII Early development of *Metopograpsus messor* (Forsk.), *Plagusia depressa squamosa* (Herbst), *Metasesarma rousseauxi* A. M. Edwards and *Sesarma terragonum* (Fabricius) of the family Grapsidae. *J. Zool. Soc. India*, Calcutta, **13**(2): 154-165.
- Rathbun, M. J., 1918. The grapsoid crabs of America. *U.S. Nat. Mus. Bull.*, **97**: 1-461. ? pl.
- Sakai, K., 1999. J. F. W. Herbst-Collection of decapod Crustacea of the Berlin Zoological Museum, with remarks on certain species. *Naturalists*, **5**: 1-45, pl. 1-21.
- Schubart, C. D., J. A. Cuesta, R. Diesel & D. L. Felder, 2000. Molecular phylogeny, taxonomy, and evolution of non-marine lineages within the American grapsoid crabs (Crustacea: Brachyura). *Mol. Phylogenetic Evol.*, **15**(2): 179-190.
- Schubart, C. D., J. I. Gonzalez-Gordillo, N. Reyns, H.-C. Liu & J. A. Cuesta, in press. Are Atlantic and Indo-Pacific populations of the rafting crab, *Plagusia depressa*, distinct? New evidence from larval morphology and mtDNA. *Raffles Bull. Zool.*
- Schmitt, W. L., J. C. McCain & E. Davidson, 1973. Decapoda I. Brachyura I. Fam. Pinnotheridae. *Crustaceorum Catalogus*, Dr. W. Junk, Den Haag, **3**: 1-160.
- Stimpson, W., 1858. Prodromus descriptionis animalium evertibratorum, quae in Expeditione ad Oceanum Pacificum Septentrionalem, a Republica Federata missa, Cadwaladaro Ringgold et Johanne Rodgers Ducibus, observavit et descripsit. Pars V. Crustacea Ocypodoidea. *Proc. Acad. Nat. Sci. Philadelphia*, **1857**: 93-110.
- Stimpson, W., 1860. Notes on North American Crustacea, in the Museum of the Smithsonian Institution. No. II. *Ann. Lyc. Nat. Hist., N.Y.*, **7**: 177-246, pls. 2-5.
- Udekem d'Acoz C. d', 1999. *Inventaire et distribution des crustacés décapodes de l'Atlantique nord-oriental, de la Méditerranée et des eaux continentales adjacentes au nord de 25°N*. Collection "Patrimoines Naturels" (Mus. Natn. Hist. Nat. / S.P.N.), Paris, 40. 383 pp.
- Zimsen, E., 1964. *The type material of I. C. Fabricius*. Copenhagen, pp. 1-656. 2 pls.