

PHYLOGENETIC RELATIONSHIPS OF THE PLAGUSIIDAE DANA,
1851 (BRACHYURA), WITH DESCRIPTION OF A NEW GENUS AND
RECOGNITION OF PERCNIDAE ŠTEVČIĆ, 2005, AS AN
INDEPENDENT FAMILY

BY

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ABSTRACT

A molecular and morphological analysis of representatives of the family Plagusiidae, including all members of *Plagusia* Latreille, 1804, and the recently established *Davusia* Guinot, 2007, was carried out. Due to marked differences in adult and larval morphology, as well as mitochondrial and nuclear DNA, two species of *Plagusia*, viz., *P. chabrus* (Linnaeus, 1758), and *P. dentipes* De Haan, 1835, are considered sister taxa but distinct from other members of the genus. They are transferred to a new genus, *Guinusia*. A molecular phylogeny suggests that *Guinusia* is not closer related to *Plagusia* than to the plagusiid genera *Euchirograpsus* H. Milne Edwards, 1853, and *Miersiograpsus* Türkay, 1978. Furthermore, with new evidence from mitochondrial and nuclear DNA as well as a reappraisal of the larval morphology, the genus *Percnon* Gistel, 1848, is formally removed from the Plagusiidae and recognized as a separate family, Percnidae Števíć, 2005.

RÉSUMÉ

Une analyse moléculaire et morphologique des représentants de la famille des Plagusiidae comprenant tous les membres du genre *Plagusia* Latreille, 1804, et le genre récemment établi *Davusia* Guinot, 2007, a été réalisée. Pour tenir compte des nettes différences dans la morphologie adulte et larvaire ainsi que sur l'ADN nucléaire et mitochondrial, deux espèces de *Plagusia*, *P. chabrus* (Linnaeus, 1758), et *P. dentipes* De Haan, 1835, sont considérées comme espèces sœurs et transférées dans le genre *Guinusia*. Une phylogénie moléculaire suggère que ce genre n'est pas plus proche du genre *Plagusia* que des genres de Plagusiidae *Euchirograpsus*

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H. Milne Edwards, 1853 et *Miersiograpsus* Türkay, 1978 et justifie donc sa séparation. Par ailleurs, considérant les nouvelles preuves des l'ADN mitochondriaux et nucléaires et une réévaluation de la morphologie larvaire, le genre *Percnon* Gistel, 1848 est ici formellement enlevé de la famille des Plagusiidae et placé dans une famille propre, les Percnidae Števíć, 2005.

INTRODUCTION

The genus *Plagusia* Latreille, 1804, underwent a period of taxonomic confusion and re-definitions towards the end of the 19th century (Miers, 1878; De Man, 1883; Alcock, 1900; see Schubart & Ng, 2000), but this largely stabilized with the monograph by Rathbun (1918). The modern composition of the genus, and the status of species (and subspecies) were more recently summarized by Dawson (1987) and Schubart & Ng (2000). Schubart et al. (2001) addressed the issue of the subspecific status within *Plagusia depressa* (Fabricius, 1775), and recognized *Plagusia squamosa* (Herbst, 1790) (formerly referred to as *P. depressa tuberculata* Lamarck, 1818, see Schubart & Ng, 2000) as a full species. Guinot (2007) then removed *P. glabra* Dana, 1851, from *Plagusia* and placed it in a new genus, *Davusia*. This left seven species of *Plagusia* and unclear phylogenetic relationships among the genus *Davusia* and the remaining members of the family Plagusiidae.

The higher classification of *Plagusia* and its allies has also experienced recent changes. The description of the larval stages of *Euchirograpsus americanus* A. Milne-Edwards, 1880, by Wilson (1980) and *Plagusia depressa* by Wilson & Gore (1980) revealed close morphological similarities between these species, which at that time were classified in different subfamilies of the family Grapsidae, i.e., Varuninae H. Milne Edwards, 1853, and Plagusiinae, respectively. Cuesta & Schubart (1997) discussed the subfamilial arrangement based on larval morphology and confirmed that the larvae of *Euchirograpsus* were more closely related to *Plagusia* than to those of the subfamily Varuninae. They also cited unpublished evidence from mitochondrial DNA for a close phylogenetic relationship between these two genera, suggesting a “systematic position of *E. americanus* in close relationship to *P. depressa* and not linked to the main group of the Varuninae” (Cuesta & Schubart, 1997: 296). Sternberg & Cumberlidge (2000) had come to a similar conclusion in a morphological cladistic analysis, with Guinot & Bouchard (1998) having previously noted that the morphology of the male abdominal press-button locking mechanism of *Euchirograpsus* suggested that this genus was misplaced in the Varuninae. The molecular results stated in Cuesta & Schubart (1997) were

published by Schubart et al. (2000), officially transferring *Euchirograpsus* to the Plagusiidae: “The Plagusiinae, next to the type genus *Plagusia*, would now also include *Euchirograpsus* (see also d’Udekem d’Acoz, 1999) and the taxonomic position of *Percnon* awaits future comparisons (i.e., incertae sedes [sic])” (Schubart et al., 2000: 184). The inclusion of *Euchirograpsus* within the Plagusiidae was reiterated by Schubart et al. (2002), and a similar fate was suggested for *Miersiograpsus*. This was confirmed by Davie (2002), who after examining adult morphology, independently transferred *Miersiograpsus* to the Plagusiidae giving the evidence of fused abdominal somites 3-6 as an autapomorphy for *Euchirograpsus*, *Miersiograpsus*, and *Plagusia*. Also around this time, two papers argued that the former grapsid subfamilies should be raised to family level (Schubart et al., 2000; Sternberg & Cumberlidge, 2000) returning to a taxonomic system that initially Guinot (1978) had put forward, but was not followed in later classifications.

The position of *Percnon* within the Plagusiinae or Plagusiidae has also been questioned repeatedly (Schubart et al., 2000, 2006). Consequently, Števíć (2005) established a new tribe for the genus, Percnini, which was later adopted as a subfamily Percninae within the Plagusiidae by Ng et al. (2008). Published molecular results have placed representatives of *Percnon* (i.e., *P. gibbesi* (H. Milne Edwards, 1853) and *P. planissimum* (Herbst, 1804)) in a polyphyletic relationship to other members of the family Plagusiidae (see Schubart et al., 2000, 2006).

In the present contribution, we use phylogenetic analyses based on adult and larval morphology, as well as mitochondrial and nuclear DNA, to examine intrageneric relationships within *Plagusia*, and intergeneric relationships among plagusiid and potentially related genera. Our results show that there is sufficient morphological and molecular diversity within the genus *Plagusia*, that a new genus can be described for two of its constituent species. In addition, *Percnon* is officially removed from the Plagusiidae and placed in its own family within the Thoracotremata. The superfamily Grapsoidea is avoided in this context following the reasoning of Schubart et al. (2006) and new evidence based on nuclear DNA markers by Landstorfer et al. (unpubl.).

MATERIAL AND METHODS

Specimens examined are deposited in museums as listed in table I. New DNA sequences were obtained between 1999 and 2009. DNA extractions and selective amplification of mitochondrial and nuclear DNA were carried out

as reported in Schubart et al. (2006). PCR-amplifications of the 16S rDNA were run with four minutes denaturation at 94°C, 40 cycles with 45 s 94°C, 1 min. 48°C, 1 min. 72°C and 10 min. final denaturation at 72°C, and the primers 16L2 or 16L29 and 16H2 or 16HLeu (see Schubart, 2009). In addition, nuclear DNA of the histone H3 gene was obtained for at least one specimen of all key taxa with a cycling program of 30 s 94°C, 30 s 48°C, 30 s 72°C (otherwise as above) and the primers H3af and H3ar (Colgan et al., 1998). PCR products were purified with Microcon 100 filters (Microcon) or Quick-Clean (BioLine) and subsequently sequenced with the ABI BigDye terminator mix followed by electrophoresis in an ABI Prism 310 Genetic Analyzer (Applied Biosystems, Foster City, CA, U.S.A.). New sequence data were submitted to the European molecular database EMBL (see table I for accession numbers). In addition, the following 16S mtDNA ingroup sequences archived in molecular databases were included in our analyses: *Guinusia dentipes* (as *Plagusia dentipes* AJ308421), *Plagusia depressa* (AJ250649, AJ311791-AJ311793), *Plagusia squamosa* (AJ311794-AJ311796), *Percnon planissimum* (AM180693) in addition to Genbank sequences for outgroups (see table I).

The model of DNA substitution that fitted our data best was determined using the software MODELTEST 3.6 (Posada & Crandall, 1998). Two methods of phylogenetic inference were applied to our dataset: Bayesian Inference (BI) as implemented in MrBayes v. 3.1 (Huelsenbeck & Ronquist, 2001) and Minimum Evolution (ME) as implemented in MEGA 4.1 (Tamura et al., 2007) with pairwise deletions, the Maximum Composite Likelihood model, heterogeneous pattern among lineages, and gamma distributed rates among sites. Gamma shape was established and BI trees were calculated using the suggested model of evolution by MODELTEST. The Bayesian analysis was run with four MCMC (Markov chain Monte Carlo) chains for 2 000 000 generations, saving a tree every 500 generations (with a corresponding output of 4000 trees) and with *Carpilius* sp. as the outgroup. The $-\ln L$ converged on a stable value between 15 000 and 20 000 generations (burn-in phase) so that the first 25 000 generations were always excluded from the analysis to optimize the fit of the remaining trees. The posterior probabilities of the phylogeny were determined by constructing a 50% majority-rule consensus of the remaining trees. ME confidence values were established by running 2000 bootstrap pseudoreplicates.

The mitochondrial dataset consisted of 43 sequences resulting in 675 aligned characters, of which 322 were conserved, 249 parsimony-informative, and 350 variable. GTR + G + I was selected as the best-fitting evolutionary

TABLE I

List of crab specimens of which DNA (16S mtDNA or H3 nDNA) was sequenced and used for phylogenetic reconstruction or morphological comparisons [authorities of species names mentioned in the main text are not repeated here]

Species	Collection locality and date	Collection #	16S / H3 accession #
Plagusiidae			
<i>Guinustia chabrus</i>	Australia: Cape Peterson; 38°40'S 145°37'E; 23.1.2000	NMV J47112	FM539005 / FN434050
<i>Guinustia chabrus</i>	New Zealand: Katkoura, 11.1997	SMF-24560	FM539005
<i>Guinustia dentipes</i>	Japan: Honshu, Chiba-ken, Banda Tateyama, 5.7.1997	SMF-24559	AJ308421 / FN434051
<i>Davusia glabra</i>	Australia: SE Queensland, P. Lookout, 1998	QM W23974	FM539009 / FN434052
<i>Euchirograpsus americanus</i>	USA: Louisiana, Sackett Bank (61-76 m), 25.3.1996	ULLZ. 3626	FM539010 / FN434055
<i>Euchirograpsus timorensis</i>	New Caledonia: 23°37.8'S 167°42.7'E, 29.1.1993	SMF-34761	FM539011 / FN434056
<i>Mierstograpsus australiensis</i>	New Caledonia: 24°44.55'S 170°08.85'E, 26.10.1991	SMF-34762	FM539012 / FN434053
<i>Mierstograpsus kingsleyi</i>	SE Atlantic off Namibia: 27°25'S 14°50'E, 21.7.1983	ICMD2/2004	FM539013 / FN434054
<i>Plagusia depressa</i>	Ghana: Cape Coast, 4.7.2001	SMF-34728	FM538999 / FN434046
<i>Plagusia depressa</i>	São Tomé and Príncipe: Bom-Bom ~1°N-7°E, 3.2004	SMF-34729	FM539000
<i>Plagusia immaculata</i>	Clipperton: 10°18.80'N 109°12.50'W, 18.1.2005	MNHN B-31976	FM539002 / FN434048
<i>Plagusia immaculata</i>	Maldives: Rasdhoo Atoll, Kuramathi, 12.7.1999	SMF-24941	FM539003
<i>Plagusia immaculata</i>	Vietnam: Hon Miao Nhatrang, 23.11.1999	MNHN B-27676	FM539004
<i>Plagusia spectosa</i>	Clipperton: "crête récifale à mer très basse", 2005	MNHN B-30681	FM539008
<i>Plagusia spectosa</i>	Taiwan: Pingtung, Fongtzuetsisha, 5.9.1999	SMF-pending	FM539007 / FN434049
<i>Plagusia squamosa</i>	Maldives: Rasdhoo Atoll, Kuramathi, 12.7.1999	SMF-24943	FM539001
<i>Plagusia squamosa</i>	Hawaii: Oahu Kewalo, 2000	ZRC 2000.0412	AJ311796 / FN434047
Percnidae			
<i>Percnon gibbesi</i>	Spain: Ibiza, Cala Llenya, 1.4.2001	SMF-34760	FM539014 / FN434058
<i>Percnon guinotae</i>	Maldives: Rasdhoo Atoll, Kuramathi, 14.7.1999	SMF-24946	FM539015 / FN434059
<i>Percnon planissimum</i>	Kenya: Malindi: Watamu, 6.11.1999	MZUF 2735	AM180693 / FN434057

TABLE I
(Continued)

Species	Collection locality and date	Collection #	16S / H3 accession #
Outgroups			
<i>Cardisoma carnifex</i> (Herbst, 1794)	Thailand: Phuket: Ao Tang Khen, Dec. 1999	ZRC 1999.0787	FM539017 / FN434044
<i>Discopax hirtipes</i> (Dana, 1852)	Taiwan: Pingtung: Hsiang-Chiao-Wan, 19.5.1998	ZRC 1998.398	FM863830 / FN434045
<i>Gecarcinus lateralis</i> (Fréminville, 1835)	Mexico: Veracruz: Pta. Delgada, 18.4.1998	ULLZ 3722	AJ130804 / FN434043
<i>Gecarcoidea lalandii</i> H. Milne Edwards, 1837	Taiwan: Pingtung: Hengchun, 19.5.1998	ZRC 1998.423	AM160684 / FN434042
<i>Grapsus grapsus</i> (Linnaeus, 1758)	Mexico: Veracruz: Pta. Delgada, 18.4.1998	ULLZ 3709	AJ250650 / FN434067
<i>Pachygrapsus transversus</i> (Gibbes, 1850)	Brazil: Ilha Sta. Catarina: Praia Ingleses, Nov. 2004	MZUSP-16887	FM539016 / FN434068
<i>Chiromantes haematocheir</i> (de Haan, 1835)	Japan: Wakayama: Samusaura, 11.6.1998	SMF-25989	AJ308414 / FN434063
<i>Sexarma reticulatum</i> (Say, 1817)	USA: Delaware, Woodland Beach, 17.9.1994	ULLZ 3835	AJ130799 / FN434062
<i>Cyclograpsus integer</i> (H. Milne Edwards, 1837)	Mexico: Veracruz: Pta. Delgada; 18.4.1998	ULLZ 3704	AJ250639 / FN434061
<i>Varuna litterata</i> (Fabricius, 1798)	Kenya: Mida Creek	MZUF 2503	AJ308419 / FN434060
<i>Glyptograpsus jamaicensis</i> (Benedict, 1892)	Jamaica: Non Such, 21.3.1997	SMF-25987	AJ308420 / FN434065
<i>Platychoirapsus spectabilis</i> De Man, 1896	USA: Florida: Tampa Bay, Alafia R., June 1996	SMF-24567	AJ250645 / FN434064
<i>Xenograpsus testudinatus</i> Ng et al., 2000	Taiwan: I-Lan, Kueishan, 16 m depth; 18.4.1999	ZRC 2009.0866	FM863827 / FN434066
<i>Ocypode quadrata</i> (Fabricius, 1787)	USA: Georgia: Jekyll Island, 24.8.2000	ULLZ 4261	FM539018 / FN434069
<i>Ucides cordatus</i> (Linnaeus, 1763)	Puerto Rico: Boquerón, July 1994	tissue only	FM539019 / FN434070
<i>Palicou obesus</i> (A. Milne-Edwards, 1880)	Gulf of Mexico, 1989	ULLZ 3852	AJ130808 / FN434071
<i>Carpilius</i> sp.	French Polynesia: Îles Australes, 17.8.1991	SMF-32771	FM208748 / FM208786
ICMD, Instituto de Ciencias Marinas, Barcelona, Spain; MNHN, Muséum national d'Histoire naturelle, Paris, France; MUZSP, Museu de Zoologia Universidade de São Paulo, Brazil; MZUF, Museo Zoologico Università di Firenze, Italy; NMV, National Museum Victoria, Melbourne, Australia; SMF, Forschungsinstitut und Museum Senckenberg, Frankfurt a.M., Germany; ULLZ, University of Louisiana Zoological Collection, Lafayette, USA; QM, Queensland Museum, Brisbane, Australia; ZRC, Zoological Reference Collection, Raffles Museum at the National University of Singapore, Singapore.			

model by MODELTEST and implemented for subsequent Bayesian analysis. The ME bootstrap consensus tree resulted in an identical topology for all significant nodes. This topology with confidence values of both methods exceeding 50% is shown in fig. 1. The histone H3 nuclear dataset consisted of 31 taxa with a fixed length (no indels) of 328 basepairs. It was added to the 16S alignment for combined evidence, resulting in an alignment of 1003 basepairs (544 were conserved, 322 parsimony-informative, and 456 variable). Again, GTR + G + I was selected as the best-fitting evolutionary model by MODELTEST and implemented for subsequent Bayesian analysis. The resulting consensus tree with BI and ME topologies exceeding 50% is shown in fig. 2.

SYSTEMATIC ACCOUNT

Family PLAGUSIIDAE Dana, 1851

Plagusinae [sic] Dana, 1851: 288; 1852: 333, 368.

Plagusiinae — Miers, 1878: 147; Alcock, 1900: 289, 436; Guinot, 1978: 285; 1979: 106, 144, 151, 155, 206, 209; Manning & Holthuis, 1981: 238; Williams, 1984: 462; Hartnoll, 1992: 51; Ng, 1998: 1139; Guinot & Bouchard, 1998: 664. [All partim.]

Plagusiidae — Schubart et al., 2000: 183-184; Von Sternberg & Cumberlidge, 2000: 120, 133; Martin & Davis, 2001: 75; Ng et al., 2001: 47; Schubart et al., 2002: 29; Davie, 2002: 436; Števcíć, 2005: 126; Schubart et al., 2006: 193, 198; Ng et al., 2008: 30, 218. [All partim.]

Type genus. — *Plagusia* Latreille, 1804 (type species *Cancer depressus* Fabricius, 1775, by monotypy and designation by Latreille, 1810: 422). Gender feminine.

Guinusia n. gen.

Plagusia — Dana, 1852: 370-371 (pro parte); Miers, 1878: 148, 152-153 (pro parte); Rathbun, 1918: 336-337 (pro parte); Barnard, 1950: 134-137 (pro parte); Griffin, 1968: 209-213; Benech, 1978: 104; Guinot, 1979: 144, 151, 209 (pro parte); Wear & Fielder, 1985: 73-76; Dawson, 1987: 37-44; Guinot & Bouchard, 1998: 664 (pro parte); González-Gordillo et al., 2000: 144-149 (pro parte); Schubart & Ng, 2000: 334 (pro parte); Guinot, 2007: 30 (pro parte).

(Not *Plagusia* Latreille, 1804.)

Type species. — *Guinusia chabrus* (Linnaeus, 1758) new combination, described as *Cancer chabrus* Linnaeus, 1758, by present designation. Gender feminine.

Other species included. — *Guinusia dentipes* (De Haan, 1835) new combination, described as *Grapsus (Plagusia) dentipes* De Haan, 1835.

Etymology. — This genus is dedicated to our esteemed and admired colleague Danièle Guinot in recognition for her decisive contributions to the understanding of the Brachyura, her Thoracotremata, the family Plagusiidae, and the genus *Plagusia*. Her recent recognition of *Davusia* as a new genus

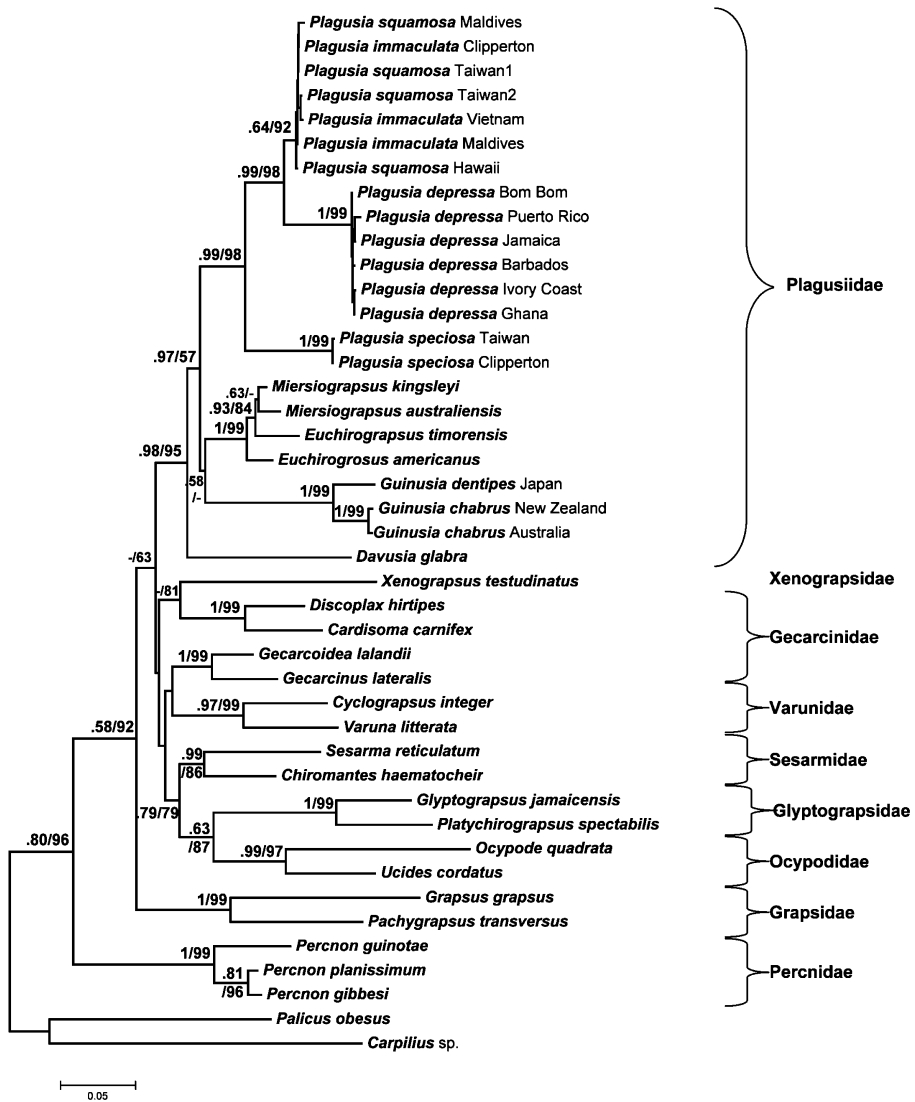


Fig. 1. Phylogenetic consensus tree of representatives of the Plagusiidae and thoracotreme outgroups based on 675 basepairs of mtDNA (16S rRNA). Bayesian Inference (BI) and Minimum Evolution (ME) confidence intervals (only ≥ 50) corresponding to BI posterior probabilities/ME bootstrap values. *Carpilius* sp. was used as outgroup.

triggered the finalization of this long-planned study. The genus name is composed of the four initial letters of Danièle Guinot's last name in addition to the ending *usia*, expressing morphological similarity to the genera *Plagusia* and *Davusia*. Gender feminine.

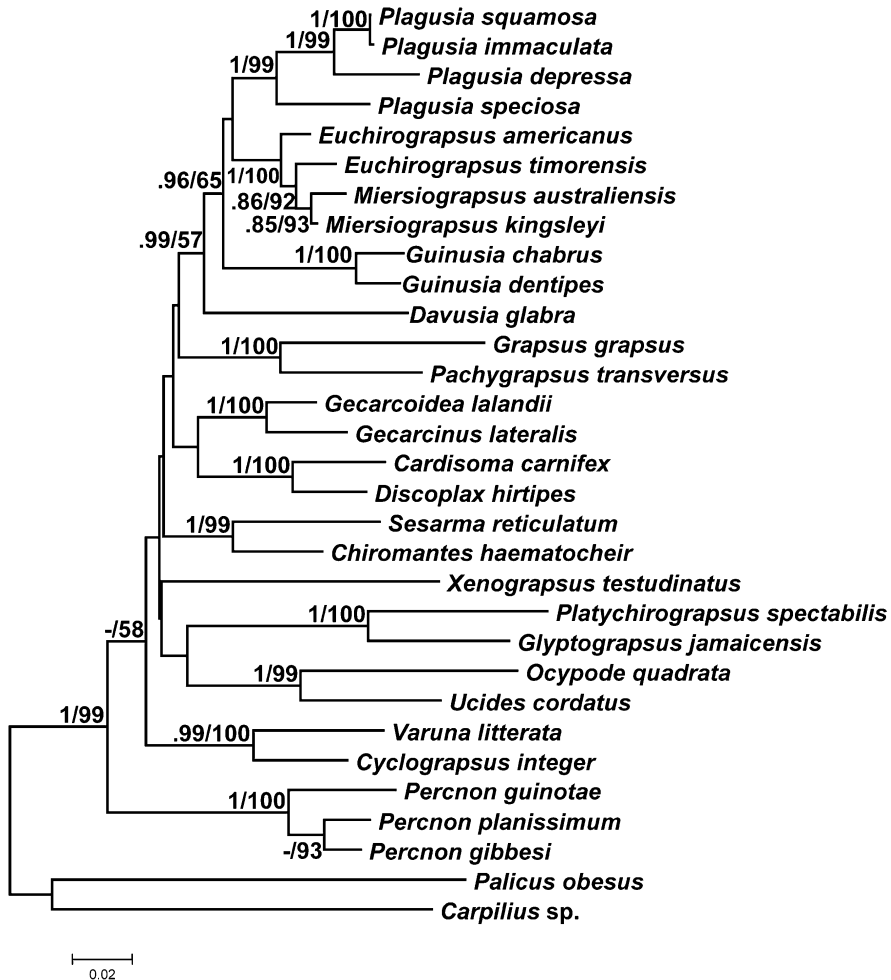


Fig. 2. Phylogenetic consensus tree of representatives of the Plagusiidae and thoracotreme outgroups based on 1003 basepairs (bp) of combined DNA (675 bp 16S rRNA, 328 bp histone H3). Bayesian Inference (BI) and Minimum Evolution (ME) confidence intervals (only ≥ 50) corresponding to BI posterior probabilities/ME bootstrap values. *Carpilius* sp. was used as outgroup.

Diagnosis. — Joints of the meri of all ambulatory legs with a series of spines on their upper margin (as opposed to one subterminal and one terminal spine in *Plagusia*) (fig. 3). Carapace almost entirely destitute of tubercles (as opposed to tuberculate in *Plagusia*) (fig. 4). Larval characters as listed in table II. Other studied characters not differentiating diagnostically from *Plagusia*.

Remarks. — Guinot (2007) lists a number of characters that separate her new genus *Davusia* from the remaining species of *Plagusia*. One of these

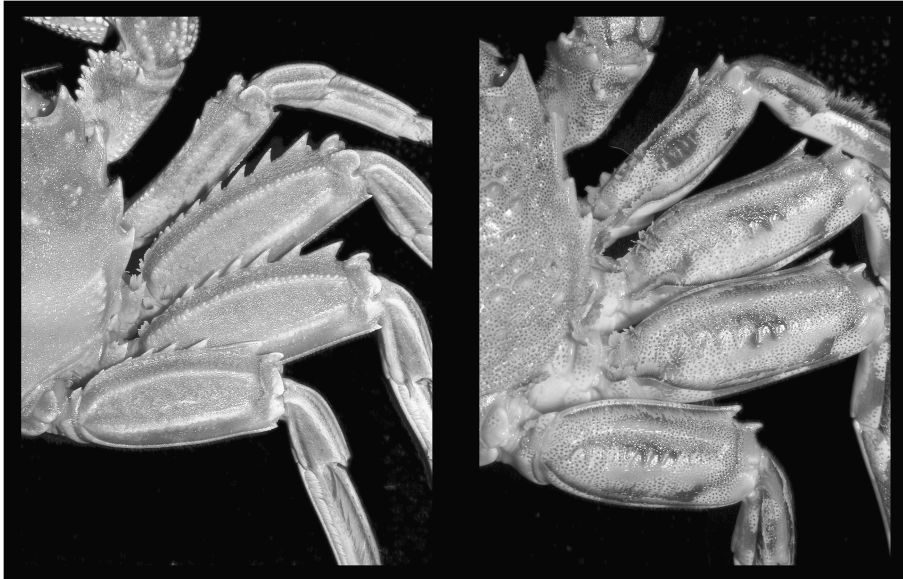


Fig. 3. Morphology of meri of walking legs in *Guinusia* gen. n. and *Plagusia*. Left, *Guinusia dentipes* (De Haan, 1835), Japan (SMF-24559); Right, *Plagusia depressa* (Fabricius, 1775) Ghana (SMF-34728).

characters is the presence of a palp on the exopods of the third maxillipeds. This palp is absent in the other species of *Plagusia*, except for *P. dentipes*, where it may be present in the form of a flagellum. She then concludes that “the generic position of *P. dentipes* should be re-examined” (Guinot, 2007: 30). On the other hand, the gonopod of *Davusia glabra* turns out to be similar to the one of *P. chabrus*. These characters are therefore not consistent in the separation of the newly recognized genus *Davusia* and suggest a mosaic of characters within the genus *Plagusia* in its former sense.

More conclusive adult morphological characters to consistently separate two species of the genus *Guinusia* n. gen., *G. chabrus* and *G. dentipes*, from the species of *Plagusia* (and *Davusia*) have in fact already been provided much earlier by Miers (1878). He separated his first group consisting of *Plagusia depressa*, *P. tuberculata* (= *P. squamosa*), *P. immaculata* Lamarck, 1818, *P. speciosa* Dana, 1852, and *P. glabra* from his second group, with *P. dentipes* and *P. chabrus*, on the basis of the absence or presence of a “series of spines” on the upper margin of the ambulatory merus and, to a lesser extent, of the presence or absence of tubercles on the carapace. It is precisely these characters (figs. 3, 4) in addition to larval morphology (fig. 5) and molecular



Fig. 4. Morphology of carapace structures in *Guinusia* gen. n. and *Plagusia*. Top, *Guinusia dentipes* (De Haan, 1835), Japan (SMF-24559); Bottom, *Plagusia depressa* (Fabricius, 1775), Ghana (SMF-34728).

TABLE II

Morphological and meristic differences between zoeal and megalopal stages of those species of Plagusiidae with known larval data. Abbreviations: (–) no data; (?) zoea collected in plankton samples, number of stage attributed by the author; antenna type (A) refers to exopod present as a small simple seta, (B) refers to exopod less than 1/6 of the protopod length with 1-2 terminal setae, longer one never reaching the middle of protopod length; (C) refers to exopod longer than 1/6 of the protopod length with small terminal spines and 2 terminal setae, longer one almost reaching the tip of the protopod [authorities of species names have been mentioned in the main text]

Species	No. zoeal stages	Zoeal stages		Megalopa stage	
		Antenna type	Setation of 1 st maxilliped basis	No. segment on exopod of 3 rd maxilliped	No. cincinuli on endopod of pleopods
<i>Euchirograpsus americanus</i>	5(+6)	B	2,2,2,2	–	–
<i>Guinusia chabrus</i>	12(?)	B	2,2,3,3	–	–
<i>Guinusia dentipes</i>	–	B	2,2,3,2	2	13-15
<i>Plagusia depressa</i>	6(?)	C	2,2,2,2	1	9
<i>Plagusia speciosa</i>	–	C	2,2,2,2	–	–
<i>Plagusia squamosa</i>	–	C	2,2,2,2	1	8-9
<i>Percnon abbreviatum</i>	–	–	–	–	11-15
<i>Percnon gibbesi</i>	6(?)	A	2,2,3,2	1 ⁽¹⁾	13-17
<i>Percnon guinotae</i>	–	–	–	–	11-14
<i>Percnon planissimum</i>	–	–	–	1	11-14

⁽¹⁾ Cuesta & Schubart, unpublished data.

datasets (figs. 1, 2) that we here use as distinguishing characters for the new genus.

Supporting characters for separating the two species here included in *Guinusia* n. gen. from the remaining representatives of *Plagusia* were indeed found in the larval morphology, despite the fact that larval descriptions of Plagusiidae are incomplete and scarce (no larvae yet known for *Davusia* and *Miersiograpsus*, and only an incomplete description of the zoea of *Euchirograpsus americanus*, as opposed to published larval data for four out of seven recognized species of *Plagusia*). Zoeal data are known for *P. chabrus* (zoea I by Wear, 1970, and zoea V? and XII? by Wear & Fielder, 1985), *P. dentipes* (zoea I by Terada, 1987), *P. depressa* (zoea I-V by Wilson, 1980), and *P. squamosa* (zoea I by Schubart et al., 2001). Included in the present study are the unpublished results (by J. Cuesta, H.-C. Liu & C. D. Schubart) of the first zoea of a fifth species, *P. speciosa*.

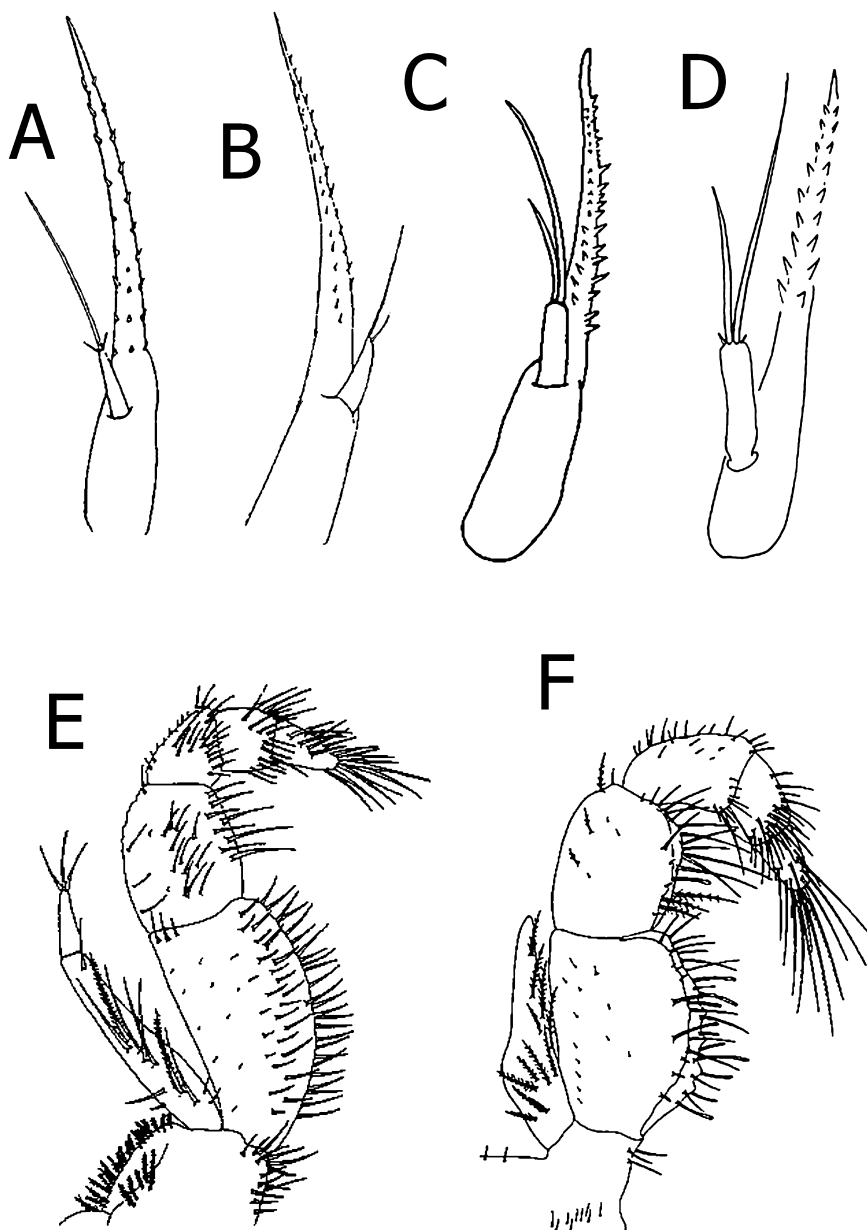


Fig. 5. Antennal morphology of zoea I of: A, *Guinusia chabrus* (Linnaeus, 1758); B, *Guinusia dentipes* (De Haan, 1835); C, *Plagusia depressa* (Fabricius, 1775); D, *Plagusia speciosa* Dana, 1852 (after Wear, 1970; Terada, 1987; Schubart et al., 2001; Cuesta, Liu & Schubart, unpubl., respectively). Third maxilliped (detail of exopod) of the megalopa of: E, *Guinusia dentipes*; F, *Plagusia depressa* (after González-Gordillo et al., 2000; Schubart et al., 2001, respectively).

All zoea I of *Plagusia* sensu stricto share a setal count of 2,2,2,2 at the basis of the first maxilliped, whereas *Guinusia dentipes* and *G. chabrus* have a 2,2,3,2 and 2,2,3,3 setal pattern, respectively. Another important difference is found in the antennal exopod, which is relatively shorter (less than 1/6 of protopod length) in *G. chabrus* and *G. dentipes*, and ends in a long seta that can reach, as maximum size, half the protopod length, with two (*G. chabrus*) or one (*G. dentipes*) additional short setae. In the species of *Plagusia* sensu stricto, the exopod is longer (more than 1/6 of protopod length) and with two long setae, the longer one reaching almost to the tip of the protopod and presenting minute terminal spines (not observed in *G. chabrus* and *G. dentipes*) (fig. 5).

The morphology of the megalopa stage also appears to be useful in distinguishing species of *Guinusia* from *Plagusia*. The megalopa has only been described for *Guinusia chabrus* (without details by Barnard, 1950; Wear, 1970; Wear & Fielder, 1985), *G. dentipes* (several descriptions, the most detailed by González-Gordillo et al., 2000), *Plagusia depressa* (Schubart et al., 2001), and *P. squamosa* (Muraoka, 1965). Three characters show important differences that allow telling apart the megalopae of *G. dentipes* (and *G. chabrus*) from those of *P. depressa* and *P. squamosa*. Firstly, the exopod of the third maxilliped, is 2-segmented in *G. dentipes*, but unsegmented in *P. depressa* and *P. squamosa* (no data available for *G. chabrus*). Secondly, the endopod of the pleopods has less than 10 (8 or 9) cincinnuli in *P. depressa* and *P. squamosa*, but more than 12 (13-17) in *G. dentipes* (no data available for *G. chabrus*). Finally, the rostrum is rather short and broadly bilobed in *G. dentipes* and *G. chabrus*, whereas it projects well forward and is bifid at the tip in *P. depressa* and *P. squamosa*.

Previous mtDNA phylogenies have included only one or two species of *Plagusia* (e.g., Schubart et al., 2001, 2006). The molecular trees generated for this study include all currently recognized species of *Plagusia* with the exception of *Plagusia integripes* Garth, 1973, from the Easter Islands, which is so far only known from the type. Morphological examination of the type specimen allowed the conclusion that the species should remain in the genus *Plagusia* based on the pattern of spines on the meri of the ambulatory legs. However, no amplifiable DNA could be obtained from it. The use of mitochondrial 16S rRNA and the nuclear histone H3 gene allowed both the recognition of intrageneric genetic distances and the construction of more robust gene phylogenies based on separate DNA sources, which should reflect the species' phylogeny. Three main clusters within *Plagusia* (sensu Schubart & Ng, 2000) could be recognized, one consisting of the type species *P. depressa*

(Atlantic) in addition to *P. squamosa*, *P. immaculata*, and *P. speciosa* (Indo-Pacific). Schubart et al. (2001) documented morphological (adult and larval) and genetic differences between the allopatric *P. depressa* and *P. squamosa*, warranting the specific status of both. In the present analysis, however, the two sympatric Indo-Pacific species, *P. squamosa*, and *P. immaculata*, could not be genetically distinguished based on the fragment used, or histone H3. This could be due to a very recent separation event, which is not expressed in the analysed DNA. However, the main morphological difference between these two species is the setation surrounding the tubercles of the carapace and in the sulcae of the pereopods, present in *P. squamosa* but absent in *P. immaculata* (see Schubart & Ng, 2000). In most cases, this pubescence is easy to discern under a dissecting microscope, but some individuals have a faintly developed setation (C. Schubart, pers. obs.), so that we are inclined to consider these two species conspecific with a variable degree of pubescence. However a final decision on synonymy will have to await more comprehensive morphological study, and genetic comparisons with more variable markers (Schubart et al., in progress).

The genetically (and morphologically) most distinct of all former *Plagusia* species is *Davusia glabra*. The monotypic status of *Davusia* Guinot, 2007, is confirmed by the long branch with a single species at the tip (no close sister species). The molecular results indicate that *Davusia glabra* is phylogenetically basal to all other species of *Plagusia* and *Guinusia* n. gen.) and to the analysed species of *Euchirograpsus* and *Miersiograpsus*.

The third phylogenetic cluster consists of the two species, *G. chabrus*, and *G. dentipes*, which are here placed in the new genus *Guinusia*. Despite the clear morphological differences between these two species, they seem closely related genetically, forming the tip clades of a long branch with high confidence values. Also in this case, genetic distances to the remaining species of *Plagusia* are not lower than those between *Guinusia* and *Euchirograpsus*-*Miersiograpsus*, the latter two genera forming a fourth monophyletic clade within the Plagusiidae.

The final putative member of the Plagusiidae is the genus *Percnon*. The present molecular data support the results of Schubart et al. (2000, 2006), in showing that *Percnon* species do not cluster close to the Plagusiidae, but represent a basal split within the Thoracotremata. The current study included three species, viz., *Percnon gibbesi*, *P. planissimum*, and *P. guinotae* Crosnier, 1965, and evidence from mitochondrial, and for the first time also from nuclear DNA (figs. 1, 2), enforces support for an independent phylogenetic origin of

Percnon, and strengthens the insight that it should not be maintained within the Plagusiidae. This differs from the conclusion by Ng et al. (2008), who gave the Percninae subfamily status within the Plagusiidae according to the following reasoning (their p. 219): “With regards to *Percnon*, DNA (Schubart et al., 1999 [2000]) and larval evidence (J. Cuesta, pers. comm.) have suggested that *Percnon* is different and doubtfully placed in the Plagusiidae. On the basis of adult morphology, we concur that *Percnon* species are highly derived, and have many unique generic apomorphies, probably related to their unusual habit of living subtidally on rock faces exposed to heavy wave action. These, combined with unusual sternal characters and the unique grapsoid condition of the male abdomen having only segments 3-5 fused, lead us to support the recognition of a separate subfamily, Percninae, a taxon first erected as a tribe by Števcíć (2005)”. However, the here provided combined evidence of mtDNA, nDNA, and larvae fully support separation of the Percnidae as a full family, suggesting that apparent adult morphological similarities to the Plagusiidae are due to convergence.

Data on the larvae of *Percnon* are, unfortunately, restricted to incomplete descriptions of the development of *P. gibbesi* (see Lebour, 1944; Paula & Hartnoll, 1989) combining material reared in the laboratory and collected in the plankton, the megalopa stage of *P. planissimum* (see Muraoka, 1967), brief descriptions of the megalopa stages of *P. abbreviatum* (Dana, 1851), and *P. guinotae* and *P. planissimum* (see Hartnoll, 1992). Despite the limited data, significant differences in larval morphology also support exclusion of *Percnon* from the Plagusiidae. With regards to the zoeae, the antennal exopod has a small simple seta as in Grapsidae (sensu Schubart et al., 2002, see Cuesta & Schubart, 1999), all the cephalothoracic spines are well developed (especially dorsal and rostral ones), covered by spinules, and the tips of these spines are extended in a lanceolate fashion. The abdomen is long, thin, and with a telson having long furcal arms and a deep cleft; this is a shape not found in any other “grapsoid” family and resembles that of Dorippidae and Dotillidae (see Paula, 1991; Ng et al., in press). The setation of the endopod of the maxilla of zoea I of *P. gibbesi* has a setation of 2,2, which in the zoea III changes to 2,3, and in zoea V and VI to 2,4 according to Paula & Hartnoll (1989); this is very unusual and awaits confirmation. In all known brachyuran zoeae, this setation remains constant throughout development (Cuesta et al., 2006). The megalopae are also distinct, with 10 segments on the antennular flagellum (eight in Plagusiidae) and a trifid rostrum (bilobate or bifid at the tip in Plagusiidae).

In an mtDNA phylogeny of selected Thoracotremata, Schubart et al. (2006) found two representatives of the Plagusiidae (*Plagusia depressa* and *Euchi-*

rograpsus americanus) clustering with low support among the Gecarcinidae, suggesting an apparent paraphyletic relationship of the latter family. Due to the low confidence values and limited number of taxa, this was not discussed in detail (except perhaps by Ng et al., 2008: 214), and Schubart et al. (2006: 196) concluded that “Further studies with all gecarcinid taxa and additional molecular markers are necessary to confirm their phylogenetic relationship and their position within the Thoracotremata”. The molecular trees in the present study support monophyly of the Plagusiidae (now including all the genera) with confidence values always exceeding 0.95 posterior probability, and show no affinity to gecarcinid representatives. In contrast, the phylogenetic status of the Gecarcinidae as well as the basal relationships among the families of Thoracotremata remain unresolved (see also N. K. Ng et al., 2007). Very remarkable, however, is the close relationship of *Ocypode* and *Ucides* so that, in contrast to Ng et al. (2008), for the time being, we continue recognizing *Ucides* as member of the family Ocypodidae (and the Ucididae Števcíć, 2005 a junior synonym of the Ocypodidae). Further studies are currently underway to resolve basal relationships among the Thoracotremata, including more conserved nuclear markers (28S and nuclear coding genes) (Schubart et al., in prep.; Landstorfer et al., in prep.).

The present study represents a comprehensive phylogenetic study of the Plagusiidae and has resulted in recognition of the new genus *Guinusia* and the establishment of a new phylogenetic understanding of relationships among four genera and 11 species of the family Plagusiidae. In order to make the Plagusiidae monophyletic we formally exclude *Percnon* and the subfamily Percninae from the Plagusiidae, and hereby recognize the independent family Percnidae Števcíć, 2005.

Family PERCNIDAE Števcíć, 2005 [new status]

Subfamily PERCNINAE Števcíć, 2005 (see Ng et al., 2008)

Tribe PERCNINI Števcíć, 2005

Type genus. — *Percnon* Gistel, 1848 (only genus in family).

Type species. — *Acanthopus planissimus* Herbst, 1804.

Other species. — *Percnon abbreviatum* (Dana, 1851), *P. affine* (H. Milne Edwards, 1853), *P. gibbesi* (H. Milne Edwards, 1853), *P. guinotae* Crosnier, 1965; *P. sinense* Chen, 1977.

Diagnosis. — Carapace conspicuously flattened; front with two antennal clefts, third maxillipeds with reduced exopod and lacking palp (shared with Plagusiidae); meri of walking legs always with several spines on dorsal crest, male abdomen with somites 3-5 fused (3-6 in Plagusiidae).

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REFERENCES

- ALCOCK, A., 1900. Materials for a carcinological fauna of India. No. 6. The Brachyura Catometopa, or Grapsoidea. Part II. Journal of Asiatic Society of Bengal, **69** (3): 279-456.
- BARNARD, K. H., 1950. Descriptive catalogue of South African decapod Crustacea. Annals of the South African Museum, **38**: 1-837.
- BENECH, S. V., 1978. Ocean transport of a community of the grapsid crab *Plagusia dentipes* (De Haan, 1833). *Crustaceana*, **35**: 104.
- COLGAN, D. J., C. McLAUGHLIA, G. D. F. WILSON, S. P. LIVINGSTON, G. D. EDGE-COMBE, J. MACARANAS, G. CASSIS & M. R. GRAY, 1998. Histone H3 and U2 snRNA DNA sequences and arthropod molecular evolution. Australian Journal of Zoology, **46**: 419-437.
- CUESTA, J. A., G. GUERAO, H.-C. LIU & C. D. SCHUBART, 2006. Morphology of the first zoeal stages of eleven Sesamidae (Crustacea, Brachyura, Thoracotremata) from the Indo-West Pacific, with a revision of larval characters of the family. Invertebrate Reproduction and Development, **49** (3): 151-173.

- CUESTA, J.A. & C. D. SCHUBART, 1998. The first zoeal stage of *Glyptograpsus impressus*, with comments on the subfamilial arrangement of Grapsidae (Crustacea: Brachyura). *Cahiers de Biologie Marine*, **38**: 291-299 [as 1997].
- — & — —, 1999. First zoeal stages of *Geograpsus lividus* and *Goniopsis cruentata* from Panama confirm consistent larval characters within the subfamily Grapsinae (Crustacea: Brachyura: Grapsidae). *Ophelia*, **51** (3): 163-176.
- DANA, J. D., 1851. On the classification of the Crustacea Grapsoidea. *American Journal of Science and Arts*, (2) **12**: 283-290.
- —, 1852. Crustacea. United States Exploring Expedition during the years 1838, 1839, 1840, 1841, 1842 under the command of Charles Wilkes, U.S.N., **13** (1): i-viii, 1-685. (C. Sherman, Philadelphia).
- DAVIE, P. J. F., 2002. Crustacea: Malacostraca: Eucarida (Part 2): Decapoda-Anomura, Brachyura. In: A. WELLS & W. W. K. HOUSTON (eds.), *Zoological Catalogue of Australia*, **19.3B**: i-xiv, 1-641. (CSIRO Publications, Melbourne).
- 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. *National Museum of New Zealand Records*, **3** (4): 37-45.
- GONZÁLEZ-GORDILLO, J. I., S. TSUCHIDA & C. D. SCHUBART, 2000. Redescription of the megalopa of *Plagusia dentipes* (Brachyura: Plagusiidae) from Japan. *Crustacean Research*, **29**: 143-151.
- GRIFFIN, D. J. G., 1968. The designation of a neotype for *Cancer chabrus* Linnaeus and the status of *Plagusia capensis* De Haan (Decapoda, Grapsidae). *Crustaceana*, **15** (2): 209-213.
- GUINOT, D., 1978. Principes d'une classification évolutive des Crustacés Décapodes Brachyours. *Bulletin Biologique de la France et de la Belgique*, **112** (3): 211-292.
- —, 1979. Données nouvelles sur la morphologie, la phylogénèse et la taxonomie des Crustacés Décapodes Brachyours. *Mémoires du Muséum national d'Histoire naturelle*, (A, Zoologie) **112**: 1-354.
- —, 2007. A new genus of the family Plagusiidae Dana, 1851, close to *Plagusia* Latreille, 1804 (Crustacea, Decapoda, Brachyura). *Zootaxa*, **1498**: 27-33.
- GUINOT, D. & J.-M. BOUCHARD, 1998. Evolution of the abdominal holding systems of brachyuran crabs (Crustacea, Decapoda, Brachyura). *Zoosystema*, **20** (4): 613-694.
- HARTNOLL, R. G., 1992. Megalopae and early postlarval stages of East African *Percnon* (Decapoda: Brachyura: Grapsidae). *Journal of Zoology, London*, **228**: 51-67.
- HUELSENBECK, J. P. & F. RONQUIST, 2001. MrBayes: Bayesian inference of phylogenetic trees. *Bioinformatics*, **17**: 754-755.
- LATREILLE, P. A., 1804. Crustacés (1). Crustacea. Classe Septième. Tableau méthodique des Crustacés. In: *Nouveau Dictionnaire d'Histoire Naturelle*, **24**: 123-127.
- —, 1810. Considérations générales sur l'ordre naturel des animaux composant les classes des Crustacés, des Arachnides et des Insectes; avec un tableau méthodique de leurs genres, disposés en familles: 1-144. (F. Schoell, Paris).
- LEBOUR, M. V., 1944. Larval crabs from Bermuda. *Zoologica*, **29**: 113-128.
- MAN, J. G. DE, 1883. Carcinological studies in the Leyden Museum. No. 3. Notes of the Leyden Museum, **5** (15): 150-169.
- MANNING, R. B. & L. B. HOLTHUIS, 1981. West African brachyuran crabs (Crustacea: Decapoda). *Smithsonian Contributions to Zoology*, **306**: i-xii, 1-379.
- MARTIN, J. W. & G. E. DAVIS, 2001. An updated classification of the recent Crustacea. *Natural History Museum of Los Angeles County, Science Series*, **39**: 1-124.

- MIERS, E. J., 1878. Revision of the Plagusiinae. *Annals and Magazine of Natural History*, (5) **1**: 147-154.
- MURAOKA, K., 1965. On the post-larval stage of *Plagusia depressa tuberculata* Lamarck (Grapsidae). *Research on Crustacea*, **2**: 83-90.
- , 1967. On the post-larval stages of *Percnon planissimum* (Herbst), Grapsidae. *Research on Crustacea*, **3**: 61-67.
- NG, N. K., P. J. F. DAVIE, C. D. SCHUBART & P. K. L. NG, 2007. Xenograpsidae, a new family of grapsoid crabs (Crustacea: Brachyura) associated with shallow water hydrothermal vents. *Raffles Bulletin of Zoology*, (Supplement) **16**: 233-256.
- 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*, **2**. Cephalopods, crustaceans, holothurians and sharks: 1045-1155. (Food and Agriculture Organisation, Rome).
- NG, P. K. L., P. F. CLARK & J. A. CUESTA, in press. Establishment of a new subfamily for *Shenius anomalus* (Shen, 1953) (Decapoda, Brachyura, Dotillidae). *Journal of Natural History*, London.
- NG, P. K. L., D. GUINOT & P. J. F. DAVIE, 2008. Systema Brachyurorum: Part I. An annotated checklist of extant brachyuran crabs of the world. *Raffles Bulletin of Zoology*, (Supplement) **17**: 1-286.
- NG, P. K. L., C. H. WANG, P. H. HO & H. T. SHIH, 2001. An annotated checklist of brachyuran crabs from Taiwan (Crustacea: Decapoda). *National Taiwan Museum Special Publications Series*, Taipei, **11**: 1-186.
- PAULA, J., 1991. The zoeal stages of the crab *Medorippe lanata* (Linnaeus, 1767) (Brachyura, Dorippidae) reared in the laboratory, and the larval characters of the Dorippidae. *Journal of Natural History*, London, **25**: 75-89.
- PAULA, J. & R. G. HARTNOLL, 1989. The larval and post-larval development of *Percnon gibbesi* (Crustacea, Brachyura, Grapsidae) and the identity of the larval genus *Pluteocaris*. *Journal of Zoology*, London, **218**: 17-37.
- POSADA, D. & K. A. CRANDALL, 1998. MODELTEST: testing the model of DNA substitution. *Bioinformatics*, **14**: 817-818.
- RATHBUN, M. J., 1918. The grapsoid crabs of America. *U.S. National Museum Bulletin*, **97**: 1-461, pls. 1-161.
- SCHUBART, C. D., 2009. Mitochondrial DNA and decapod phylogenies: the importance of pseudogenes and primer optimization. In: J. W. MARTIN, K. A. CRANDALL & D. L. FELDER (eds.), *Decapod crustacean phylogenetics*. *Crustacean Issues*, **18**: 47-66. (Taylor & Francis/CRC Press, Boca Raton, Florida).
- SCHUBART, C. D., S. CANNICCI, M. VANNINI & S. FRATINI, 2006. Molecular phylogeny of grapsoid crabs (Decapoda, Brachyura) and allies based on two mitochondrial genes and a proposal for refraining from current superfamily classification. *Journal of Zoological Systematics and Evolutionary Research*, **44** (3): 193-199.
- SCHUBART, C. D., J. A. CUESTA, R. DIESEL & D. L. FELDER, 2000. Molecular phylogeny, taxonomy, and evolution of nonmarine lineages within the American grapsoid crabs (Crustacea: Brachyura). *Molecular Phylogenetics and Evolution*, **15** (2): 179-190.
- SCHUBART, C. D., J. A. CUESTA & D. L. FELDER, 2002. Glyptograpsidae, a new brachyuran family from Central America: larval and adult morphology, and a molecular phylogeny of the Grapsoidea. *Journal of Crustacean Biology*, **22** (1): 28-44.
- SCHUBART, C. D., J. I. GONZÁLEZ-GORDILLO, N. REYNS, H.-C. LIU & J. A. CUESTA, 2001. Are Atlantic and Indo-Pacific populations of the rafting crab, *Plagusia depressa*, distinct? New evidence from larval morphology and mtDNA. *Raffles Bulletin of Zoology*, **49** (2): 301-310.

- SCHUBART, C. D. & P. K. L. NG, 2000. 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). Raffles Bulletin of Zoology, **48** (2): 327-336.
- STERNBERG, R. VON & N. CUMBERLIDGE, 2000. Taxic relationships within the Grapsidae MacLeay, 1838 (Crustacea: Decapoda: Eubrachyura). Journal of Comparative Biology, **3** (2): 115-136 [as 1998].
- ŠTEVČIĆ, Z., 2005. The reclassification of brachyuran crabs (Crustacea, Decapoda: Brachyura). Natura Croatica, **14** (supplement 1): 1-159.
- TAMURA K., J. DUDLEY, M. NEI & S. KUMAR, 2007. MEGA4: Molecular Evolutionary Genetics Analysis (MEGA) software version 4.0. Molecular Biology and Evolution, **24**: 1596-1599.
- TERADA, M., 1987. Zoeal forms of 14 species of crabs from Enshunada. Research on Crustacea, **16**: 93-120.
- UDEKEM D'ACCOZ, 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", **40**: 1-383. (Muséum national d'Histoire naturelle, Paris).
- WEAR, R. G., 1970. Life-history studies on New Zealand Brachyura. 4. Zoa larvae hatched from crabs of the family Grapsidae. New Zealand Journal of Marine and Freshwater Research, **4** (1): 3-35.
- WEAR, R. G. & D. R. FIELDER, 1985. The marine fauna of New Zealand: Larvae of the Brachyura (Crustacea, Decapoda). New Zealand Oceanographic Institute Memoir, **92**: 1-90.
- WILLIAMS, A. B., 1984. Shrimps, lobsters, and crabs of the Atlantic coast of the eastern United States, Maine to Florida: 1-550. (Smithsonian Institution Press, Washington, D.C.).
- WILSON, K. A., 1980. Studies on decapod Crustacea from the Indian River region of Florida. XV. The larval development under laboratory conditions of *Euchirograpsus americanus* A. Milne-Edwards, 1880 (Crustacea: Decapoda: Grapsidae) with notes on grapsid subfamilial larval characters. Bulletin of Marine Science, Miami, **30** (4): 756-775.
- WILSON, K. A. & R. H. GORE, 1980. Studies on decapod Crustacea from the Indian River region of Florida. XVII. Larval stages of *Plagusia depressa* (Fabricius, 1775) cultured under laboratory conditions (Brachyura: Grapsidae). Bulletin of Marine Science, Miami, **30** (4): 776-789.

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