Genetic diversity of freshwater crabs (Brachyura: Sesarmidae) from central Jamaica with description of a new species

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Abstract

Jamaica is the only island of the Greater Antilles where freshwater streams are not populated by representatives of the old lineage of freshwater crabs, the Pseudothelphusidae. Instead, a very diverse fauna of endemic sesarmid crabs inhabits freshwater and terrestrial habitats throughout the island, thereby showing complete independence from the sea. They have been reported thriving in bromeliad leaf axils, rock rubble, empty snail shells, caves and mountain streams. Otherwise, the Sesarmidae are typical inhabitants of soft-sediment littoral habitats like marshes and mangroves. For many years, crabs from Jamaican mountains streams had been considered to belong to a single species, Sesarma bidentatum Benedict 1892. However, recent morphological and molecular studies have shown that crabs from mountain streams of different regions of the island belong to different species. Consequently, four new crab species have been described over the last 10 years. In this study, we give evidence that freshwater streams in central Jamaica also host two different species of crabs. In streams draining to the north we exclusively found the species S. windsor Türkay and Diesel, 1994, while streams draining to the south were inhabited by a closely related but undescribed species of crab. The southern species is here described as new and is referred to as Sesarma meridies sp. n. Morphological and molecular (12S and 16S mtDNA) evidence is provided that allows these two species of freshwater crabs from central Jamaica to be distinguished. The species richness of Jamaican endemic sesarmids thereby increases to 10, which makes the island unique in terms of its diversity of land-dwelling crabs.

Keywords: Crustacea, decapoda, Sesarma meridies, Sesarma windsor, mtDNA sequence

Introduction

The Caribbean island of Jamaica is one of only two places world-wide where sesarmid crabs complete their life cycle in total independence of the sea. Otherwise, crabs of this family are typical inhabitants of marshes and mangroves. Some sesarmid crabs live as adults in lower reaches of rivers (e.g. Diesel and Schuh 1998; Schubart et al. 2000a) and a few representatives belonging to the closely related families Varunidae and Glyptograpsidae migrate several hundred kilometres upstream, to spend their adult lives in fresh water (Schubart et al. 2002). In almost all of these cases, however, the crabs have a marine planktonic development and adults have to migrate back to the sea or have the currents

carry the larvae downstream in order for larval development and dispersal to take place in the world's oceans (Anger 1995; Diesel et al. 2000). The only exceptions known for this mode of reproduction in thoracotreme crabs are sesarmid crabs of the genus Geosesarma in South-East Asia and the endemic Sesarmidae (genera Sesarma and Metopaulias) from Jamaica. These crabs have an abbreviated or reduced larval development and complete their life cycle on land or in fresh water. While Geosesarma was for a long time known to be a species-rich genus, due to its occurrence from Thailand to Taiwan and its presence on all of the larger Indonesian islands (Ng et al. 2004), the Jamaican Sesarmidae until 10 years ago were thought to consist of only five endemic species (four species of Sesarma and the monotypic Metopaulias depressus Rathbun, 1896). Interestingly, these five species all occupy different ecological niches (freshwater streams, caves, rock rubble, snail shells and bromeliad leaf axils) and can be easily distinguished by their distinct morphology, thus representing different ecotypes and morphotypes (Hartnoll 1964, 1971; Chace and Hobbs 1969; Abele 1992; Diesel & Horst 1995). In consequence, Hartnoll (1964, 1971) assumed that these crabs experienced an adaptive radiation on the island. A molecular systematic study including the Jamaican endemic Sesarmidae and all the other American representatives of the genus Sesarma showed that the Jamaican endemic crabs are indeed monophyletic and thus most likely colonized Jamaica only once. This colonization was estimated to have taken place 4.5 million years ago, while initial speciation may have occurred approximately 3.5 million years ago (Schubart et al. 1998a).

During the last 10 years, detailed morphological and molecular work has allowed the recognition and description of four additional species of endemic crabs from Jamaica, within the eco- and morphotypes from freshwater streams (Türkay and Diesel 1994; Schubart et al. 1997, 1998b, 1999; Reimer et al. 1998). While the above-mentioned and first-described five species of Jamaican crabs overlapped geographically, but could easily be told apart by their morphology and ecology, later species descriptions were based on less marked morphological, but clear molecular differences. Since these newly described crab species all belong to the same ecotype, it is not surprising that they exclude (or substitute) each other geographically. After the most recent description of Sesarma ayatum Schubart et al., 1998b, the following distribution was valid for five species of crabs inhabiting mountain creeks from western to eastern Jamaica: (1) S. dolphinum Reimer et al., 1998, from Hanover and Westmoreland; (2) S. fossarum Schubart et al., 1997, from St James, St Elizabeth and western Trelawny; (3) S. windsor Türkay and Diesel, 1994, from eastern Trelawny, Manchester and Clarendon; (4) S. bidentatum Benedict, 1892, from the western Blue Mountains (St Ann, St Mary, St Catherine, St Andrew); and (5) S. ayatum from the eastern Blue Mountains and the John Crow Mountains (Portland and St Thomas). All these species, except for S. windsor, are known to include populations from rivers draining to the north as well as to the south of the island of Jamaica, which are genetically homogeneous (e.g. Schubart et al. 1998b). The description of S. fossarum made a redecription of S. windsor necessary, which was then based only on individuals from a subterranean part of a river, which drains to the north coast of Jamaica (Schubart et al. 1997). In subsequent years we collected and analysed freshwater crabs from all neighbouring rivers in central Jamaica draining to the north as well as to the south. It turned out that all crabs inhabiting rivers draining to the north are morphologically and genetically similar and must be included in the species Sesarma windsor. On the other hand, crabs from four river systems draining to the south differed from all S. windsor examined in their morphology and in two mitochondrial genes. Consequently, they are here described as a new species.

Material and methods

Freshwater crabs were collected from eight different river systems at 15 localities in central Jamaica between 1995 and 2003. The entire area between Christiana in the south, Troy in the west, Albert Town in the north and Lluidas Vale in the east was thereby covered and all surface waters sampled. In addition, one locality was sampled from the Rio Magno system, a tributary of the Rio Cobre in St Catherine. Overall, 112 crab specimens were examined.

Crab tissue for DNA sequencing was preserved in 75% ethanol. Genomic DNA was isolated from the muscle tissue of walking legs from nine crabs using the extraction kit of Puregene (Gentra). Selective amplification of a 559 base-pair region from the mitochondrial large ribosomal subunit (16S rRNA) and a 585 base-pair region from the small ribosomal subunit (12S rRNA) gene was carried out by polymerase chain reaction (PCR) with 35-40 cycles and the following temperature profile: 45 s denaturing at 94° C, 1 min annealing at 46–48°C and 1 min extension at 72°C. The following primers were used: 16S-L2 (5'-TGCCTGTTTATCAAAAACAT-3') (modified from 16sar) and 16S-1472 (5'-AGATAGAAACCAACCTGG-3') (see Schubart et al. 2000b) for 16S mtDNA; the newly designed 12L4 (5'-GTGCCAGCCGCCGCGGTTA-3') and 12H2 (5'-ATGCACTTTCCAGTACATCTAC-3') (see Fratini et al. in press) for 12S mtDNA. PCR products were purified with Millipore filters (Microcom) and both strands were sequenced in an automated sequencer ABI 310 (Perkin Elmer). Alignments were done by hand using the multisequence editing program ESEE (Cabot and Beckenbach 1989). Sequences of the different haplotypes have been deposited in the EMBL database (AJ621819–AJ621830).

Type specimens have been deposited at the Senckenberg Museum Frankfurt (SMF), Germany; Natural History Museum (NHM), London, UK; Nationaal Natuurhistorisch Museum (RMNH), Leiden, The Netherlands; Naturhistorisches Museum Wien (NHMW), Vienna, Austria; Academy of Natural Sciences, Philadelphia (ANSP), PA, USA; National Museum of Natural History (USNM), Smithsonian Institute, Washington DC, USA; and the Zoological Reference Collection (ZRC), National University of Singapore, Republic of Singapore.

Abbreviations and measurements used in the text are: cw, maximum carapace width; cl, carapace length; bh, body height; iw, interorbital width; el, extraorbital tooth length; prh, chelar propodus height; prl, chelar propodus length; dal, chelar dactylus length; 4prp, ventral length of pereiopod 4 (all in mm); CDS, private collection Christoph D. Schubart; JBS, Jamaican Biological Survey carried out by the the Academy of Natural Sciences, Philadelphia.

Results

Morphological comparisons showed consistent differences in crab populations from the northern and the southern drainages in central Jamaica. These differences include the shape of the carapace, the male chelae and the male pleon. Crabs from the southern drainages are overall significantly flatter than those from the northern drainages (body height/carapace width= 0.47 ± 0.01 as opposed to 0.48 ± 0.01 , *t*-test *P*=0.0001; *n*=83). The exorbital tooth is shorter and less curved than in the northern drainages (exorbital length/carapace length= 0.15 ± 0.01 as opposed to 0.21 ± 0.01 , *t*-test *P*=0.013; *n*=97) (Figure 4A). The tubercles on the dactylus on the male claw are much more prominent and broader in crabs from the northern drainages as compared to the southern populations.

Finally, the male pleon is slightly vaulted from a fronto-ventral perspective and the margins of the single segments are straight in crabs from the southern drainages. In contrast, the male pleon is straight from a fronto-ventral perspective and the margins of the single segments are convex in crabs from the northern drainages (Figure 4B).



Figure 1. Plot of genetic distances (Kimura 2-parameter), not including indels, among nine freshwater crab specimens from central Jamaica based on (A) 585 base pairs of the 12S rRNA mitochondrial gene and (B) 559 base pairs of the 16S rRNA mitochondrial gene.

	Mouth R.	Printed C.	Quashies R.	Hectors R.	Crooked R.	Pindars R.	Pedro R.	$\begin{array}{c} \text{Magno R.} \\ \times 2 \end{array}$
Mouth R.	_	0.34	0.51	0.85	2.56	2.56	2.56	3.08
Printed C.	0	_	0.17	0.51	2.22	2.22	2.22	2.74
Quashies R.	0.18	0.18	_	0.34	1.88	1.88	1.88	2.39
Hectors R.	0.54	0.54	0.36	_	2.39	2.39	2.39	2.91
Crooked R.	1.79	1.79	1.97	1.97	_	0	0	0.51
Pindars R.	1.97	1.97	2.15	2.15	0.18	_	0	0.51
Pedro R.	1.79	1.79	1.97	1.97	0	0.18	-	0.51
Magno R. $\times 2$	1.79	1.79	1.97	1.97	0.36	0.54	0.36	-

Table I. Percentage genetic divergence between crabs from eight localities in central Jamaica.

Upper right values, 585 base pairs of 12S mtDNA; lower left values, 559 base pairs of 16S mtDNA.

The comparison of 585 base pairs of mtDNA sequence of the 12S rRNA gene (12S) and 559 base pairs of the 16S rRNA gene (16S) from nine crabs collected at eight different localities revealed the existence of six different haplotypes for both genes. Plotting the populations on a diagram according to genetic distances, they formed two clearly distinct groups with identical species compositions for both genes (Figure 1). Populations from the southern drainages in central Jamaica (Crooked River, Pindars River, Pedro River) had identical 12S haplotypes and differed in no more than one mutation (0.18%) in 16S. Two crabs from another southern drainage, but more to the east (Magno River), showed a slightly higher genetic distance to the other three populations: three mutations in 12S (0.51%) and two to three in 16S (0.36-0.54%). Intraspecific mutations among the populations from the northern drainages (Mouth River, Printed Creek, Quashies River, Hectors River) are similarly low and never exceed 1% genetic divergence (0.34–0.85% in 12S; 0–0.54% in 16S). In contrast, genetic divergence between southern and northern drainages always were higher than 1.5% and in the range of 1.88–3.08% in 12S and 1.79– 2.15% in 16S (Table I). Between the two drainage systems and potential species, 12 diagnostic positions (eight transitions, two transversions and two indels) were found in 585 base pairs of 12S and eight diagnostic positions (six transitions and two indels) were found in 559 base pairs of 16S, which consistently separate the populations from northern and southern drainages, thereby supporting their distinctness.

Morphological and molecular methods thus suggest the existence of two distinct species among the studied material, all of which would have been previously assigned to *Sesarma windsor* Türkay and Diesel, 1994. The redescription of this species (Schubart et al. 1997) revealed that the type locality is Printed Circuit Cave in the Mouth River system which drains to the north. The name *S. windsor* will therefore be used for the populations from the northern drainages, while crabs from the populations of the southern drainages will be described as a new species.

Systematic account

Sesarma meridies sp. n. (Figures 2–4)

Material examined. HOLOTYPE: one male (SMF 29338), Jamaica (Clarendon): Crooked River, tributary to Rio Minho (~18°08'N, 77°20'W), 12 March 1995, leg. C. D. Schubart and R. Diesel.



Figure 2. Sesarma meridies sp. n., male holotype (SMF 29338), carapace. (A) Dorsal view; (B) frontal view. Scale bars: 1 cm.

PARATYPES: one male and five females (SMF 29339), same data as holotype; two males and two females (RMNH D 50431), Jamaica (Clarendon): Grantham, tributary to Rio Minho (18°09'19.3"N, 77°23'48.1"W, 345 m), 14 March 2003, leg. C. D. Schubart, R. Brodie, T. Santl and T. Weil; two males and two females (USNM 1020443), same data as RMNH D 50431; one male and one female (NHM 2004. 74–75), same data as RMNH D 50431; one male and one female (NHMW 19934), same data as RMNH D 50431; one male and one female (NHMW 19934), same data as RMNH D 50431; one male and one female (Clarendon): Pindars River (=Bullhead River) and tributary, between Kellits and Brandon Hill (JBS 383; 18°10.19'N, 77°14.85'W; 456 m), 11 October 2000, leg. C. D. Schubart and G. Rosenberg; two males and seven females (ANSP CA7304), Jamaica (St Ann–Clarendon): Pedro River,



Figure 3. *Sesarma meridies* sp. n., male holotype (SMF 29338). (A) Left cheliped dorsal view; (B) left chela outer face; (C) anterior and posterior face of second walking leg; (D) gonopods, right one denuded. Scale bars: 1 cm (A–C); 1 mm (D).

next to bridge (JBS 382; $18^{\circ}11.72'$ N, $77^{\circ}13.08'$ W; 464 m), 11 October 2000, leg. C. D. Schubart and G. Rosenberg.

Other material: one male and one female (CDS), same data as RMNH D 50431; three males and two females (CDS), Jamaica (Clarendon): Thomas River between Nine Turns



Figure 4. Comparison of *Sesarma meridies* sp. n., male holotype (SMF 29338) and *S. windsor* Türkay and Diesel, 1994 (R-148). (A) Anterior carapace with anterolateral tooth; (B) male pleon and sternum. Upper drawings, *Sesarma meridies* sp. n.; lower drawings, *S. windsor*. Scale bars: 1 cm.

and Smithville, 14 March 2002, leg. C. D. Schubart, R. Brodie, T. Santl and T. Weil; two males and four females (ANSP CA7305), Jamaica (St Catherine): Knollis River (tributary to Rio Magno) between Rio Magno and Ham Walk (JBS 398; 18°13.06'N, 76°57.63'W; 323 m), 14 October 2000, leg. C. D. Schubart and I. Muratov.

Etymology. The name '*meridies*' is Latin and means 'south'. It is used as a noun in apposition and thus is independent of the gender of the genus name (in this case neuter). The name makes reference to the fact that the newly described species is so far the only Jamaican freshwater crab restricted to river systems draining to the south of the island.

Diagnosis. General body form flattened, body height 0.47 times carapace breadth. Carapace comparatively broad and smooth; all regions well defined. Anterolateral borders with one comparatively short and straight exorbital tooth. Row of 10–14 horny-tipped tubercles on dactyli of male chelae not very prominent and not reaching distal end. Walking legs comparatively short: merus less than 2.4 times as long as broad in all legs, pereiopod 4 approximately twice as long as carapace length. Male pleon vaulted and with straight lateral margin of segments, telson relatively short. Gonopod slender, terminal horny endpiece slightly deflexed.

Description. Body form flattened (bh/cw=0.47 + 0.01, n=21). Carapace broader than long $(cl/cw=0.86\pm0.01, n=21)$ widening posteriorly. Greatest width at posterior angles (cw at tooth/posterior cw= 0.98 ± 0.01 , n=21). Carapace regions clearly delimited, especially gastric ones. Carapace surface mostly glabrous and smooth, evenly covered with small and coarse granules. Branchial regions with various oblique striae of different lengths and scattered setae (Figure 2A). Interorbital region subdivided into four frontal lobes. Median ones more bulged and broader than lateral ones. Lateral lobes often with row of granules; median lobes with short and oblique row of granules (if any). Posterior frontal lobes reduced (in large animals a slight elevation still visible), instead a short row of granules usually present. Front relatively narrow (iw/cb= 0.48 ± 0.01 , n=21) with ventral border granular, lateral margins subparallel and median emargination (Figures 2A, 4A). Exorbital tooth triangular; anterolateral margin anterior to deep notch comparatively short and straight (el/cl= 0.15 ± 0.01 , n=21). Anterolateral tooth triangular and bent upwards, the tip thus pointing dorsofrontally (Figures 2A, 4A). Posterior to tooth, a distinct bulge, where anterior striae of branchial regions meet anterolateral borders, representing a second, now rudimentary anterolateral tooth. Posteriorly carapace slopes ventrally. Lateral carapace border ventrally fringed by a row of long setae on the upper branchiostegite. The setal row is interrupted several times by gaps subdividing it into five to six distinct groups; gaps tend to be at same height as anterolateral teeth and carapace striae. Lateral carapace border and parallel row of setae meet ventral carapace at height of third ambulatory leg without fusing, thus leaving small gap between them. Pterygostomian region and branchiostegite covered with dense and regular reticulation. Anterior triangular area, separated by grooves, with shorter non-reticulated setae. Epistome setose, with endostomial cristae along ventral border. Epistomial wings in close connection with base of the second antennae. Setae delimiting Verwey's groove mostly reduced. Orbit lined with setae. Cornea of eyes broader than eyestalk (Figure 2B). Gap between third maxillipeds clearly exposes mandibles and palps of second maxillipeds.

Chelipeds in adult animals homochelous, but sexually dimorphic, those of females markedly smaller and weaker (prh/cw= 0.35 ± 0.07 in 10 males, 0.28 ± 0.01 in 11 females,

t-test P=0.0025). Merus triangular in cross-section, all three borders with regular row of granules. Upper border with subdistal projection and rounded distal tip. Inner face ventrally bulged, with two longitudinal rows of setae, lower one extending over full length, upper one only extending to proximal half. Dorsal to upper row, presence of an irregular field of short and stout setae. Ventral face triangular, smooth and glabrous. Outer face with several transverse rows of granules of varying length. Carpus with regular longitudinal row of granules on proximal border and tuft of grooming setae in close connection with ventral setal row from inner face of merus. Outer face with mostly granular crests of different length. Palm approximately 0.5 times as high as long $(prh/prl=0.55\pm0.04 \text{ in } 10 \text{ males})$ 052 ± 0.01 in 11 females; t-test P=0.038). Dorsal row of granules semi-continuous; often broken once at half its length, sometimes the granules are of irregular size and distance. Upper inner face often with oblique lines of larger-sized granules (Figure 3A). Outer face completely covered with coarse granules. Inner face irregularly granulate, with a patch of larger granules in its centre. Palm about 1.6-1.7 times as long as dactylus (1.63+0.03 in 10)males, 1.68 ± 0.02 in 11 females; t-test P=0.0005). Regular row of 10-14 small hornytipped tubercles on dorsal edge of dactylus from proximal to about three-quarters length (Figure 3A). Fingers in large animals slender and curved, resulting in an oval gap between the cutting edges (Figure 3B); not so in small animals. Cutting edges with teeth along their whole length. Tips of fingers with horny edges, pointed in dactylus fitting into groove from pollex (immovable finger). Tufts of setae parallel to teeth on inner side of fingers

Pereiopods 2-5 moderately long; fourth longest, ventral length about twice carapace length (4prp/cl= 2.01 ± 0.05 , n=21). Merus of walking legs less than 2.4 times as long as broad (pereiopod 2: 2.31+0.09; pereiopod 3: 2.35+0.1; pereiopod 4: 2.37+0.08; pereiopod 5: 2.27 ± 0.1 ; n=20-21). Upper border crested and with subdistal tooth. Posterior faces with transverse granular striae in pereiopods 2-4. Anterior faces smooth and glabrous (Figure 3C). Upper border of carpus with weakly granulated crest; all posterior faces with two and anterior faces of pereiopods 2-4 with one longitudinal granular crest. Propodus with oblique longitudinal crest on proximal half of anterior face of pereiopods 2-4 (Figure 3C), not in pereiopod 5; similarly oblique crest on posterior face of all pereiopods. Ventral face and dorsal border of propodi in males with pubescence gradually decreasing from pereiopod 2 to 5: dorsal border of pereiopod 2 is almost completely covered with setae, while ventral border is only covered to two-thirds its length; dorsal border of pereiopod 5 covered to one-third its length and ventral face only with few distal spines; pereiopods 3 and 4 with an intermediate pubescence. Females with no pubescence on ventral face of propodi except distal end of pereiopod 2. Dactyli slightly curved with six longitudinal rows of setae: dorsal, antero-dorsal, postero-dorsal, ventral, antero-ventral and postero-ventral; distal end horny-tipped and without setation (Figure 3C)

Sternite III weakly granulated and mostly glabrous (Figure 4B). Other sternites smooth and glabrous. In males, pleon conspicuously vaulted from fronto-ventral view, third abdominal segment broadest; lateral borders of fourth and fifth abdominal segment comparatively straight. Sixth abdominal segment with lateral borders convex. Telson relatively short, about as long as wide at base (Figure 4B). Female pleon broadly oval; telson invaginated in sixth abdominal segment, about as long as broad. Male gonopods slender, slightly twisted and distally deflexed with horny apex (Figure 3D).

Colour in life. Sesarma meridies sp. n. has a more or less homogeneous dark orange to rusty colour.

Measurements. The following measurements refer to the largest male (SMF 29338) and female (Rio Magno) from the material studied, respectively: carapace width 23.44/23.05 mm; carapace length 20.22/19.94 mm; body height 11.09/11.15 mm; frontal breadth 11.20/11.41 mm.

Type locality. Holotype from tributary of Rio Minho (Crooked River) next to road between Crooked River and Trout Hall.

Discussion

The species richness and ecological diversity of the Jamaican Sesarmidae is striking, not only in comparison to the crab fauna of other Caribbean islands, but also in comparison to the South-East Asian Sesarmidae, the only other group within this family that achieved complete independence from the sea. The more we learn about the Jamaican crabs, the more it becomes evident that differentiation and speciation within the endemic crabs of Jamaica seems to be acting at two different levels. On one hand, the comparison of different ecotypes within the Jamaican crabs suggests that some sort of ecological differentiation coupled with morphological adaptations has played an important role in giving rise to so many different species in a relatively small area. Today, these ecotypes occur sympatrically (up to four species) in many regions of the island. Different use of the available niches within the same habitat and thus avoidance of competition facilitates the present coexistence of these species. However, it is still not possible to explain how these different ecotypes evolved, whether in sympatry or in allopatry with secondary range extensions. The second level of differentiation is the one within the different ecotypes. Our recent studies on crabs from freshwater streams (stream ecotype) have shown that several different species belong to the same ecotype, make use of the same habitat and exclude each other geographically (Schubart et al. 1997, 1998a; Reimer et al. 1998). Preliminary results suggest that also in some of the other ecotypes (bromeliad ecotype) and (rock-rubble ecotype) there are geographically separated cryptic or semi-cryptic species. In this case of species differentiation, it seems very likely that we are dealing with the outcome of allopatric speciation. Nevertheless, it would be wrong to assume that these geographically separated and morphologically similar species within the same ecotype are relatively young and came into existence after an initial divergence into different ecotypes. At least in the case of the stream ecotype, preliminary results suggest that these crabs are basal within the Jamaican Sesarmidae and some of the other ecotypes evolved after initial speciation events within the stream ecotype (Schubart et al. 1998a). Also in their morphology, the crabs from the stream ecotype seem to be basal within the Jamaican sesarmids since their morphology is closest to the one from their marine relatives found in marshes and mangroves. Therefore a comprehensive study of the crabs belonging to the stream ecotype and the inclusion of the different genetic forms comprised within this ecotype seems essential for constructing phylogenies and understanding speciation processes within the Jamaican endemic Sesarmidae.

In this study, the comparison of morphological features and of 12S and 16S mtDNA allowed separation of two species occurring in central Jamaica and the description of one of them as new to science. It is the first time that a geographic separation between Jamaican freshwater crabs is not in a strict west–east direction, but more in a north–south fashion, even though *Sesarma windsor* seems to reach more to the west (Hectors River) and *S. meridies* sp. n. far more to the east (Rio Magno), thereby becoming a southern counterpart to *S. bidentatum* rather than to *S. windsor* over most of its range. This study also sheds light

on the exact distribution of *S. windsor*, which according to the published information could have been considered to be restricted to a cave of the Mouth River near Albert Town: 'Further collecting is necessary to determine whether *S. windsor* occurs exclusively in caves...' (Schubart et al. 1997: 417). Here we show that *S. windsor* occurs in four river systems (Mouth River, Quashies River, Hectors River and Cave River), which all end as limestone sinks, explaining the presence of these crabs outside as well as inside caves. *Sesarma windsor* is thus a troglophile and not a troglobite and morphological adaptations to life in caves (see Schubart et al. 1997) may be due to phenotypic plasticity. Interestingly, the waters of the four above-mentioned rivers all surface again in the northern coastal plains (Fincham 1997), but so far there has been no record of *S. windsor* from there, corroborating the fact that these crabs need mountainous fast-flowing streams.

Most of the specimens used for the description of Sesarma meridies sp. n. were from the Rio Minho drainage system and include Rio Minho proper and its tributaries Yankee River, Crooked River as well as probably Pindars River and Pedro River, both of which disappear in sinks. This is here considered the core distribution of Sesarma meridies sp. n. Nevertheless, similar crabs in terms of morphology and genetics were also found more to the east, in the Rio Magno which most likely forms part of the Rio Cobre drainage system. Consistent molecular differences between these animals and those from the Rio Minho system could be found in both of the studied genes, suggesting that there is a lack of gene flow between these populations and possibly the existence of a different taxon. However, the genetic divergence is within the range of what has been considered intraspecific in other species of Jamaican sesarmids and we therefore refrain from describing a new species. Furthermore, at this point there is not sufficient material from the Rio Cobre drainage system for detailed morphological comparisons. In any case, we have to realize that the freshwater crabs of Jamaica will have to be further subdivided and more independently evolving groups have to be considered in the future, if we want to do justice to the genetic structuring that becomes discernible at smaller geographic scales.

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