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DIFFERENTIATION WITHIN A RIVER SYSTEM: ECOLOGY OR GEOGRAPHY DRIVEN? EVOLUTIONARY SIGNIFICANT UNITS AND NEW SPECIES IN JAMAICAN FRESHWATER CRABS

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ABSTRACT

Freshwater habitats of the Caribbean island Jamaica are unique, in so far that they are not inhabited by freshwater Decapoda Reptantia with a long evolutionary history in fresh water, like crayfish or old lineages of freshwater crabs. Instead, a relatively young invasion and radiation of originally coastal crabs from the family Sesarmidae took place, resulting in currently ten endemic sesarmid species that are recognized from the island. Six of those have been described from Jamaican brooks and streams (river crabs), whereas the other four species thrive in caves and more terrestrial habitats. After establishing and describing the diversity of Jamaican river crabs at the species level, ongoing studies are designed to highlight presumed intraspecific differentiation within the recognized species, as a means of understanding the diversification and rapid speciation processes of this adaptive radiation. Here we use mitochondrial DNA sequences of the ND1 gene and morphometrics to document diversity within river crabs from western Jamaica so far considered to belong to *Sesarma dolphinum*, complementing a recent population genetics study with nuclear DNA. Distinct evolutionary lineages can be recognized, of which two are so clearly separated that they do not share mitochondrial haplotypes nor do they show any overlap in morphometry. Interestingly, these lineages co-occur within the same river system, allowing first insights into the mechanisms of differentiation of these crabs. Ecological restriction to upper reaches of rivers isolates the crabs in different tributaries and thus genetic connectivity is apparently more likely to be maintained in overland dispersal between headwaters than within the river system. The distinct evolutionary lineage from the southeastern range of the distribution area of *S. dolphinum* is here described as a new species in order to highlight its uniqueness and to make it a management unit. A nested clade analysis reveals that the genetic relationship of populations of *S. dolphinum* is the result of restricted gene flow with isolation by distance. A literature review compiles other published reports for freshwater Crustacea with different evolutionary lineages in the same water catchment.

INTRODUCTION

Less than twenty years ago, secondary freshwater crabs from Jamaican brooks and streams (Grapsoidea: Sesarmidae) were considered to belong

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to a single species, *Sesarma bidentatum* Benedict, 1892. A closer look at representatives of different regions of the island, however, allowed recognition and description of six distinct species, based on morphological characters alone (Türkay & Diesel, 1994; Schubart et al., 1997; Reimer et al., 1998) or a combination of morphological and molecular features (Schubart et al., 1998a, 1999; Schubart & Koller, 2005). The distinctness of the two closest species, *Sesarma windsor* Türkay & Diesel, 1994, and *Sesama meridies* Schubart & Koller, 2005 from central Jamaica, previously established by morphology and mitochondrial DNA (mtDNA) (Schubart & Koller, 2005), was later confirmed with the highly variable ITS1-5.8S-ITS2 region of the nuclear genome by Schubart et al. (2010). The latter study also revealed measurable intraspecific genetic structure within these two sister species as well as in the river crab species *Sesarma dolphinum* Reimer, Schubart & Diesel, 1998. Our own unpublished results confirm this for the other three river crab species and two of the more terrestrial crab species. The role of geographic structure and ecology in shaping intraspecific genetic variability, and the recognition of evolutionary significant units combined with their nomenclatural treatment, will be the topic of this and upcoming contributions concerning the radiation of endemic Sesarmidae in Jamaica, first documented in Schubart et al. (1998b).

The concept of evolutionary significant units (ESU) was originally introduced by Ryder (1986) and defined as "*Subsets of the more inclusive entity species, which possess genetic attributes significant for the present and future generations of the species in question*". Moritz (1994), Crandall et al. (2000) and many others adjusted and re-defined the concept for conservation biology purposes. This was reviewed by Fraser & Bernatchez (2001) resulting in a return to a more general definition of the concept of ESU as "*A lineage demonstrating highly restricted gene flow from other such lineages within the higher organizational level* (*lineage*) *of the species*". Used in this sense, ESUs can be applied to recognized intraspecific isolated lineages, regardless of the conservation status or the respective ecological exchangeability (cf. Crandall et al., 2001) or, as stated by Fraser & Bernatchez (2001: 2742): "*We emphasize that the strengths and weaknesses of various operational criteria should not encumber conservation efforts but rather aid managers in conducting sound conservation plans specific to the situation at hand*".

The comparison of 232 clones corresponding to the nuclear ITS regions of 32 specimens of *Sesarma dolphinum* throughout its distribution range in westernmost Jamaica revealed several genetic lineages (Schubart et al., 2010: table 3), of which three alone are encountered in the Cabarita River

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system. Even before studying the genetic population structure of this species, in the original description of the species Reimer et al. (1998) already noted some morphological differences of individuals inhabiting the Roaring River, a southeastern tributary of the Cabarita River. Those authors point out that "The three specimens of *S. dolphinum* from Roaring River (Westmoreland) differed from the other material of the species by having shorter legs (4^{th} pereiopod length/carapace length: 1.91 ± 0.06). In these specimens, the dorsal row of granules on the palm of the chela is not always continuous and the number of tubercles on the dactylus of the chela varied between 0 and 4. These specimens might possibly be a distinct subspecies, but further material will be needed for confirmation" (Reimer et al., 1998: 194). Those authors also note that preliminary results based on the 16S rRNA gene of the mtDNA did not support a separation. This genetic marker, however, is relatively conserved within the mitochondrial genome and thus population studies including more populations and more variable markers would be necessary. The molecular data provided by Schubart et al. (2010) based on the ITS nDNA region confirm genetic separation of the Roaring River Deans Valley River populations. However, with one exception, this analysis also distinguished between all other sampled populations within this species (partly due to non-independence of the data by including several clones from single individuals) and suggested limited connectivity among all of the inhabited river systems.

The question remains of how to deal with genetically isolated and in part quite differentiated evolutionary units. In the present study, we provide new genetic (mtDNA) and morphometric evidence for the distinctness of the geographic population comprising crabs from the Deans Valley and Roaring rivers and compare these to other representatives of *Sesarma dolphinum*, including individuals from the type locality from the Hog-Davis Cove river system (near Kingsvale). In conclusion we consider the Deans Valley River and Roaring River populations to comprise a well-defined lineage of *Sesarma* that is described here as a new species.

MATERIAL AND METHODS

More than one hundred specimens of *Sesarma dolphinum* (Decapoda: Brachyura: Thoracotremata: Sesarmidae) were collected from 13 localities from throughout its distributional range in western Jamaica (fig. 1) during several sampling trips between 1997 and 2005. From those, 83 were used for

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morphometric comparisons and 42 for DNA isolation (see table I) and 40 for amplification and sequencing of mitochondrial DNA.

Genetics. — Tissue was extracted from the muscle of a walking leg and DNA isolation was performed using a modified Puregene method from Gentra Systems. Dried genomic DNA was resuspended in 20 μl TE buffer and the concentration was ascertained on agarose gels. From the corresponding dilutions of the DNA solution 1 μl was used for polymerase chain reactions. A >800 basepair (bp) fragment of the mitochondrial NADH1 dehydrogenase subunit 1 (ND1) was amplified with NDL4 (5′-AAAADKCTAATTRTTTTGTG-3′) (corrected from Schubart et al., 2011) and NDH2 (5′-GCTAAATATATWAGCTTATCATA-3′) (Schubart, 2009) and the internal primers NDL5 (5′-TTGCTGGWTGRTCTTCWAATTG-3′) (new) and NDH5 (5′-GCYAAYCTWACTTCATAWGAAAT-3′) (Schubart, 2009). For PCR, a standard 25 μl reaction was prepared containing 2.5 μl of 10× buffer, 2.5 μl of 1.25 mM dNTPs, 0.5 μl of both primer (20 mM), 2 μl of 25 mM $MgCl_2$, 1 μl of 0.5 U/μl TAQ and 15 μl of double-distilled water in addition of 1 μl gDNA. 40 cycles were run with 45 s at 94°C, 1 min at 48°C as an annealing temperature, and 1 min at 72°C. PCR products were cleaned using QuickClean (Bioline) and sequenced with an ABI-PRISM 310 (Applied Biosystems). Sequences were proofread for possible errors made by the computerized analysis provided with ChromasLite (http://www.technelysium.com). Due to the lack of indels, the corrected sequences were aligned by eye using BioEdit (Hall, 1999). Sequences of all detected haplotypes were submitted to the EMBL molecular database and archived as HF678402-HF678413. The nexus file of the ND1 dataset was then used to construct a statistical parsimony network using the algorithm outlined in Templeton et al. (1992) and implemented in the TCS software package version 1.21 (Clement et al., 2001). Based on the obtained haplotype network of the ND1 data a nested clade analysis (NCA) was performed (Templeton et al., 1995; Templeton, 2004) to test the null hypothesis of no association between the geographic distribution of haplotypes. The haplotype network was converted into a nested statistical design using the instruction given in Templeton and Sing (1993) and in Crandall & Templeton (1996). To test for an association between the genetic composition and the geographic distribution of the haplotypes, two distances were calculated. First, the clade distance Dc, which estimates how geographically widespread a clade is, and second, the nested clade distance Dn, which measures the relative distribution of a clade compared to the other clades in the same higher clade level. All calculations were

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TABLE I

List of western Jamaican localities, from where *Sesarma abeokuta* n. sp. and *S. dolphinum* were collected for genetic and morphometric analyses, including the number of individuals used for both methods and the museum collection number

	Location	N_{DNA}	Haplotypes	N_{morpho}	Museum #
Sesarma abeokuta					
Deans Valley R.-Abeokuta, 2005	18°14′43.08″N/78°02′38.58″W	2	12	1	NHMW 25418
Deans Valley R.-Galloway, 1997	~18°15.5′N/78°02′W	3	12	2	SMF-34538
Roaring R.-Spring, 1997 & 2005	18°17′15.54″N/78°02′43.80″W	2	7	15	SMF-34539
Sesarma dolphinum					
Flint R.-Cascade, 2003	18°23′52.19″N/78°05′39.12″W	2	1	8	SMF-34540
Upper Cabarita-Buxton, 2003	18°22′24.00″N/78°06′1.38″W	4	1, 4	4	SMF-34541
Lucea East R.-Tom Spring, 2003	18°24′11.95″N/78°08′6.38″W	0	n.a.	12	SMF-34542
Lucea West R.-Harvey, 2003	18°24′6.81″N/78°09′15.24″W	3	1, 5	5	SMF-34543
Lucea West R.-Askenish, 2003	18°22′42.47″N/78°09′07.30″W	0	n.a.	5	SMF-34544
Green Island R.-Rock Spring, 2003	18°21′30.42″N/78°14′32.58″W	5	1, 6, 8	5	SMF-34545
New Savannah R.-Jerusalem, 2003	18°18′53.73″N/78°14′10.26″W	3	2, 3	12	SMF-34546
Lances R.-Dias, 2005	18°23′59.88″N/78°11′29.64″W	4	8	0	SMF-34547
Morgan R.-Flamstead, 2005	18°22′28.18″N/78°12′20.02″W	4	8, 11	8	SMF-34548
Upper Cabarita-Bath Mt., 2005	18°20′26.22″N/78°05′57.42″W	2	1	2	SMF-34549
Upper Cabarita-nr. Cash Hill, 2005	18°22.400′N/78°06.023′W	0	n.a.	3	SMF-34550
Green Island R.-Kendal, 2005	18°21′56.49″N/78°13′50.41″W	4	1, 8	0	SMF-34551
Davis Cove R.-Paradise, 1997	18°23′0.17″N/78°12′45.79″W	4	8, 9, 10	1	Not available

done with the software GEODIS 2.5 (Posada et al., 2000) using 1 000 000 permutations and direct distances. The direct distances option was favoured over river distances as all species in this study are freshwater species with no marine form, which would be necessary to connect certain rivers. The direct distances between the single sample locations were measured in GoogleEarth (http://earth.google.com). To infer the historical events that caused the observed genetic population structure we used the most recent inference key from Templeton (http://darwin.uvigo.es/software/geodis.html).

Morphometry. — Data on the relative proportions of morphological characters of specimens were collected to detect phenotypic differences among populations. A mechanical calliper gauge with a digital display was used to record the corresponding measurements. The following characters were recorded: carapace width, measured at two separate positions: at the widest anterior part including the exorbital tooth (CWf) and at the posterior broadest part of the carapace (CWb); carapace length (CL) and body height (BH), measured along the median line of the carapace; frontal width (FW) between the two orbits, and length of the exorbital tooth (ET). Three chelar measurements were taken, the height (PrH) and ventral length (PrL) of the propodus and the dorsal length of the dactylus (DaL). From pereiopods three and four, the length (3L, 4L) and width (3W, 4W) of the meri were recorded. Finally, the pleon (PlW) was measured at its widest part. To minimize possible errors due to allometric growth (see Reuschel & Schubart, 2006) only individuals considered to be adult (or very close to it: CL $>$ 12 mm) were measured. All measurements were logarithmically transformed to further minimize the effect of possible allometric growth. Measurements were tested for normal distribution using the one-sample Kolmogorov-Smirnov test. Those which showed normal distribution were included in a canonical discriminant function analysis. The variable which had the greatest weight on the outcome of the discriminant function analysis was calculated. The discriminant function analysis was then re-done without this variable to assure that the observed differences are not the result of a single factor. All calculations were performed in SPSS version 16 (SPSS Inc., Chicago, IL).

RESULTS

Genetics. — A fragment of 834 bp mtDNA of the ND1 gene was successfully sequenced from 40 individuals of *Sesarma dolphinum* and aligned, resulting in 12 different haplotypes (ht). Base frequencies were A = 0.2870,

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C = 0.0855, G = 0.1795 and T = 0.4480. Initial tests of pairwise distinctness between neighbouring localities with low representation failed to show differences. Therefore the following populations were pooled for subsequent analyses: two tributaries of Deans Valley River; the upper Cabarita River and its tributary near Bath Mountain; West and East Lucea rivers; neighbouring Davis Cove and Lances rivers (Davis/Lances rivers). The 13 collecting sites for which DNA sequences became available were pooled into 9 populations (see codes in map fig. 1). The statistical parsimony network (fig. 1) revealed the existence of two major clades (ht I-VI versus ht VII-XII) separated by a relatively high number of 12 (with ht VI) or 16 (without ht VI) mutations. The software considers ht-I as the ancestral haplotype. This haplotype can be found in the northernmost samples from the Flint River, both Lucea rivers, the upper Cabarita tributaries, and in two individuals from the Green Island River (n = 10). Four haplotypes (ht II-ht V) are derived from ancestral ht-1 in a star-like pattern and differ by only one or two substitutions. Haplotypes II (n = 1) and III (n = 2) are exclusively found in samples from the southwestern New Savannah River system, ht-V is present twice in the Lucea rivers, and ht-IV (n = 1) was found in one sample from the upper Cabarita system. Haplotype VI was encountered in one individual from the Green Island River and differs from the first major clade with ht-I by four substitutions and from the second major clade by at least 12. The second major clade consists of three common haplotypes, of which two are characteristic and exclusive for single populations. Haplotype VIII has the highest frequency (n = 10). It contains most samples from the Green Island River, the Morgan River (western tributary to Cabarita River) and the Davis/Lances rivers. Also three of the four haplotypes which are connected to ht VIII by one or two substitutions belong to individuals collected in these three river systems (ht IX and ht X from the Davis Cove River, and ht XI from the Morgan River, all n = 1). All these river systems are found in the northwestern part of the distribution area. Haplotype VII is found on the connecting line between ht-I and ht-VIII, only one mutational step away of the latter. This haplotype was exclusively found in the five sequenced samples from the Roaring River, which is another tributary to the Cabarita River, but in the southeastern distribution limit of *Sesarma dolphinum*. Haplotype XII departs from ht VII and is separated by four mutations. This haplotype was found in all sequenced animals from the Deans Valley River (n = 5). This river lies even further southeast than the Roaring River and marks the border between *Sesarma dolphinum* and *Sesarma fossarum* Schubart, Reimer, Türkay & Diesel, 1997.

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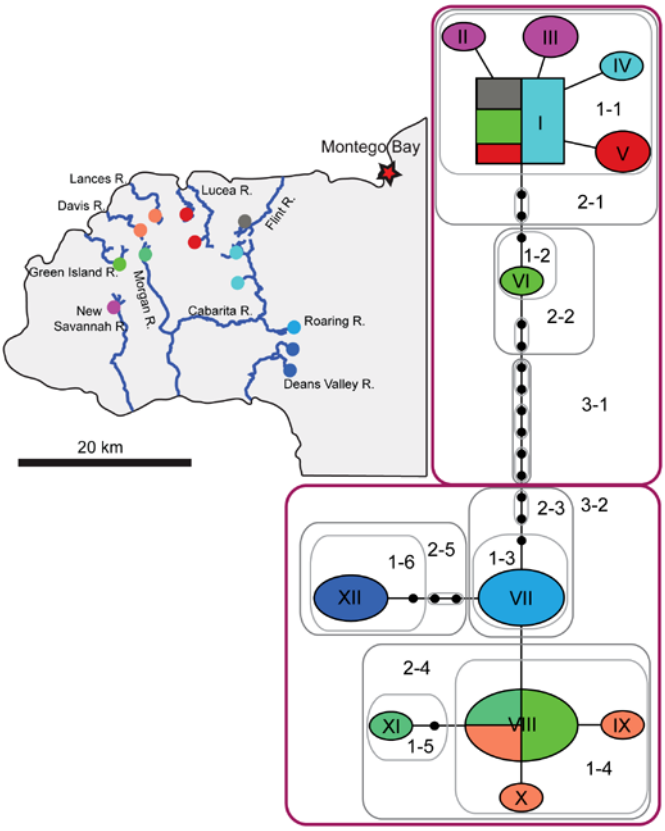

Fig. 1. Left: map of the western part of Jamaica (Greater Antilles) showing selected rivers and sampling sites where specimens of *Sesarma dolphinum* Reimer, Schubart & Diesel, 1998 and *S. abeokuta* n. sp. were collected. Right: Statistical parsimony network constructed with TCS based on a 834-basepair fragment of the ND1 gene (N = 37) and the corresponding nesting design for the Nested Clade Analysis. Each line represents one substitution; dots on the lines indicate additional substitutions separating two haplotypes. Coloration corresponds to sample sites on map. The size of the circle is representative for the frequency of the haplotypes (small: N = 1; medium: N = 2-3; large: N = 4-5; largest: N > 10; square: proposed ancestral haplotype). Light grey lines enclose the 1-step clades (1-..), dark grey lines enclose 2-step clades (2-..) and red lines enclose 3-step clades (3-1 and 3-2).

The resulting ND1 statistical parsimony network displays the genetic relationships between the different populations of *Sesarma dolphinum*. However, it does not tell us how these genetic relationships originated. To investigate such a question a nested clade analysis was performed. The twelve haplotypes constitute units at the smallest level, i.e. the 0-level clades. Based on these 0-level clades, seven 1-level clades, five 2-level clades and two 3-level clades were constructed, which formed the total cladogram. At the 1-level,

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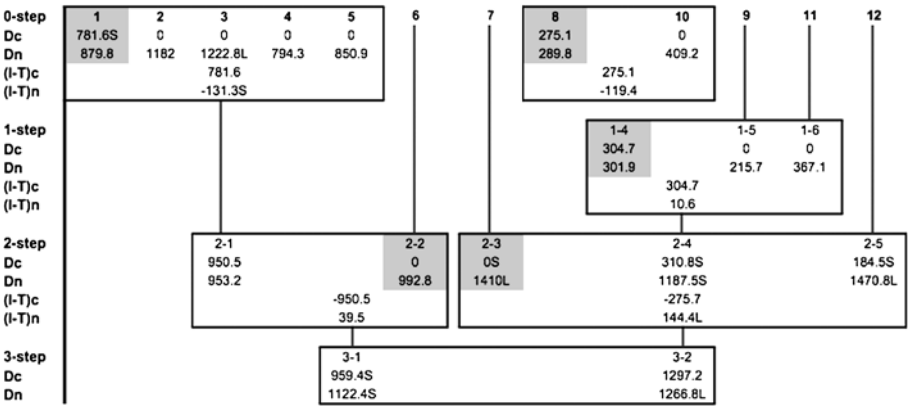
two clades show geographic association, but only the clade 1-1 has significant values for the within- and nested-clade distances and the interior to tip within- and nested-clade distances. The analysis of clade 1-1 with the inference key resulted in an inconclusive outcome. From the 2-level clades, only one has geographic associations, but does not show any significant values. At the 3-level, again two clades have geographic associations, of which clade 3-2 displayed significant values. Analyzing these values with the inference key, gives three scenarios, how the present state could come into place: either by past fragmentation, or by long distance colonization, or by a combination of these two possibilities. The total cladogram also infers geographic associations and the analysis produced significant values for the within- and nested-clade distances. This time, the inference key suggested a single outcome: the present state of the *Sesarma dolphinum* populations under research is the result of restricted gene flow with isolation by distance, which seems to be the most important result to understand differentiation in this species. The nesting design is shown in fig. 1 and the analysis of the geographic associations in table II.

Morphometry. — The same nine pooled populations as above, and as depicted in fig. 1, were used for the statistical analyses of the morphometry, in which 83 individuals were included (see table I). From the 15 characters mea-

TABLE II

Nested clade distance analysis of ND1 haplotypes observed in *Sesarma dolphinum* and *S. abeokuta*. The nested design is given in fig. 1. Dc and Dn are clade and nested clade distances, respectively (for details see Templeton et al., 1995). Interior vs. tip contrasts for Dc and Dn are indicated with 'I-T' in the corresponding clade. Interior clades are identified by shading. The S and L superscripts refer to significantly small and large values at the 0.05 level, respectively. Significance of values is based on permutation analysis using 1 000 000 resamples



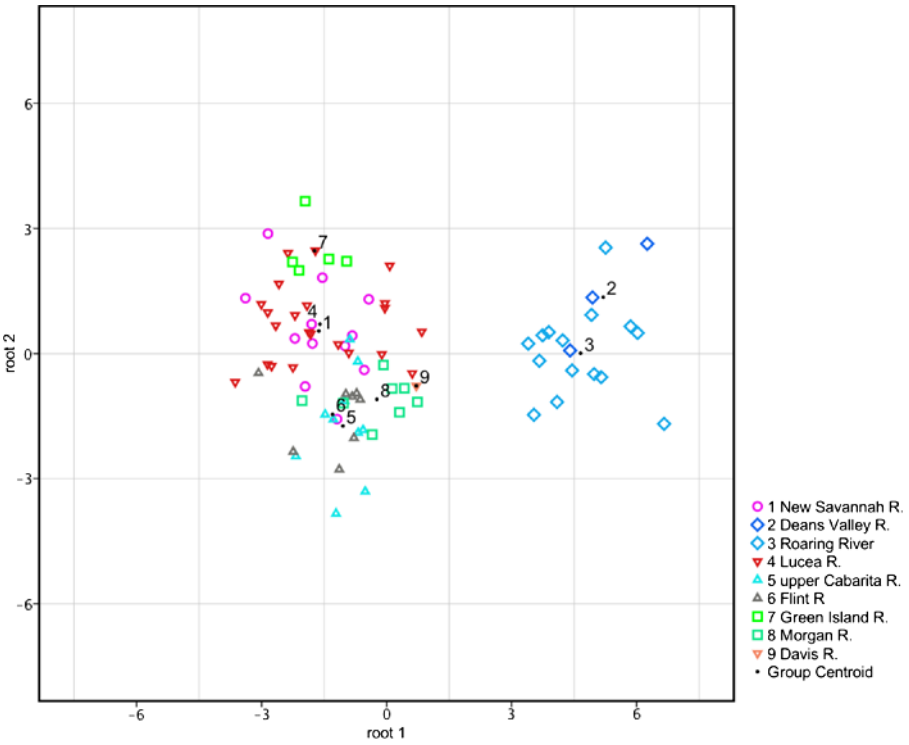


Fig. 2. Canonical analysis showing discrimination by morphometric measurements between nine populations of *Sesarma dolphinum* Reimer, Schubart & Diesel, 1998 and *S. abeokuta* n. sp. from western Jamaica; plot of the first discriminant function (root 1) against the second (root 2).

sured, all showed normal distribution in the Kolmogorov-Smirnov test. The Wilk's Lambda for the overall model is 0.015 with $p \leqslant 0.001$, which indicates a very good discrimination, also shown in the overall correct classification of 71.4%. In fig. 2, a two-dimensional plot of the first two canonical values is shown. These two canonical values together explain 85.1% of the variables found in the dataset. In the plot, two separate clusters are clearly visible. One cluster contains only samples from the southeastern distribution range of *Sesarma dolphinum*, namely from the Deans Valley River system and the Roaring River. In the second cluster, the remaining populations do not appear much differentiated, but certain clusters can nevertheless be recognized. This is also reflected in the classification matrix (table III). This matrix indicates the percentage of animals from each site which are correctly grouped according to the discriminant analysis. The two southeastern sites have 100% correct placement, if pooled. Wrongly placed individuals can be found in the corresponding

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TABLE III

Percentage of correct classification based of the morphometric classification function for nine western Jamaican populations of *Sesarma dolphinum* and *S. abeokuta* n. sp. (overall correct classification: 71.4%)

Population	1	2	3	4	5	6	7	8	9
1 New Savannah R.	75	0	0	8.3	0	0	8.3	8.3	0
2 Deans Valley R.	0	66.7	33.3	0	0	0	0	0	0
3 Roaring R.	0	26.7	73.3	0	0	0	0	0	0
4 Lucea rivers	9.1	0	0	68.2	0	0	18.2	4.5	0
5 Upper Cabarita R.	10	0	0	10	40	40	0	0	0
6 Flint R.	0	0	0	0	37.5	62.5	0	0	0
7 Green Island R.	0	0	0	0	0	0	100	0	0
8 Morgan R.	0	0	0	0	0	0	0	100	0
9 Davis Cove R.	0	0	0	0	0	0	0	0	100

other population. Similarly, the Flint River and upper Cabarita River taken together almost reach 100% correct classification, with 62.5% correct placement of Flint River animals, whereas the remaining 37.5% are all attributed to the nearby upper Cabarita River population. Vice versa, the upper Cabarita population has 40% correct placements and another 40% are assigned to the Flint River population. The three northwestern sites together, Green Island River, Davis Cove River and Morgan River, have all correct placement at 100% respectively. They also belong to different drainage systems and are geographically quite close. The remaining New Savannah River and pooled Lucea rivers also have remarkably high correct individual placements with 75% and 68.2% respectively. Overall, the populations show good to very good classification by means of their morphometric characters.

Taxonomy. — According to the above results, in combination with those of Schubart et al. (2010), we consider to have gathered sufficient evidence to recognize the southeastern population from *Sesarma dolphinum*, colonizing the Deans Valley and the Roaring rivers, as an evolutionary significant unit. The mtDNA network from fig. 1 gives evidence for genetic isolation even between these two rivers and suggests possible founder effects resulting in genetic bottlenecks (both rivers having unique ND1 haplotype, separated by four mutation steps), but the nuclear DNA (Schubart et al., 2010) and the morphometry (see fig. 2) suggest a close relationship and common origin of these two populations. We therefore describe individuals from both populations jointly as a new species.

Sesarma abeokuta new species
fig. 3A-D

Sesarma dolphinum Reimer, Schubart & Diesel, 1998, specimens from Roaring River (Reimer et al., 1998); specimens from Roaring & Deans Valley rivers (Schubart et al., 2010).

Material examined. — Holotype: 1 male (20.9 × 17.6 (carapace width × carapace length in mm)) (SMF-34537), Jamaica, Westmoreland, Galloway, Deans Valley River system, wet gravel at foot of hillside, 17 Mar. 1997, leg. R. Diesel, J. Reimer, C. D. Schubart (DNA extr. 7 Jul. 2004 ×4). Paratypes: 3 males (19.0 × 16.4, 19.06 × 16.53, 17.96 × 15.32), 2 females (16.7 × 14.14, 16.96 × 14.1) (SMF-34538) same data as holotype (DNA extr. 10 Oct. 1997; 7 Jul. 2004 ×3); 2 males (15.73 × 13.12, 13.33 × 10.94), 2 females (19.2 × 15.8, 16.6 × 14.0) (NHMW 25418), Jamaica, Westmoreland, Abeokuta Nature Park, near Galloway, tributary to Deans Valley River, 128 m, 18°14.718′N-78°02.643′W, 16 Oct. 2005, leg. C. D. Schubart, S. Reuschel, T. Santl; 2 males (19.70 × 16.50, 15.16 × 12.91), 2 females (18.02 × 15.11, 16.62 × 14.19) (ZRC 2013.0451), same data as previous; 2 males (19.08 × 16.09, 17.19 × 14.21), 2 females (18.97 × 15.73, 16.88 × 14.54) (RMNH.CRUS.D.55074), same data as previous; 9 males (21.35 × 18.72, 18.0 × 15.89, 17.23 × 14.55, 15.66 × 13.71, 15.6 × 13.65, 15.5 × 13.08, 14.72 × 12.78, 12.91 × 11.02, 12.63 × 10.78), 1 female (18.75 × 16.2) (SMF-34539), Jamaica, Westmoreland, spring of Roaring River nr. Shrewsbury, tributary to Cabarita River, 98 m, 18°17′16″N-78°02′44″W, 16.3.1997, leg. C. D. Schubart, J. Reimer, R. Diesel (DNA extr. 26 Jul. 2005 ×10); 2 males (14.98 × 12.83, 13.27 × 11.58), 4 females (21.2 × 18.43, 16.85 ×

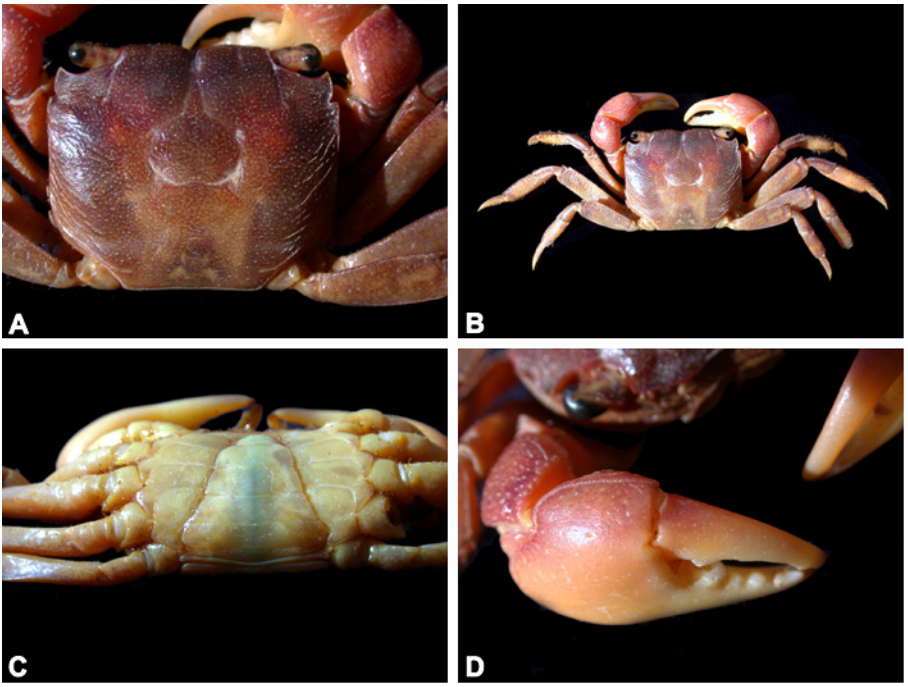

Fig. 3. *Sesarma abeokuta* n. sp., holotype (SMF-34537). A, dorsal carapace; B, dorsal view; C, sternum and male pleon; D, dorsal and outer face of chela.

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14.65, 13.82 × 11.88, 11.96 × 10.28) (ZSMA20130013), same locality as previous, 16 Oct. 2005, leg. C. D. Schubart, S. Reuschel, T. Santl (DNA extr. 14 Nov. 2005 ×6).

Other material.— 1 male (16.36 × 14.19), 2 females (19.23 × 16.19, 17.23 × 14.61) (Collection R. Diesel), Jamaica, Westmoreland, Roaring River Spring, tributary to Cabarita River, 18°17′16″N-78°02′44″W, 19 Mar. 1995, leg. R. Diesel, C. D. Schubart; 21 juveniles (collection C. D. Schubart), Jamaica, Westmoreland, Abeokuta Nature Park, near Galloway, tributary to Deans Valley River, 18°14.718′N-78°02.643′W, 16 Oct. 2005, leg. C. D. Schubart, S. Reuschel, T. Santl.

Comparative material. — *Sesarma dolphinum* Reimer, Schubart & Diesel, 1998: Holotype: 1 male (25.3 × 21.44) (SMF-23304), Jamaica, Hanover, tributary to Hog River-Davis Cove River system, road between Paradise Great House and Kingsvale (~18°23.1′N/78°12.75′W), 19 Mar. 1995, leg. R. Diesel, C. D. Schubart; 4 specimens (CDS private), same locality as holotype, Mar. 1997, leg. R. Diesel, J. Reimer, C. D. Schubart (DNA extr. ×4); 7 males, 5 females (SMF-34540), Jamaica, Hanover, Flint River between Cascade and Pondside (18°23′52.19″N/78°05′39.12″W), 17 Mar. 2003, leg. C. D. Schubart, T. Weil, T. Santl (DNA extr. ×2); 8 males, 7 females, 2 juv. (SMF-34541), Jamaica, Hanover, upper Cabarita River near Buxton (18°22′24.00″N/78°06′1.38″W), 17 Mar. 2003, leg. C. D. Schubart, T. Weil, T. Santl (DNA extr. ×4); 7 males, 3 females, 1 juv. (SMF-34542), Jamaica, Hanover, Lucea East River near Tom Spring (18°24′11.95″N/78°08′6.38″W), 17 Mar. 2003, leg. C. D. Schubart, T. Weil, T. Santl (DNA extr. ×2); 2 males, 3 females (SMF-34543), Jamaica, Hanover, nr. Harvey River, right tributary to Lucea West River (18°24′6.81″N/78°09′15.24″W), 17 Mar. 2003, leg. C. D. Schubart, T. Weil, T. Santl (DNA extr. ×1); 4 males, 5 females (SMF-34544), Jamaica, Hanover, Askenish, tributary to Lucea West River (18°22′42.47″N/78°09′07.30″W), 17 Mar. 2003, leg. C. D. Schubart, T. Weil, T. Santl (DNA extr. 1 male 8.5.2003); 2 males, 3 females (SMF-34545), Jamaica, Hanover, Rock Spring, Green Island River tributary (18°21′30.42″N/78°14′32.58″W), 18 Mar. 2003, leg. C. D. Schubart, T. Weil, T. Santl (DNA extr. ×5); 9 males, 5 females (SMF-34546), Jamaica, Westmoreland, 3 km E of Jerusalem Mountain, New Savannah River tributary (18°18′53.73″N/78°14′10.26″W), 18 Mar. 2003, leg. C. D. Schubart, T. Weil, T. Santl (DNA extr. ×3); 2 males, 2 females, 1 juvenile, 1 exuvia (SMF-34547), Jamaica, Hanover, Dias, upper Lances River (198 m, 18°23.920′N/78°11.542′W), 15 Oct. 2005, leg. C. D. Schubart, S. Reuschel, T. Santl (DNA extr. ×4); 2 males, 5 females (SMF-34548), Jamaica, Hanover, Flamstead, South of Kingsvale, Morgan River (90 m, 18°22′28.18″N/78°12′20.02″W), 15 Oct. 2005, leg. C. D. Schubart, S. Reuschel, T. Santl (DNA extr. ×4); 4 males, 6 females (SMF-34549), Jamaica, Hanover, tributary to Jackass River and Cabarita River near Bath Mountain (94 m, 18°20′26.22″N/78°05′57.42″W), 22 Oct. 2005, leg. C. D. Schubart, S. Reuschel, T. Santl (DNA extr. ×2); 7 males, 8 females, 3 juv. (SMF-34550), Jamaica, Hanover, upper Cabarita River, 2.8 km south of Cash Hill (219 m, 18°22.400′N/78°06.023′W), 22 Oct. 2005, leg. C. D. Schubart, S. Reuschel, T. Santl (DNA extr. ×2); 2 males, 3 females, 1 juv. (SMF-34551), Jamaica, Hanover, Green Island River near Kendal (62 m, 18°21′56.49″N/78°13′50.41″W), 15 Oct. 2005, leg. C. D. Schubart, R. Brodie, S. Reuschel, T. Santl (DNA extr. ×4) (see table I).

Diagnosis. — See species diagnosis of *S. dolphinum* (Reimer et al., 1998) with exception of: Legs relatively short and stouter, with ratio 4th pereiopod length/carapace length smaller than 2. Carapace broadest anteriorly, next to epibranchial teeth. MtDNA sequences of the ND1 gene rendering two unique haplotypes, corresponding to haplotype VII (Roaring River, GenBank

HF678408) and haplotype XII (Deans Valley River, GenBank HF678413) in fig. 1.

Description. — See species description of *S. dolphinum*, with exception of walking legs which are relatively short and stout with 4th pereiopod length/carapace length = 1.91 ± 0.06 (see Reimer et al., 1998); merus of fourth pereiopod/anterior carapace width in the range of 0.58-0.66 (as opposed to 0.63-0.75 in *S. dolphinum*, see Gaß, 2012: fig. 48). Carapace broadest anteriorly, next to epibranchial teeth: CWb/CWf in the range of 0.96-1.005 (as opposed to CWb/CWf in the range of 0.99-1.06 in *S. dolphinum*, see Gaß, 2012: fig. 47).

Etymology. — This species is named after the locality Abeokuta Hills in the Galloway area in southwestern Jamaica (Province Westmoreland), in the vicinity of which this species was encountered in three different localities, belonging to two river systems. The name is used as a noun in apposition.

Remarks. — While documenting and mapping the distribution of *Sesarma dolphinum* for the present study, we noticed that coordinates given in the original description of the species by Reimer et al. (1998) are imprecise, or mistaken by the magnitude of 10 min. Therefore we here provide correct coordinates (see also table I): *Sesarma dolphinum*: Holotype SMF-23304 from upper Hog-Davis Cove river system, ~18°23.1′N-78°12.75′W. Paratypes: SMF-19576-77, USNM 284155 from Askenish, Lucea West River system, ~18°22.75′N-78°09.12′W; SMF-23305 from Flamstead, tributary to Morgan River, 18°22′28.18″N-78°12′20.02″W. Other material: Collection R. Diesel from Roaring River Spring (now *Sesarma abeokuta* n. sp.): 18°17′15.54″N-78°02′43.80″W. The latter is the material that Reimer et al. (1998) referred to when describing morphological differences and considering the establishment of a new subspecies (not material from Galloway as wrongly quoted in Schubart et al., 2010: 346).

DISCUSSION

Entirely freshwater organisms that do not exit their native waters via terrestrial migrations or via planktonic dispersal in coastal waters are genetically isolated in specific drainage systems (watersheds). These watersheds thus represent units and interesting case studies in island biogeography in the sense of MacArthur and Wilson (1967) and Diamond (1975). Depending on its ecology, a species may inhabit the entire drainage area, which most often consists

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of a main river and varying number of tributaries, or only thrive in specific sections of the drainage that meet certain ecological demands. This habitat specificity (for example in higher reaches of rivers) may cause isolation of freshwater organisms even within a river system. Examples of such isolation are summarized in table IV and in Decapoda include among others the Japanese freshwater palaemonid shrimp *Macrobrachium nipponense* (see Mashiko & Numachi, 2000); the Australian atyid shrimp *Paratya australiensis* (see Cook et al., 2006, 2007); the European astacid crayfish *Austropotamobius torrentium* in the Danube system (Trontelj et al., 2005; Schubart & Martin, 2006); North American cambarid crayfish (Fetzner & Crandall, 2003; Buhay et al., 2007), and Taiwanese potamid freshwater crabs of the genus *Geothelphusa* (see Shih et al., 2004, 2007, 2010).

Better known are the cases of diversification and speciation of Crustacea in ancient lakes, representing a similar case of within-catchment genetic isolation and speciation, but with less evident allopatric mechanisms: Amphipoda Gammaridea in Lake Baikal (Sherbakov et al., 1998), Atyidae and Potamonautidae in East African Lake Tanganyika (Fryer, 2006; Marijnissen et al., 2006, 2009) and Southeast Asian Atyidae and Gecarcinucidae in ancient lakes of Sulawesi (von Rintelen et al., 2007, 2010; Schubart et al., 2008). There are thus two important scenarios of isolation and genetic diversification in freshwater Crustacea, one is more obvious and results from allopatric separation in unconnected fresh waters, whereas the other case appears less obvious, as it takes place in the same catchment area and may be driven by the ecology and/or behaviour of the species, and thus can be parapatric or sympatric. This is in agreement with an ongoing paradigm shift away from allopatric speciation towards an ecological adaptive one, as recently advocated and summarised by Dieckmann et al. (2004).

Also for Jamaican river crabs of the family Sesarmidae, two cases of different genetic lineages within single catchment systems are mentioned by Schubart et al. (2010). In one case, *Sesarma bidentatum* and *S. meridies* inhabit different tributaries of the Rio Cobre. In another case, three different genetic lineages of the westernmost species *Sesarma dolphinum* are found in the Cabarita River system (Schubart et al., 2010: 343). This second case has been more thoroughly studied and results are confirmed within the present paper. Interestingly, the populations inhabiting the different tributaries of the Cabarita system are closer related to other populations from nearby rivers, corresponding to different catchment areas (Upper Cabarita R.-Flint R.; Morgan R.-Davis/Lances and Green Island rivers; Roaring R.-Deans Valley R.)

TABLE IV

Compilation of the known cases in which differentiation and speciation has been recorded within freshwater stream for Decapoda and other Crustacea

Species name	Taxonomy	Locality	Species status	References
Kinnecaris solitaria complex	Copepoda: Parastenocarididae	Australia	Species	Karanovic & Cooper, 2011
Asellus aquaticus	Isopoda: Asellidae	Danube catchment	Intraspecific	Verovnik et al., 2004
Eophreatoicus species	Isopoda: Phreatoicidae	Danube catchment	Intraspecific	Wilson et al., 2009
Paratya australiensis	Atyidae	Eastern Australia	Intraspecific	Hurwood et al., 2003; Cook et al., 2006, 2007; etc.
Troglocaris anophthalmus	Atyidae	Danube catchment	Intraspecific	Zakšek et al., 2009
Macrobrachium nipponense	Palaemonidae	Japan	Intraspecific	Mashiko & Numachi, 2000
Austropotamobius pallipes	Astacidae	Western Europe	Intraspecific	Trontelj et al., 1995
Austropotamobius torrentium	Astacidae	Danube catchment	Intraspecific	Trontelj et al., 1995
Orconectes luteus	Cambaridae	Southern USA	Intaspecific	Fetzner & Crandall, 2003
Cambarus hamulatus	Cambaridae	Southern USA	Intaspecific	Buhay et al., 2007
Euastacus species	Parastacidae	Eastern Australia	Species	Baker et al., 2004
Geothelphusa species	Potamidae	Taiwan	Species	Shih et al., 2004, 2007, 2011
Potamonautes perlatus	Potamonautidae	South Africa: Olifants R.	Intraspecific	Daniels et al., 1999
Sesarma dolphinum-abeokuta	Sesarmidae	Jamaica: Cabarita R.	Species	Current study
Sesarma meridies-bidentatum	Sesarmidae	Jamaica: Cobre T.	Species	Schubart & Koller, 2005

than they are among each other. This suggests that overland dispersal between nearby headwaters in forested areas is more likely than genetic mixing in the lowland part of the rivers, despite the fact that all river crabs from Jamaica with known development have two larval stages (Hartnoll, 1964; Anger & Schubart, 2005; González-Gordillo et al., 2010) and thus relatively high distribution potential compared to other freshwater crabs with direct development. However, in both these cases documented in Jamaica, i.e. the Cabarita and the Cobre rivers, the lower sections of the corresponding rivers are broad and fast-flowing lowland streams that lack rocky structures and are thus not suitable for adult nor larval crabs. This explains, how different crab species or populations can become ecologically and geographically isolated and evolve independently, even within single river systems, providing important insights for the reconstruction of the rapid adaptive radiation of Jamaican crabs that took place during the past 4.5 million years (Schubart et al., 1998b). Future analyses with larger sample sizes and more variable markers are planned to allow statistical quantification of gene flow and its direction among all sites, and thus provide a better understanding of the underlying patterns of diversification and speciation.

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