Taxonomy, Distribution and Ecology of the Genus Sesarma (Crustacea, Decapoda, Grapsidae) in Eastern North America, with Special Reference to Florida

LAWRENCE G. ABELE

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Taxonomy, Distribution and Ecology of the Genus Sesarma (Crustacea, Decapoda, Grapsidae) in Eastern North America, with Special Reference to Florida[1]

LAWRENCE G. ABELE[2]
Smithsonian Tropical Research Institute, P.O. Box 2072, Balboa, Canal Zone

ABSTRACT: Six species of the grapsid crab genus *Sesarma* are reported from eastern North America. A key for their identification is presented and their diagnostic characters are illustrated. Their distributions in the western Atlantic are reviewed and a map is given of their distributions in Florida, an area where all six species occur. Field observations on the biology and ecology of four species are presented. Character divergence occurs between two closely related, partially sympatric species. Several factors are suggested to account for the observed patterns of distribution.

INTRODUCTION

Six species of the grapsid crab genus *Sesarma* have been reported from eastern North America (Rathbun, 1918; Tabb and Manning, 1961; Abele, 1972). There has been some uncertainty concerning the status of these species in Florida, especially in areas where three or more species occur together.

While studying some collections of *Sesarma* from southern Florida, I found it necessary to re-examine extensive material of the genus from eastern North America, as well as material from other localities identified with North American species. Study of this material in the National Museum of Natural History, Washington, D. C., the museum of the Rosenstiel School of Marine and Atmospheric Science, Miami, Fla., and collections made by myself and others revealed that many distribution records were based on misidentified material.

This report presents a key to the six species of *Sesarma* known to occur in eastern North America. Diagnostic characters of all species are illustrated, three for the first time. A distribution map of all six species in Florida is presented and their known distributions in the western Atlantic are given. Some data are presented on the size at which sexual maturity is reached, the development of secondary sexual characters and the time of spawning. Field observations on ecological distribution are presented as well as observations on character divergence in an area of sympatry.

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[2] Present address: Department of Biological Science, Florida State University, Tallahassee 32306.

The abbreviation USNM refers to the National Museum of Natural History, Washington, D. C., UMML to the museum of the Rosenstiel School of Marine and Atmospheric Science and *cb* to carapace breadth. The gonopod is the first pleopod of the male.

Key to the species of *Sesarma* in eastern North America

1. Movable finger of male chela (Fig. 1B) normal, not greatly enlarged proximally; apex of gonopod without two sutures 2
   Movable finger of male chela (Fig. 1A) greatly enlarged proximally; apex of gonopod with two sutures (Fig. 1G) ..... *benedicti*
2. Carapace without tooth or lobe posterior to outer orbital angle 3
   Carapace with tooth (Fig. 1C) or lobe (Fig. 1D) posterior to outer orbital angle 5
3. Gonopod with endpiece central, not curved (Fig. 1J); merus of second walking leg with length greater than 2.6 times width ..... *ricordi*
   Gonopod with endpiece lateral, curved (Fig. 1H or 1I); merus of second walking leg with length less than 2.6 times width 4

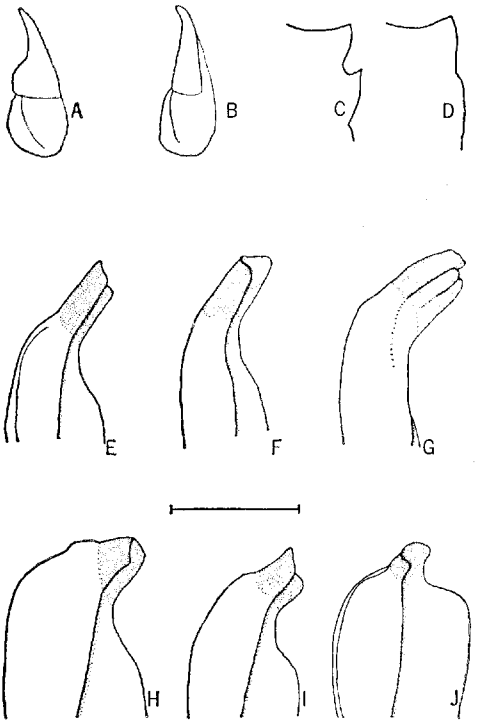

Fig. 1.—A, male chela of *S. benedicti*. B, chela of *S. cinereum*. C, anterolateral portion of carapace of *S. curacaoense*. D, anterolateral portion of carapace of *S. reticulatum*. E-J, apex of male gonopod. E, *S. reticulatum*. F, *S. curacaoense*. G, *S. benedicti*. H, *S. cinereum*. I, *S. miersii*. J, *S. ricordi*. Scale = 1 mm for E-J, 4 mm for A, B, 2 mm for C, D

4. Dactylus of fourth walking leg unarmed dorsally ..... *miersii*
   Dactylus of fourth walking leg armed dorsally with short black spines ..... *cinereum*
5. Tooth behind outer orbital angle deeply cut into carapace (Fig. 1C) .... *curacaoense*
   Tooth behind outer orbital angle little more than a lobe (Fig. 1D) .... *reticulatum*

DESCRIPTION OF SPECIES

Sesarma (Holometopus) cinereum (Bosc, 1801-1802)

Florida material examined.—5 males, 4 females; Apalachicola; USNM 49910.—6 males, 5 ovigerous females, 12 nonovigerous females; Alligator Harbor, Franklin Co.; UMML.—32 males, 49 nonovigerous females; Cedar Keys, Levy Co.; USNM 6413.—1 male, 1 female; Sarasota Bay, Sarasota Co.; USNM 71160.—1 female; Gasparilla Island, Tampa, Pinellas Co.; USNM 15261.—1 male, 4 females; Tampa Bay, Pinellas Co.; USNM 26113.—3 females; Inglewood, Sarasota Co.; USNM 74545.—30 specimens; Punta Rassa, Lee Co.; USNM 15072.—5 males, 6 females; Naples, Collier Co.; USNM.—1 male, Dayton (? = Daytona), Volusia Co.; USNM 71158.—1 male, 5 females; Jupiter, Palm Beach Co.; UMML.

Description.—Williams, 1965: 222, Fig. 206.

Distribution.—Magathy River, Chesapeake Bay, Maryland to Palm Beach Co. on the E coast of Florida; Collier Co. on the W coast of Florida to Vera Cruz, Mexico. Records of this species from the West Indies and elsewhere were found to be based on juvenile specimens of *Sesarma ricordi* H. Milne Edwards, 1853 and *S. americanum* De Saussure, 1853.

Habitat.—This species occurs from above the high water mark to about 50 m inland. Specimens were collected from high areas of a *Spartina* marsh, along the edge of a mangrove swamp (*Rhizophora mangle*), at the edge of a pine woods and from a supratidal grassy area in shallow burrows (*see also* Ecological Distribution).

Remarks.—*Sesarma cinereum* is sexually dimorphic in several characters. The usual differences between brachyuran sexes in the form and number of the pleopods and in the width of the abdomen were noted. In addition to these differences, mature males of *S. cinereum* have more robust chelae than females and have a row of dark, heavy pubescence along the ventral border of the dactylus and distal portion of the propodus of the second and third pereiopods which is lacking on the females. Secondary sexual characters of both sexes appear to develop over a period of time rather than following a single molt.

Thirty-two males were examined for gonopod development, fringe of pubescence and robustness of the chelae. The size range was *cb* 4.7 to 14.7 mm. Males of *cb* 4.7 to 7.5 mm were at a similar stage of sexual development. A small, naked gonopod was present, pereiopodal pubescence was lacking and the chelae were not robust. Males *cb* 8.1 to 10.1 mm had the gonopod well developed with setae present, a fringe of pubescence on the second pereiopod, a few setae on the third

pereiopod and chelae which were stronger than those of the previous group. Males *cb* 10.0 to 14.7 mm had all male secondary sexual characteristics. The overlap between this group and the former consisted of two specimens of *cb* 10.0 mm.

A sequential development of secondary sexual characters occurred in females. Females *cb* 5.0 to 5.4 mm had a narrow abdomen and very small pleopods with no setae present. Females *cb* 5.4 to 6.6 mm had a slightly wider abdomen with a few setae present on the pleopods. Females *cb* 8.0 to 9.3 mm had well-developed pleopods with setae present but the abdomen was not covering the sternum. All secondary sexual characters were present on females of *cb* 11.2 to 17.2 mm. Ovigerous females ranged in size from *cb* 11.2 to 17.2 mm. Females appear to attain a larger size than males.

Sexually mature females were observed during January, February, March, April, June, July and November. Only those collected during June (Florida) and July (Texas) were ovigerous (specimens collected 31 July had eggs early in development so August can be included) suggesting spawning occurs during the summer. Williams (1965) reported ovigerous females from May to November in the Carolinas. Each female carried many small eggs (diam, 0.25 mm), the number apparently depending of the size of the female.

Discussion.—*S. cinereum* is close to both *S. ricordi* and *S. miersii*. It can be distinguished from *S. ricordi* by its broader walking legs, less inflated carapace and form of the gonopod. The mean length/width ratio of the merus of the third pereiopod is 2.50 for *S. cinereum*. Specimens from Collier Co. had a ratio of 2.43 while those from Palm Beach Co. had a ratio of 2.59. Specimens of *S. ricordi* had a mean ratio of 2.86 in all areas of Florida. Specimens from Bermuda and the West Indies had a ratio of 3.0 or greater. Holthuis (1959) reported small specimens with a ratio of 2.60 and adults with a ratio of 3.0. The propodi of the walking legs of *S. cinereum* are more heavily armed with short black spines than are those of *S. ricordi*. The carapace of *S. cinereum* is less inflated than that of *S. ricordi*. The gonopods of the two species are dissimilar (compare Figs. 1H and 1J).

Sesarma cinereum can be separated from *S. miersii* by the form of the gonopod and the spination of the dactylus of the fifth pereiopod. The gonopod of *S. cinereum* (Fig. 1H) has a small hump on the distomesial margin slightly poximal to the short robust endpiece. The gonopod of *S. miersii* (Fig. 1I) lacks this hump and the endpiece is not as short or as robust. The dactylus of the fifth pereiopod of *S. cinereum* is armed dorsally and ventrally with short, strong, black spines while that of *S. miersii* has only a few ventral spines.

Sesarma (Holometopus) ricordi H. Milne Edwards, 1853

Florida material examined.—5 males; Shell Key off St. Petersburg, Pinellas Co.; USNM 75554.—2 males, 3 females; Naples, Collier Co.: USNM.—4 males, 2 females, 1 ovigerous female; Key Biscayne, Dade Co.; UMML.—1 male, 5 females (2 parasitized); Coconut Grove,

Dade Co.; USNM 58430.—1 male; Bahia Honda, Monroe Co.; USNM 48581.— 11 males, 6 females, 2 ovigerous females; Key West, Monroe Co.; USNM 71151, 71166, 71295, 71298.

Description.—Chace and Hobbs, 1969: 183, Fig. 62k.

Distribution.—Shell Key off St. Petersburg, Fla. to Surinam (Holthuis, 1959); Bermuda; West Indies (Chace and Hobbs, 1969). Records of this species from Mississippi have been determined to be *S. cinereum* (*cf.* Chace, in Hedgepeth, 1953). Material from Brazil was determined to be *S. angustipes* Dana, 1852 (*see* Abele, 1972).

Habitat.—Specimens were collected from above the high water mark to about 30 m inland. Crabs were common in a low-lying pine woods, along the edge of a mangrove swamp (*Rhizophora mangle*), and in shallow burrows in grass above sandy beaches. This species was uncommon on a rock-limestone substrate among supratidal litter (*see also* Ecological Distribution).

Remarks.—Primary and secondary sexual characters of *S. ricordi* are similar to those described for *S. cinereum* and appear to develop in a similar pattern. Males of *cb* 10.7 mm and smaller were immature while those of *cb* 10.7 to 16.3 mm were mature, the overlap consisting of a single specimen. Females of *cb* 10.0 mm and smaller were immature while those of *cb* 13.2 to 20.6 mm were mature. Ovigerous females ranged from *cb* 15.1 to 17.0 mm. Each female carried many small eggs (diam. 0.25 mm), the number apparently depending on the size of the female.

Sexually mature females were observed in April, May, August, September, November, December, January and March. Those collected in Florida during May, June, and August were ovigerous, and those collected in Panama during January were ovigerous.

Discussion.—*See S. cinereum.*

Sesarma (*Holometopus*) *benedicti* Rathbun, 1897

Florida material examined.—1 female; Key West, Monroe Co.; A. S. Packard (?1881); MCZ 6236 (Museum of Comparative Zoology, Harvard University).

Description.—Rathbun, 1918: 316, pl. 93.—Holthuis, 1959: 248, Fig. 62.

Distribution.—Key West, Florida; Guyana; Surinam; Brazil.

Habitat.—Holthuis (1959) reported that this species was common on the banks of brackish or almost fresh-water rivers and under wood or stones on the banks.

Remarks.—None.

Discussion.—This is a most distinctive species in a number of characters. The enlarged proximal portion of the movable finger of the chela is unique among American species of *Sesarma*. The gonopod is no less distinctive. This distal portion is folded over on itself twice rather than the usual single fold of species of *Sesarma*. The distal portion of the major fold is fused and the smaller second fold is partially fused (*see* Fig. 1G). It was so unusual that several specimens

were examined to be sure that the specimen figured was not aberrant; it was not.

Sesarma (Holometopus) miersii Rathbun, 1897

Florida material examined.—1 male, 2 females; Key West; Monroe Co.; USNM 74536, 74554.

Description.—Chace and Hobbs, 1969: 180, figs. 59, 62g-i.

Distribution.—Key West, Fla.; Bahamas; Dominica; Cuba; Swan Island.

Habitat.—Chace and Hobbs (1969) reported a specimen of this species from a marsh mud flat (*see* also their pl. 4A) adjacent to Indian River on Dominica. Vegetation present was *Pterocarpus officinalis, Montichardia aborescens* and a fern *Acrostichum danaefolium.*

Remarks.—None.

Discussion.—The taxonomic and nomenclatural confusion surrounding this species was reviewed by Abele (1972). It had previously been confused with *S. ricordi* in Florida.

Sesarma (Sesarma) reticulatum (Say, 1817)

Florida material examined.—1 ovigerous female; Bald Point outside of Alligator Harbor, Franklin Co.; UMML.—1 male; 2 km W of St. Theresa, Franklin Co.; UMML.—2 females; Sarasota Bay, Sarasota Co.; USNM 71169.—3 males, 1 female; Travertine Quarry, Manatee Co.; USNM 71302.

Description.—Williams, 1965: 221, Fig. 205.

Habitat.—This species commonly occurs in low areas of *Spartina* salt marshes. Specimens were also collected from under rocks in the intertidal zone of small tidal streams.

Distribution.—Woods Hole, Massachusetts S to presumably somewhere on the E coast of Florida; Calhoun Co., Texas to Sarasota Co. on the W coast of Florida.

Remarks.—There is a distinct decrease in the size of specimens southward. Specimens from Massachusetts are commonly of *cb* 26 or 27 mm while those from northern and central Florida are of *cb* 13 to 16.5 mm. An ovigerous female (*cb* 15.8 mm) was collected during May in N Florida.

The specimen referred to this species by Tabb and Manning (1961) was examined and determined to be *S. curacaoense.*

Discussion.—This species is related to *S. curacaoense.* They can be separated easily however, by the form of the lateral tooth posterior to the outer orbital angle. This tooth is an indistinct lobe in *S. reticulatum* (Fig. 1D) while it is distinct and deeply cut into the carapace in *S. curacaoense* (Fig. 1C).

Sesarma (Sesarma) curacaoense De Man, 1896

Florida material examined.—5 males, 2 females; Jupiter, Palm Beach Co.; UMML.—2 males, 7 females; Caximbas, Marco Cut near

Coon Key, Collier Co.; USNM 74859.—1 male, 1 female; Naples, Collier Co.; UMML.—2 males, 3 females; Flamingo, Monroe Co.; USNM.—3 males; Everglades National park near Whitewater Bay, Monroe Co.; UMML 32.1333, 32.13337.—2 males, 1 female; Miami, Dade Co.; UMML.—1 male; Key West, Monroe Co.; USNM 74837.

Description.—Chace and Hobbs, 1969: 188, Figs. 61, 62p.

Distribution.—Jupiter, Palm Beach Co., Fla., on the E coast and Collier Co. on the W coast to Estado da Bahia, Brazil.

Habitat.—Specimens were collected most commonly in mangrove swamps (*Rhizophora mangle*) under rocks and litter. This species was also collected in the intertidal zone from under clumps of oysters and rocks and from under rocks in the intertidal zone of a brackish river (salinity of 20 ppt).

Remarks.—Sexual development in this species could be followed by the increase in setation of the gonopod of the male and the increase in robustness of the male chelipeds; in females it could be followed by the increasing width of the abdomen and increased setation of the pleopods. Males from *cb* 6.5 to 10.0 mm were judged to be immature; those of *cb* 11.0 to 13.1 mm were judged to be intermediate in development; and those of *cb* 13.5 to 17.9 mm were sexually mature.

No ovigerous females were observed in the Florida material. Females of *cb* 12.0 to 17.5 mm were found to be sexually mature. Smaller females were not available with the single exception of a specimen (*cb* 11.0 mm) which was not quite mature.

Discussion.—*See S. reticulatum.*

GEOGRAPHIC DISTRIBUTION

The distribution of the genus *Sesarma* in Florida is indicated in Figure 2. *Sesarma cinereum* is known to occur S to Collier Co. and *S. reticulatum*, S to Sarasota Co. It is probable that these areas do represent the southern limit of the distribution of both species. Extensive collections made by myself and others (notably, Dr. Lowell Thomas) throughout Dade Co. failed to reveal the presence of either *S. cinereum* or *S. reticulatum*. Collections were also made throughout much of Collier Co. but *S. cinereum* was not found S of Naples and *S. reticulatum* was not found at all. There are few collection records from the E coast of Florida. *Sesarma cinereum* was collected in Palm Beach Co. on the E coast along with *S. curacaoense*. The records of *S. cinereum* from the West Indies and Central and South America were, as already mentioned, based on misidentified material. There are no records of *S. reticulatum* from the E coast, but this is probably due to insufficient collecting rather than to the absence of the species from the area.

Sesarma ricordi is common throughout Dade, Collier and Monroe counties and is known N to Pinellas Co. The species was not collected during several trips to Palm Beach Co. *Sesarma curacaoense* is common from Palm Beach Co. S through the Florida Keys, but is not known N of Collier Co. on the W coast. Both *Sesarma benedicti* and

S. miersii are known only from Key West. The record of *S. benedicti* is based on a single specimen and that of *S. miersii* is based on three specimens collected on two different occasions. Additional records of these two species in Florida are highly desirable.

The species of *Sesarma* in Florida, as well as the Florida fauna as a whole, belong to two distinct zoogeographical provinces: the *Carolinian* and the *West Indian*. *Sesarma cinereum* and *S. reticulatum* are classic examples of *Carolinian* species which have disjunct distributions in peninsular Florida (Hedgpeth, 1953). The absence of these species from the southern tropical tip of the peninsula is thought to be associated with temperature and perhaps salinity differences (Hedgpeth, 1953). However, because of the interactions between *S. ricordi* and *S. cinereum* described below, competitive habitat exclusion is more likely the reason for the absence of *S. cinereum* and, probably, *S. reticulatum* from southern Florida.

The remaining four species, *S. ricordi, S. curacaoense, S. miersii* and *S. benedicti,* are members of the *West Indian* faunal province with southern Florida being the northern continental limit to their distribution. The former two species are well established in Florida but the status of the latter two requires additional data.

ECOLOGICAL DISTRIBUTION

The general habitat data are presented in the previous section dealing with each species. As can be seen from these data, the two species of the subgenus *Sesarma* differ in several ecological features from the

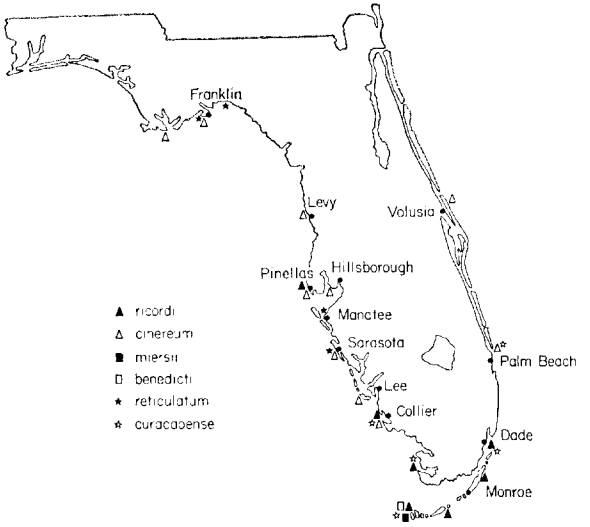

Fig. 2.—Distribution of species of the genus *Sesarma* in Florida. Localities given are county names

two species of the subgenus *Holometopus: S. reticulatum* and *S. curacaoense* occur intertidally or in seepage areas and are morphologically robust and relatively sluggish in their habits; *S. cinereum* and *S. ricordi* occur supratidally and are morphologically slender and active in their habits. Additionally, it seems that *S. reticulatum* is the northern ecological equivalent of *S. curacaoense* and that *S. cinereum* is the northern ecological equivalent of *S. ricordi*. It is suggested, based on field observations, that three factors (already noted for other animal groups) are important in permitting the sympatric species of *Sesarma* to co-exist: (1) a difference in microhabitat and behavior between species of different subgenera; (2) a habitat shift in areas of sympatry reducing competition for available resources between species of the same subgenus; and (3) character divergence of color patterns and morphological features which may act as one of the isolating mechanisms between these species of the same subgenus in the area of sympatry. Examples of each of these factors are given in the following section.

Sesarma (Sesarma) curacaoense and *S. (Holometopus) ricordi* can be found on the same fallen tree at the edge of a mangrove swamp. However, they occur on different parts of the tree: *S. curacaoense* will be found under damp bark at the ground-tree interface where water collects and in shallow excavations under the tree; *S. ricordi* will be found under loose dry bark on the upper exposed portion of the tree. The two species can also be found together under litter in mangrove swamps: *S. curacaoense* occurs in areas dampened by marine seepage and *S. ricordi* occurs on relatively dry areas of slightly higher elevation. In addition to these differences in microhabitat, there are differences in behavior between these two species. Individuals of *S. curacaoense* are sluggish and tend to feed on detritus in the immediate area. Individuals of *S. ricordi* are relatively active and feed on detritus and on other food items such as insects. The more active habits of *S. ricordi* seem to expose the crabs to a wider variety of food items than do the sluggish habits of *S. curacaoense*. Although both species feed on similar items and occur together, differences such as these in microhabitat and behavior seem to reduce competition for available resources.

Sesarma (Holometopus) cinereum and *S. (Holometopus) ricordi* are ecologically equivalent where allopatric and would appear to be in direct competition in areas of sympatry. In Dade Co., where only *S. ricordi* occurs, individuals are found in dense populations on clay-sand substrate among supratidal grass and in various other habitats already noted. In Collier Co., where *S. ricordi* and *S. cinereum* are sympatric, this habitat was occupied by dense populations of *S. cinereum* while individuals of *S. ricordi* were found only a few centimeters away among litter on a rock-limestone substrate. Observations over a 2-month period showed no change in this apparent habitat exclusion. Further observations were not possible because extensive bulkheading and urbanization destroyed the habitat. Attempts to locate a similar habitat in the area were unsuccessful for the same reasons. It should be noted

here that undisturbed populations of any semiterrestrial or terrestrial species of crabs in southern Florida are difficult to locate.

Museum records and my collections indicate that *S. cinereum* and *S. ricordi* are sympatric for about 250 km on the W coast of Florida from Pinellas to Collier Co. It seems probable that these two closely related species are able to occur sympatrically, primarily because of their lability in habitat requirements (but *see also* following remarks on *character divergence*). In attempting to colonize an area, a species may be excluded from one habitat by an ecologically equivalent species already present. Under these conditions, the colonizing species establishes populations in marginal areas where it can exist and at the same time avoid direct competition with the established species for available resources. However, these marginal populations do not appear to be very successful, as most records of both species in areas of sympatry are based on a few specimens. In an area (Collier Co.) where populations of both species are relatively dense the interactions are intense with habitat exclusion occurring along an "ecotone" of only a few centimeters width, suggesting that this habitat exclusion is a physical process.

Character divergence (*character displacement* of Brown and Wilson, 1956) was observed to occur in both *S. cinereum* and *S. ricordi* (*see* Table 1) in an area of sympatry. Individuals of *S. cinereum* in this area had a slate grey carapace with no pattern present. The frontal margin was a light green with no disruptive pattern present, and the frontal region was only slightly expanded distally. The walking legs were relatively broad with the mean (n = 11) ratio of the length/width of the merus being 1:2.43. Individuals of *S. ricordi* had a grey-brown carapace with deep purple disruptive markings present, and the frontal region was greatly expanded distally. The walking legs were relatively narrow with the mean (n = 6) ratio of the length/width of the merus being 1:2.86. In areas of sympatry, both species could easily be identified in the field on the basis of color. However, this was not

TABLE 1.—Character comparisons between allopatric and sympatric populations of *S. ricordi* and *S. cinereum* in Florida

	ricordi		*cinereum*	
	allopatric	sympatric	sympatric	allopatric
General color of carapace	grey-purple	grey-purple	grey	grey-purple
Pattern on carapace	yes	yes	no	yes
Color of frontal margin	purple-grey	purple-grey	light green	purple-grey
Expansion of frontal region	distinct	distinct	slight	distinct
Length/width ratio of merus of third pereiopod	2.86	2.86	2.43	2.59
Locality (county)	Dade	Collier	Collier	Palm Beach

the case in areas of allopatry where both species were similar in color and could not be separated by this character. Although the color pattern of allopatric populations of both species was generally similar to that of *S. ricordi* from the sympatric area, the colors were less intense and the patterns were more diffuse. The expansion of the frontal region of both species in allopatric populations was similar and the difference in the widths of the walking legs (*S. cinereum* = 1:2.59; *S. ricordi* = 1:2.86) was not as great.

This situation appears to follow the classic pattern of *character divergence* as summarized by Mayr (1963); that is, allopatric populations of two closely related species resemble each other in some character, whereas sympatric populations differ markedly in this same character. In most cases summarized by Mayr and others, however, the characters involved in *character divergence* were primarily those important in food resource partitioning (*e.g.*, bill size of birds) and are of the type described by Schoener (1965) as *character difference*. The present situation does not involve characters important in resource partitioning but rather characters which may be important in species recognition. Visual cues are highly important in sexual and intraspecific encounters in semiterrestrial crabs (Crane, 1957; Schöne, 1968), and the differences described here may be important as one isolating mechanism between these two closely related species in areas of sympatry.

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