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The Systematic Importance of Color and Color Pattern: Evidence for Complexes of Sibling Species of Snapping Shrimp (Caridea: Alpheidae: *Alpheus*) from the Caribbean and Pacific Coasts of Panama

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ABSTRACT.—Closely related species in the genus *Alpheus* Fabricius, 1798, are most easily distinguished by small but consistent differences in color and particularly color pattern. We made extensive collections of several nominal species from Panama, examining living material for evidence of discrete color morphs within described species. *Alpheus formosus* Gibbes, 1850, has two Caribbean color morphs, both distinct from the morphologically similar eastern Pacific species *A. panamensis* Kingsley, 1878. Caribbean representatives of *A. cristulifrons* Rathbun, 1900, consistently differ in color and color pattern from eastern Pacific representatives of the same species. *Alpheus paracrinitus* Miers, 1881, is found in the Caribbean in two color morphs, both of which are distinct from the eastern Pacific morph of the same species. All these morphs are also distinct in color pattern from the morphologically similar eastern Pacific species *A. rostratus* Kim and Abele, 1988. The eastern Pacific species *A. canalis* Kim and Abele, 1988, has two color morphs, both of which can be distinguished from the morphologically similar Caribbean species *A. nuttingi* (Schmitt, 1924). Earlier work with *Alpheus* symbionts of sea anemones suggests that these color morphs are likely to be separate species. Analysis of color pattern holds enormous potential for defining species boundaries in this systematically difficult genus.

RESUMEN.—En el género *Alpheus* Fabricius, 1798, existen especies estrechamente relacionadas las cuales pueden ser distinguidas fácilmente, por pequeñas pero consistentes diferencias de color y particularmente en los patrones de coloración. Hemos hecho grandes colecciones de varias especies de Panamá, examinando material vivo para determinar si existen "formas de color" dentro de las especies ya descritas. *Alpheus formosus* Gibbes, 1850, tiene dos "formas de color," y ambas difieren de la especie más similar del Pacífico-este, *A. panamensis* Kingsley, 1878. La forma del Caribe de *A. cristulifrons* Rathbun, 1900, es diferente de manera consistente en color y patrón de coloración, de la forma del Pacífico-este de la misma especie. En *A. paracrinitus* Miers, 1881, del Caribe hay dos "formas de color" las cuales son distintas a la forma presente en el Pacífico-este de la misma especie. Todas estas formas son también distintas en el patrón de color de la especie morfológicamente similar del Pacífico-este, *A. rostratus* Kim y Abele, 1988. La especie del Pacífico-este *A. canalis* Kim y Abele, 1988, tiene dos "formas de color", y ambas se pueden distinguir de la especie más similar del Caribe, *A. nuttingi* (Schmitt, 1924). En base a trabajos previos con *Alpheus* simbiontes de anémonas marinas, estas "formas de color" son probablemente especies distintas. Los análises de patrones de coloración poseen un potencial enorme para la definición de especies en este género de sistemática difícil.

INTRODUCTION

Imagine the frustration of an ornithologist confronting a collection of bleached specimens. In birds and many other groups, the importance of color and color pattern in distinguishing closely related species is indisputable. Nevertheless, descriptions of crustacean species usually provide little information on color and color pattern, and patterns are rarely illustrated. Historically, the reasons for this are obvious—preserved specimens lose their color rapidly, and most taxonomic research has necessarily relied on museum collections. With many more researchers now based close to field sites, however, it is no longer necessary to limit studies to characters seen in preserved material.

It is often easier to clarify the status of problematic taxa and to estimate the true biodiversity of morphologically defined groups by working with the characters of both living and preserved specimens (for decapod crustaceans see Knowlton 1986). An example of the value of such an approach can be seen in the genus *Alpheus*, whose notorious difficulty (Wicksten, in press) stems in part from the existence of complexes of species difficult to distinguish by traditional morpholological characters. Earlier, data on color and color pattern led to the discovery of a complex of close relatives that are all symbionts of sea anemones (Knowlton and Keller 1983, 1985). In this case, the discrete color morphs were shown to be reproductively incompatible. Here we present data on comparably distinct color morphs in free-living *Alpheus* found along the Pacific and Caribbean coasts of Panama. Electrophoretic and mating behavior data (to be published elsewhere) suggest that these morphs also merit specific status.

For this paper we concentrate on four groups: (1) *A. panamensis*

(Pacific) and *A. formosus* (Caribbean), (2) *A. paracrinitus* (Pacific and Caribbean) and *A. rostratus* (Pacific), (3) *A. cristulifrons* (Pacific and Caribbean), and (4) *A. canalis* (Pacific) and *A. nuttingi* (Caribbean). *Alpheus panamensis* and *A. formosus* are morphologically very similar species, restricted to the eastern Pacific and western Atlantic, respectively. Christofferson (1979) considered *A. panamensis* to be a junior synonym of *A. formosus*, but Kim and Abele (1988) did not concur. *Alpheus cristulifrons* is reported from both sides of the Atlantic and the eastern Pacific. *Alpheus paracrinitus* has a pantropical distribution, while *A. rostratus* is a recently described, morphologically similar species restricted to the eastern Pacific. *Alpheus canalis* and *A. nuttingi* are morphologically similar species restricted to the eastern Pacific and western Atlantic, respectively. In general, the close morphological and biochemical similarities between eastern Pacific and Caribbean taxa are thought to stem from their relatively recent separation by the rise of the Isthmus of Panama (Jordan 1908, Vawter et al. 1980, Lessios 1981) approximately 3 million years ago (Keigwin 1982).

Our goal was to assess differences between eastern Pacific and Caribbean representatives and look for evidence of sympatric sibling species within the two oceans. We deliberately avoided groups in which species have been described as morphologically highly variable (e.g., *A. armillatus*), since finding sibling species with distinct color patterns would be less surprising in these cases. Working with what are thought to be morphologically well-defined taxa provides a conservative test of the importance of color in distinguishing closely related species.

METHODS AND MATERIALS

We collected at a variety of intertidal and shallow subtidal sites on both coasts of Panama from 1989 to 1991. Collected animals were brought to the laboratory and identified to species according to the keys of Chace (1972) and Kim and Abele (1988). After initial identification, presumed conspecifics from the same side of the isthmus were examined carefully side by side for variation in color and color pattern, particularly variation appearing to fall in non-overlapping classes. When several discrete differences always occurred together, color morphs defined by these differences were identified. We then compared these within-ocean morphs with their trans-isthmian relatives and looked for diagnostic differences in color or color pattern between closely related trans-isthmian morphs. In total, we examined at least 50 individuals of each defined morph, and never found any intermediate forms.

We then described in detail the colors and color pattern for each morph, using at least eight individuals per morph, including males, females, and juveniles. Animals were illuminated by a Volpi fiber-optic light source with a daylight filter, and the color pattern of the carapace, abdomen, major and minor chela, antennae, and other body parts as appropriate was recorded. We noted the presence of both diffuse pigments and pigments clearly confined to chromatophores for these body parts, and matched pigments to the closest of 1200 color cards coded by the International Munsell Color System (see Endler 1990).

RESULTS

In all cases the Pacific and Caribbean members of a group exhibited relatively small but distinct differences in color pattern, so that any individual could be unambiguously assigned to its ocean of origin on the basis of these attributes alone. In two of the four groups, Caribbean members were found to consist of two distinct morphs that often occurred sympatrically. In a third group, the Pacific species was found to contain two often sympatric morphs. Thus our four groups (consisting of seven described species) split into twelve morphs as follows: (1) *A. panamensis*, *A. formosus*-a, *A. formosus*-b; (2) *A. cristulifrons* Pacific, *A. cristulifrons* Caribbean; (3) *A. rostratus*, *A. paracrinitus* Pacific, *A. paracrinitus* Caribbean-a, *A. paracrinitus* Caribbean-b; and (4) *A. canalis*-a, *A. canalis*-b, *A. nuttingi*.

Below we describe the most consistent and conspicuous of the differences among members of each of the four groups studied. Our purpose is to indicate the kinds of color characters that distinguish sibling species of *Alpheus*. In addition to the diagnostic differences used to define the morphs, we provide data on variable characters likely to show significant frequency differences among morphs with further sampling. We do not attempt a rigorous statistical analysis of the non-diagnostic color differences observed, however, because the sample sizes are not adequate. We are preparing a full description of the color and color patterns to be published in conjunction with new species descriptions.

Alpheus panamensis/A. formosus-a/A. formosus-b.—The three taxa in this complex can be separated unambiguously by the form of the dorsal and lateral longitudinal stripes and by the color pattern of the major chela (Table 1). *Alpheus panamensis* and *A. formosus*-b have down the center of the dorsal stripe a blue line that *A. formosus*-a lacks. *Alpheus formosus*-b always has red pigment along the edges of the rostrum that narrows the light midline stripe anteriorly; the other two taxa lack red pigment on the rostrum as juveniles, and as adults the red rostral pigment is either lacking (*A. formosus*-a) or is not restricted to the margin (*A. panamensis*). *Alpheus formosus*-b also has an isolated patch of white above the

TABLE 1. Pattern and color differences among *A. panamensis*, *A. formosus*-a, and *A. formosus*-b. All listed pigments except green on major chela and blue and orange on antennae are associated with chromotophores.

Character	*panamensis* Pacific (n = 18)	*formosus*-a Caribbean (n = 10)	*formosus*-b Caribbean (n = 8)
Diagnostic pattern differences			
Dorsal blue line	present	absent	present
Adult rostrum red	entire	absent	margin
Juvenile rostrum red	absent	absent	margin
Abdominal patch	absent	absent	present
Major chela patch	absent	entire	center
Percentage of individuals bearing various classes of pigments			
Midline stripe			
Iridescent orange	72%	100%	25%
Iridescent yellow	11%	10%	100%
Iridescent green	28%	50%	100%
Major chela			
Red	78%	80%	38%
Blue	17%	0%	100%
Green	39%	0%	0%
Antennae			
Red	31%	90%	100%
Blue	0%	100%	0%
Orange	0%	0%	100%
Frequency of occurrence[a] of most common colors			
Midline iridescent orange			
5 YR 6/12	8%	50%	50%
7.5 YR 6/10	0%	0%	50%
7.5 YR 7/14	31%	0%	0%
Midline iridescent green			
2.5 GY 7/10	0%	80%	0%
7.5 GY 7/10	60%	0%	0%
10 GY 7/10	0%	0%	88%

[a]Percentages calculated for individuals having pigments in a given class. Colors listed are the most common colors exhibited by each taxon; alphanumeric codes are those used to identify individual colors in the International Munsell Color System.

lateral white stripe on the fourth abdominal segment that the other two lack. The major chela of adults is dark in *A. panamensis*, has a light patch running the length of the inner face in *A. formosus*-a, and has a light patch restricted to the center of the inner face in *A. formosus*-b.

There are also differences in the diffuse pigments, in the proportion of individuals with various color classes of discretely visible chromatophores, and in the color of the pigments in these chromatophores (Table 1). Iridescent chromatophores along the dorsal midline are most commonly orange in *A. panamensis* and *A. formosus*-a, while in *A. formosus*-b yellow and green iridescent chromatophores are always present and orange ones are comparatively rare. The most common color identified within the orange and green color classes also differs among the morphs. In the major chela, diffuse green pigments are sometimes present in *A. panamensis* but absent in both *A. formosus* morphs. Red chromatophores are less common and blue chromatophores are more common in *A. formosus*-b than in the other two taxa. Diffuse pigments in the antennae are generally absent in *A. panamensis*, blue in *A. formosus*-a, and orange in *A. formosus*-b.

Alpheus cristulifrons Pacific/A. cristulifrons Caribbean.—The Caribbean and Pacific morphs can be readily distinguished by several pattern differences (Table 2). Most strikingly, the eastern Pacific morph has bands on the antennae, which the Caribbean morph lacks. The Pacific morph also has narrower abdominal bands with large well-defined spots and a mottled major chela, while the Caribbean morph has wider abdominal bands with smaller, less distinct spots and well-defined spots on the major chela.

The frequency of occurrence and the pigments of several chromatophore classes in the two morphs also differ (Table 2). On the carapace and abdomen, iridescent green chromatophores are more common in the Pacific morph, and the most common red and blue pigments have slightly different colors in the two morphs. Together these differences are probably responsible for the black vs. brown color of the body bands on the Pacific and Caribbean morphs, respectively. Blue and iridescent yellow chromatophores are found more commonly on the major chela of the Caribbean morph than in the Pacific morph. The second pereiopods are yellow in the Pacific morph and orange in the Caribbean morph. Diffuse blue antennal pigments are found only in the Pacific morph.

Alpheus rostratus/A. paracrinitus Pacific/A. paracrinitus Caribbean-a/A. paracrinitus Caribbean-b.—*Alpheus rostratus* and the three morphs of *A. paracrinitus* can all be reliably distinguished by pattern differences on the body and major chela (Table 3). The Caribbean-b morph of *A. paracrinitus* has a pair of dark dorsolateral spots on the third abdominal segment and a double band on the sixth abdominal segment. The major chela in both Caribbean morphs of *A. paracrinitus* has faint vertically oriented patches, while in the Pacific morph the chela is darkly pigmented ventrally. *Alpheus rostratus* most resembles the Caribbean-b morph of *A. paracrinitus*, with a similar pair of spots on the third abdominal segment, but in *A. rostratus* a wide sixth abdominal band is never completely split into a double band, and the vertical bands on the major chela are much darker.

In color (Table 3), the four taxa differ somewhat in the percentage of individuals with red, blue, and iridescent yellow chromatophores on the major chela. The most common pigments of the red chromatophores on the body and the red and iridescent yellow chromatophores on the major chela are also distinct.

Alpheus canalis-a/A. canalis-b/A. nuttingi.—The two morphs of *A. canalis* can be unambiguously distinguished by the color of the distal half of the antennae and the pattern of the major chela (Table 4). *Alpheus canalis*-a has orange antennae, a light patch and widely spaced spots on the major chela, and no dark abdominal spots. *Alpheus canalis*-b has blue antennae and closely spaced spots without a light patch on the major chela. This species also usually has two dorso-lateral dark spots on the third abdominal somite and a single midline spot on the fourth and fifth somites. *Alpheus nuttingi* most resembles *A. canalis*-b, with blue antennae and closely spaced spots on the chela, but it lacks the abdominal spots, and the chela sometimes bears a light patch. These two species additionally differ in the ratio of dark background to light spots on the body.

There is also some divergence in color apart from the diagnostic differences shown in the antennae (Table 4). Differences include the percentage of individuals with blue body pigments, the shade of blue when present in the antennae, and the dominant shade of blue, red, and iridescent yellow body pigments.

TABLE 2. Pattern and color differences between Pacific and Caribbean representatives of *A. cristulifrons*. All listed pigments except blue on antennae and yellow and orange on the second pereiopods are clearly associated with chromatophores.

Character	Pacific (n = 10)	Caribbean (n = 10)
Diagnostic pattern differences		
Antennae	banded	unbanded
Abdominal bands	narrow	wide
Abdominal band spots	large, clear	small, fuzzy
Major chela	mottled	spotted
Percentage of individuals bearing various classes of diffuse pigments		
Body		
Iridescent green	80%	30%
Major chela		
Blue	30%	80%
Iridescent yellow	20%	90%
Antennae		
Red	100%	30%
Iridescent yellow	100%	20%
Blue	100%	0%
Frequency of occurrence[a] of most common colors		
Body red		
10 R 3/10	70%	0%
10 R 4/10	0%	60%
Body blue		
2.5 B 2/2	40%	100%
2.5 B 2/6	60%	0%
Major chela red		
10 R 3/10	75%	0%
10 R 4/10	0%	75%
2nd pereiopod yellow/orange		
2.5 Y 8/10	56%	0%
5 YR 7/10	0%	22%
7.5 YR 6/10	0%	22%

[a]Percentages calculated for individuals having pigments in a given class. Colors listed are the most common colors exhibited by each taxon; alphanumeric codes are those used to identify individual colors in the International Munsell Color System.

DISCUSSION

The morphs delineated above differ in color and color pattern. In general, pattern seems to discriminate better than color alone. Several unambiguous pattern differences with no intermediates separated all the morphs, while most color differences were less clear-cut (differing percentages of individuals exhibiting particular colors, and different modal pigments within color classes). Chace

TABLE 3. Pattern and color differences among *A. rostratus*, *A. paracrinitus* Pacific, *A. paracrinitus* Caribbean-a, and *A. paracrinitus* Caribbean-b. All pigments are within chromatophores.

Character	*rostratus* Pacific (n = 10)	*paracrinitus* Pacific (n = 18)	*paracrinitus* Carib.-a (n = 10)	*paracrinitus* Carib.-b (n = 10)
Diganostic pattern differences				
Abdominal spots	present	absent	absent	present
6th abdominal band	wide	narrow	narrow	double
Major chela bands	vertical	ventral	vertical	vertical
Percentage of individuals bearing various classes of pigments				
Major chela				
Red	50%	67%	90%	100%
Iridescent yellow	10%	67%	100%	60%
Blue	30%	6%	38%	50%
Frequency of occurrence[a] of most common colors				
Body red				
5 R 3/10	0%	0%	30%	40%
10 R 3/10	20%	11%	30%	0%
10 R 4/10	80%	72%	20%	0%
Major chela red				
5 R 3/10	0%	0%	11%	40%
10 R 3/10	40%	17%	22%	0%
10 R 4/10	60%	75%	33%	0%
Major chela iridescent yellow				
2.5 Y 8/8	0%	67%	0%	50%
2.5 Y 8/10	10%	11%	40%	0%
2.5 Y 8/12	0%	0%	30%	50%

[a]Percentages calculated for individuals having pigments in a given class. Colors listed are the most common colors exhibited by each taxon; alphanumeric codes are those used to identify individual colors in the International Munsell Color System.

and Hobbs (1969) and Bruce (1978) also found pattern to be a better discriminator than color in the shrimp they studied. This is convenient, because pattern differences can be illustrated and are sometimes recognizable in recently preserved material.

The complete absence of intermediate patterns suggests to us that these morphs are separate species. This was confirmed for *Alpheus* symbionts of anemones previously studied (Knowlton and Keller 1983, 1985); the four species initially recognized by color pattern differences are incapable of interbreeding (Knowlton and Keller 1983, 1985) and also have fixed electrophoretic differences (Knowlton and Weigt, unpublished data). Similarly, mating experiments and protein electrophoresis also indicate specific distinctiveness for all taxa presented here. Nei's genetic distances for comparisons of morphs or species within groups ranged from 0.028 to 0.389, and fixed allele differences were discovered in all sympatric comparisons and all but two trans-isthmian comparisons (Knowlton and Weigt, unpublished data). Similarly, 60% of intraspecific pairs produced developing eggs in the laboratory after one month, compared to only 1% (i.e., one pair) for pairings between morphs or species within a group (Knowlton and Solórzano, unpublished data). We are currently in the process of examining type material and formally describing or resurrecting the new species. Other eastern Pacific taxa whose type localities lie outside the region are logical candidates for reexamination.

The genus *Alpheus* currently has approximately 220–250 described species (Kim and Abele 1988, Chace 1988), making it the most speciose genus of shrimp (Chace, pers. comm.). These and earlier results for the anemone symbionts (overall, two color morphs on average per morphologically defined species) suggest a true world-wide diversity of *Alpheus* closer to 500 species. Given that we confined ourselves in this study to morphologically well-defined taxa from Panama, the number of species in the genus may reach as high as 1000.

How should such daunting diversity be handled? We would like to emphasize that our concentration on color data does not imply that skeletal characters are irrelevant. Indeed, we believe that most sibling species uncovered by means of color patterns can be distinguished morphologically as well. To do so *a priori*, however, requires numerous carefully made measurements, often followed by multivariate statistical analyses. While feasible, this represents an enormous amount of work (e.g., Wicksten 1990), particularly in light of the number of taxa involved in this genus. In contrast, some aspects of color and particularly color pattern appear to be consistent within species and good discriminators between species. Whatever the biological reason behind this, the message for systematists is clear. In a few hours or days working with living material, it is often possible to erect provisional groupings which would require weeks or months of study based on preserved material alone. The specific distinctiveness of these groupings can be rapidly confirmed with mating experiments or protein electrophoresis. Previously unnoticed diagnostic morphological differences may also be found.

Several final caveats are appropriate. First, color pattern differences do not necessarily indicate the presence of undescribed species (e.g., see Bauer, 1981). As with morphological characters, variability exists, and which color characters are taxonomically useful must be empirically determined for each group. In particular, we have found that juveniles and adults often have somewhat different patterns (e.g., Table 1; Knowlton and Keller 1985), so that comparisons of similarly sized individuals are essential to rule out developmentally based differences. Since the reliability of color characters, though well supported to date, still remains relatively untested, other methods (e.g., protein electrophoresis, mating

TABLE 4. Pattern and color differences among *A. canalis*-a, *A. canalis*-b, and *A. nuttingi*. All pigments except those for antennae are within chromatophores.

Character	*A. canalis*-a Pacific ($n = 10$)	*A. canalis*-b Pacific ($n = 10$)	*A. nuttingi* Caribbean ($n = 10$)
Diagnostic pattern differences			
Chela patch	present	absent	variable
Chela spot spacing	wide	narrow	narrow
Abdominal spots	absent	present	absent
Body background:spot	intermediate	large	small
Percentage of individuals bearing various classes of pigments			
Antennae (distal)			
Blue	0%	100%	100%
Orange	100%	0%	0%
Body			
Blue	70%	50%	100%
Frequency of occurrence[a] of most common colors			
Antennae blue			
5 B 6/2	—	20%	0%
2.5 BG 8/4	—	0%	30%
7.5 BG 5/2	—	20%	20%
7.5 BG 7/2	—	20%	20%
Body red			
10 R 3/10	50%	40%	20%
10 R 4/10	30%	0%	50%
Body blue			
2.5 B 2/2	29%	100%	50%
Body iridescent yellow			
2.5 Y 8/8	43%	89%	88%

[a]Percentages calculated for individuals having pigments in a given class. Colors listed are the most common colors exhibited by each taxon; alphanumeric codes are those used to identify individual colors in the International Munsell Color System.

experiments) should be used to confirm specific distinctiveness. Second, every effort should be made to identify morphological characters that in retrospect correlate well with newly recognized species boundaries. These differences are essential for identifying most previously collected specimens (including extensive museum holdings), since color is lost from all but the freshest preserved material. Moreover, determination of diagnostic morphological characters will indicate which morphological differences are most informative in closely related species for which living material is not available. Finally, although provisional taxonomic groupings based on color and color pattern can be made relatively quickly, recording the color data in detail sufficient to permit comparisons with subsequently collected living material takes time. Most descriptions of color pattern in the literature are not adequate for making the kinds of subtle discriminations outlined above. Color standards should be used to characterize pigments, and detailed notes on pattern, together with photographs, are essential. Closely related taxa should be compared side by side if possible. Ideally, in species descriptions, color pattern should receive the same level of attention as skeletal characters, in both verbal diagnoses and figures. When available, color photographs may be published or, less expensively, deposited with type material. However, attention to color and color pattern should not come at the expense of conventional morphological descriptions and illustrations.

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