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# CRYPTIC AND SIBLING SPECIES AMONG THE DECAPOD CRUSTACEA

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ABSTRACT

Cryptic species are those which are difficult to recognize using traditional systematic methods. Among the decapod Crustacea, there are probably many unrecognized complexes of cryptic species because of dependence on preserved material. Electrophoretic and mating studies have been very useful in determining whether individuals that differ in ecology, behavior, life history, or color can potentially interbreed. Color pattern of living specimens is a particularly useful character, since it is easy to assess and appears to differentiate morphologically similar species in a number of decapod groups. Examples include species of *Uca* and various symbionts of coral reef organisms (e.g., in the genera *Trapezia* and *Alpheus* and the subfamily Pontoniinae). Although nonmorphological characters cannot be scored in most museum specimens, statistical analysis of morphometric data first collected for individuals of known identity can subsequently be used to identify preserved material. Electrophoretic analyses, such as those done for species complexes of *Uca, Trapezia,* and *Alpheus,* have also shown that cryptic species pairs may or may not be more closely related to each other than morphologically distinct congeners. For this reason the term "sibling" should be reserved for those species which have been shown to be very closely related using biochemical techniques. Various speciation patterns, including possible examples of host race speciation and speciation facilitated by sexual selection, occur within decapod species complexes.

## THE PROBLEM OF CRYPTIC SPECIES

Decapod crustaceans, like most species, are primarily described and identified by morphological characters which can be studied in preserved specimens (McLaughlin *et al.,* 1982). Although this procedure effectively delineates many species, clusters of morphologically similar but reproductively isolated taxa cannot easily be resolved using such techniques. These problematic taxa are variously called cryptic or sibling species.

The term "sibling species" has traditionally been used for sets of species which are difficult to distinguish using traditional morphological characters (Mayr, 1963). "Cryptic" when used taxonomically (as opposed to ecologically) is another frequently used term for the same concept. The latter is etymologically preferable (Henry, 1985), since "sibling" implies a particularly close relationship, a feature which Mayr (1963) asserted did not differentiate sibling from other congeneric species. More recent studies have shown, however, that species which are difficult to tell apart morphologically may or may not be as distantly related to each other, on the basis of biochemical characters, as are morphologically distinct congeners (Ayala, 1975; Henry, 1985). For this reason, I will refer to all morphologically similar species as cryptic species, unless biochemical data exist to indicate that they are in fact siblings as well.

Numerous nonmorphological characters have been used to distinguish cryptic species, depending on the group involved (Mayr, 1963). They include karyology, hybridization experiments to detect postzygotic incompatibility, distribution patterns, resource use, breeding season, life history and development, mating behavior (including visual, acoustical, and chemical signals), color pattern, and various biochemical characters (especially soluble proteins studied by gel electrophoresis). Those which directly assess either the presence of hybrids (e.g., allozyme or chromosome studies) or the potential for hybridization (e.g., mating experi-

ments) are of greatest value in the context of the biological species concept, and are often used to confirm suspected cryptic species based on ecological or life historical differences. In many cases minor morphological differences, sometimes reliably diagnostic ones, are later found which can be used to identify previously collected specimens.

In some taxa, the importance of characters not evident in preserved specimens has been recognized or suspected for some time. Examples include song-defined species of crickets (Alexander, 1962) and anurans (Blair, 1962), chromosomally defined species of *Drosophila* (Ayala, 1975) and rodents (Patton and Sherwood, 1983), and species of cichlid fishes distinguished only by color (McKaye *et al.*, 1984).

Many groups, however, including decapod crustaceans, have not been much studied in this way. In a computer search (BIOSIS) from 1981 to October 1985 of articles using the terms "cryptic species" or "sibling species" in their titles or abstracts, I found 161 articles on noncrustacean arthropods (mostly insects and one-third *Drosophila*), 29 on invertebrates other than arthropods (especially mollusks and annelids), 12 on fishes, 9 on amphibians, 4 on reptiles, 9 on birds, and 12 on mammals. Crustacean studies numbered 18, but of these only 4 concerned decapods. Given the relative scarcity of such studies, albeit underestimated by this type of computer search, it is difficult to know how important the phenomenon of cryptic species might be.

Those studies which exist reveal the potential importance of nonmorphological characters, however. Lucas (1970), for example, studied the breeding biology of two *Halicarcinus lacustris*-like forms which differed in the type of larvae produced and in geographic distribution. He found evidence for hybrid inviability and higher levels of aggression during mating attempts between forms, and on this basis described a new "sibling" species, even though morphological differences were minor and largely confined to mature females.

In the fiddler crab *Uca,* wave displays have long been recognized as species specific characters, and yet have often been ignored in systematic study when morphological differences were not apparent (Salmon *et al.*, 1979). Salmon and coworkers studied *U. speciosa* and *U. spinicarpa,* two previously synonymized forms which differ in size and color, and found clear-cut differences in visual and auditory displays. Electrophoretic differences confirmed the validity of their separate status. Two other morphologically similar species, *U. panacea* and *U. pugilator,* differ electrophoretically, in visual and auditory displays, and in color, and show evidence of hybrid incompatibility (Salmon *et al.*, 1978). Recent work on *U. mordax* and *U. burgersi,* a pair of cryptic species with very similar morphologies and wave displays, has also revealed significant differences in vibration signals (von Hagen, 1984), wave display, color, distribution, and allozymes (von Hagen, 1983). A similar situation exists in another ocypodid crab, *Macrophthalmus japonicus.* The two "forms" (which apparently should be described as separate species) differ in wave display, morphology, color, and habitat (Wada, 1978) and do not interbreed (Wada, 1984).

## The Importance of Color

In the studies of ocypodid crabs cited above, the cryptic species could be readily distinguished by color. Color is typically ignored in systematic study of decapod crustaceans, however, not only because it is quickly lost after preservation, but also because in certain instances it is known to vary within species (e.g., Chassard-Bouchaud, 1965). Yet the usefulness of color pattern in recognizing species is also

indicated by studies of various symbiotic, tropical decapods. In a list of eleven "sibling" pairs of shrimps in the subfamily Pontoniinae, Bruce (1978) noted that nine have different color patterns. For example, *Periclimenes inornatus* is described as completely transparent, while *P. ornatus* is described as having blue and white dots with red striae. These two species have no obvious morphological differences.

The color differences noted by Bruce are typically rather striking, and his confidence in defining species based on color pattern is often enhanced by differences in host as well. In the above example, *P. inornatus* is associated with anemones in the genus *Radianthus,* while *P. ornatus* lives with species of *Parasicyonis.* Four of the other eight cryptic pairs that differ in color also show no overlap or only partial overlap in host utilization.

My own work on alpheid symbionts of Caribbean sea anemones indicates, however, that differences in color patterns of cryptic species are not always striking, and that complexes of such very similar cryptic species may even share the same host. What was originally thought to be a single species of *Alpheus* living with *Bartholomea annulata* is now known to be three (in addition to a fourth species associated with *Heteractis lucida*) (Knowlton and Keller, 1983, 1985). The overall red and white color pattern is very similar in each; they differ mainly in the presence and pattern of inconspicuous green spots (Knowlton and Keller, 1985). Despite the minor nature of the differences, mating experiments indicate that males and females of different color patterns invariably behave aggressively towards each other and will not form pairs, confirming the absence of potential interbreeding and thus their specific status. Although minor morphological differences exist in such characters as the shape of the rostrum, the size of the postrostral tooth, and the shape and size of the uropodal spines in males, their importance is obvious only in retrospect, since there is partial overlap and no striking bimodality in most comparisons between species. Indeed, recognition of the significance of even the color pattern differences would have been much more difficult were the species not typically found in breeding pairs. Moreover, despite the effort to document differences in this species complex, the cues used by the shrimps themselves to distinguish conspecifics from heterospecifics have probably not been pinpointed; shrimp appear to react differentially to other individuals only after the touching of antennae (Knowlton and Keller, 1982; personal observation), implicating the importance of contact chemicals.

Bruce stressed the systematic importance of color pattern in his studies of pontoniine shrimps (Bruce, 1975, 1978), and stated that "shade and intensity of colour may vary from locality to locality, but the pattern is highly consistent" (1978). Yet because of the traditional strength of morphological characters in defining species, he did not accord specific status to forms differing only in color. Thus in describing the new species *Periclimines pilipes* (Bruce and Zmarzly, 1983), he included four strikingly different color forms, even though all heterosexual pairs observed were matched in color pattern. Similarly, the alpha and beta forms of *Coralliocaris venusta* were not given specific status (Bruce, 1978), despite their distinctive color patterns and their assortative mating in the field. In neither case are there clearly defined differences in morphology or host. Yet given the documented consistency of color pattern within a species in pontoniine shrimp and the field evidence for assortative mating, it is likely that behavioral or electrophoretic investigations will reveal the absence of potential for interbreeding.

Differences in color also provide the easiest means to separate the species of *Trapezia.* These crabs are symbionts of pocilloporid corals in the Pacific whose tendency to live in male-female pairs of like color has been recognized for some

time (Patton, 1966). Yet because of their morphological similarity, their specific status has been debated (see Huber, 1985b). Huber found, however, clear electrophoretic differences including diagnostic loci between the color forms, confirming their separate species status on the basis of color. Allometric differences have been documented as well (Huber, 1985a).

## Cryptic versus Sibling Species

Huber's (1985b) work is important in that it also provides the data necessary to determine whether the cryptic species of *Trapezia* are in fact siblings. In this case Nei genetic identity values ranged between 0.56 and 0.86 with a mean of 0.70; 86% of the 28 pair-wise comparisons had values of less than 0.80. The three Panamanian species, only recently reseparated on the basis of minor color differences (Castro, 1982), had pair-wise identities of 0.66, 0.73, and 0.80. To put this in perspective, Thorpe (1982) stated that 95% of reported congeneric identities have been less than 0.80. Hedgecock *et al.* (1982) listed interspecific identity values for 28 decapod crustaceans between 0.36 and 0.92 with a mean of 0.66; 79% fell below 0.80. Thus, Huber's results suggest that many of the relationships among the cryptic species of *Trapezia* are not extraordinarly close (although none are very distant). Instead, crypticity is a function of failure to use the right characters, in this case, especially color. *Uca speciosa* and *U. spinicarpa* are another cryptic but nonsibling pair of species (I = 0.5) (Salmon *et al.*, 1979). This pattern is probably quite common.

There may, however, be sibling species relationships between some taxa in Huber's (1985b) study which are not currently given specific status. Populations of *Trapezia ferruginea* and *T. formosa* at Enewetak had genetic identities with their respective conspecifics at other localities of only 0.84. In contrast, Huber's other comparisons of geographically isolated, conspecific populations yielded identity values exceeding 0.99, and more generally, 98% of conspecific comparisons have genetic identity values exceeding 0.85 (Thorpe, 1982). This suggests the possibility of allopatric species within these two taxa. *Trapezia digitalis* also has an unusual population structure. There were higher levels of heterozygosity, a statistically significant excess of homozygotes, and a tendency for assortative mating between color pattern variants in the laboratory (but not in the field) (Huber, 1983, 1985b).

Other true siblings among decapod cryptic species have been found in the complex of *Panopeus herbstii* (Turner and Lyerla, 1980; Williams, 1983) and in the four species of *Alpheus* symbiotic with Caribbean sea anemones. In the latter case, work in progress (Knowlton and Bert, unpublished) has revealed very high genetic identities (on the order of 0.9) which are much closer within the sibling group than with other alpheid species. The American and European lobsters *Homarus americanus* and *H. gammarus* are an example of the more unusual situation of genetically closely related species (genetic identity = 0.9) which are morphologically quite distinctive (Hedgecock *et al.*, 1977).

## Mechanisms of Speciation

The mechanisms of speciation that might be responsible for generating these cryptic complexes are potentially varied. Bert (1985, in press), for example, has documented two genetically distinct taxa within *Menippe mercenaria* (western Gulf and peninsular Florida forms) which are distinguished by fixed or nearly fixed differences at 16% of 40 loci examined and by color. The two forms hybridize in northwest Florida, but there are deficits of certain heterozygotes, indicating

partial reproductive isolation (i.e., semispecies). Bert suggested that divergence took place when eastern and western populations were divided by range constriction and changes in current patterns during the Miocene-Pliocene glaciation. There are undoubtably many examples of speciation through divergence following geographic isolation (Mayr, 1963), although the nature of the geographic barrier will often remain unspecified.

There is increasing evidence, however, for the role of other, less traditional mechanisms in the generation of these cryptic and sibling species complexes. For example, the cryptic pontoniine species listed by Bruce (1978) which show differences in host use may have formed through what Bush (1975) calls host race speciation. This can be thought of as a finer grained form of gene pool division (Templeton, 1981); speciation occurs because individuals preferring different hosts do not interbreed, allowing divergence to take place.

West-Eberhard (1983) identified the sexually selected species of *Uca* as an example of the pattern of prolific speciation discussed by her and also by Lande (1981). They suggested that sexual selection facilitates speciation because in isolated populations, random changes in female mating preferences will initiate a process of runaway selection leading to novel secondary sexual characteristics in males which will serve as barriers to interbreeding with other populations.

Finally, Huber (1983) has suggested the possibility of sympatric speciation in crabs of the genus *Trapezia,* based on Rosenzweig's (1978) model of competitive speciation, as a partial explanation for the co-occurrence of several species using the same hosts and differing only or mainly in color. Individuals possessing unusual color patterns are assumed to have an ecological advantage because they will not be evicted from coral occupied by crabs of different color types. Assortative mating based on color, leading to speciation, is also favored because the offspring will then share the same advantage. This scenario, as Huber recognized, makes a number of assumptions about the biology of *Trapezia.* In addition, the theoretical constraints on this type of model are considerable (see Templeton's (1981) discussion of habitat divergence). Yet at least some of the biological assumptions seem reasonable, and the ecology of the species is not incompatible with the theoretically required conditions.

The examples above illustrate the diversity of the potential mechanisms which could generate the species complexes discovered to date. As in other taxa (Futuyma and Mayer, 1980) we still lack most of the information necessary to determine the validity of the suggested speciation modes in these groups. But the behavioral complexity of decapod crustaceans (e.g., the varied types of cues used in mate recognition) makes them promising subjects for this kind of analysis.

## Some Practical Considerations

Given the potential importance of undiscovered cryptic species complexes in the decapod Crustacea, what can be done to facilitate their detection? The studies reviewed above suggest several methods which currently could be used with only a modest increase in effort and expense. Of these, the most readily applied and still often underemphasized would be simply to give more weight to color pattern of living individuals in systematic descriptions and identification keys. The potential importance of this approach is indicated by the fact that almost all the cryptic species mentioned above can be so distinguished. Although color photographs will often be too expensive to publish, they could be sent to museums with type material for reference. Hues could be matched to internationally recognized color standards (e.g., Munsell, 1929) and the results provided in systematic

works. Since pattern rather than exact shade is in many cases the critical component, detailed descriptions and line drawings comparable to those used for hard parts (e.g., Bruce and Zmarzly, 1983) would be extremely valuable. At the very least such information will allow other investigators to determine whether the forms they are examining are different from those previously described. For species that can be readily collected alive, studies of breeding behavior and success (e.g., Lucas, 1970; Salmon *et al.,* 1978; Knowlton and Keller, 1985) and electrophoretic analysis of proteins (e.g., Salmon *et al.,* 1979; Huber, 1985b; reviews by Hedgecock *et al.,* 1982; McLaughlin *et al.,* 1982) should be attempted when other information (e.g., color, behavior, life history, larval development, ecology, or minor morphological differences) leads one to suspect the existence of cryptic species.

As these types of studies become more common, it will be increasingly easy to assess the relative importance of nonmorphological characters for various groups of decapod crustaceans. This will, of course, be of no help in sorting out previously collected material. For this reason, efforts to find diagnostic morphological characters must still be continued in those groups where species are more readily identified by other means. Sophisticated statistical techniques (e.g., discriminant function analysis) can define suites of morphological characters useful in discriminating individuals of known identity; the same methods can then be used with the more difficult preserved specimens (see Sneath and Sokal, 1973; McLaughlin *et al.,* 1982).

## Conclusion

The problem of cryptic and sibling species is not an insuperable one. Yet should we spend valuable time and resources subdividing morphologically defined species when there is still so much work to do both in the description of species which are distinctive morphologically and in sorting out relationships within higher taxa? There are several reasons why this kind of systematic study merits more attention. First, all biological investigations, be they behavioral, ecological, or physiological, depend on accurate identifications of species for their validity. Particularly with abundant species, which are most likely to be the subject of such studies, identification of cryptic species is essential to avoid misinterpretation. My earlier documentation of patterns of sexual dimorphism in *Alpheus armatus* (Knowlton, 1980), for example, could now be interpreted rather differently with the knowledge that more than one species was involved. Second, many complexes of sibling species hold great promise for testing current evolutionary theories in ecology and behavioral biology. One of the biggest problems with the comparative method, as it is typically used in such studies, is that the species differ in so many ways that it is difficult to sort out the factors responsible for the pattern being investigated. Sibling species facilitate comparative studies, because so few differences exist between them; one approaches, in essence, the kind of controlled situation characteristic of experimental research (see also Felsenstein, 1985). Third, I would argue that our entire conception of biological diversity, biogeography, and population genetics is dependent on knowing how many species there are in a group and where they are found. There is an enormous difference, for example, in terms of evolutionary potential between a circumtropical species and a complex of many more geographically limited ones. Finally, information of this type adds to our understanding of the process of speciation. What are the relative importances of the different modes of speciation? In which groups is speciation a fundamentally difficult or easy process, and why? These are evolutionary questions of long standing and general interest to which studies of decapod crustaceans can contribute.

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## Literature Cited

Alexander, R. D. 1962. The role of behavioral study in cricket classification.—Systematic Zoology 11: 53–72.

Ayala, F. J. 1975. Genetic differentiation during the speciation process.—Evolutionary Biology 8: 1–78.

Bert, T. M. 1985. Geographic variation, population biology, and hybridization in *Menippe mercenaria* and evolution in the genus *Menippe* in the southwestern north Atlantic Ocean.—Ph.D. Thesis, Yale University, New Haven, Connecticut.

———. (In press.) Speciation in stone crabs: geological processes and climatic events shape species distributions.—Marine Biology.

Blair, W. F. 1962. Non-morphological data in anuran classification.—Systematic Zoology 11: 72–84.

Bruce, A. J. 1975. Coral reef shrimps and their colour patterns.—Endeavor 34: 23–27.

———. 1978. The evolution and zoogeography of shallow-water tropical shrimps.—Information Series, Department of Scientific and Industrial Research, New Zealand 137: 337–355.

———, and D. L. Zmarzly. 1983. *Periclimenes pilipes*, new species, a crinoid associate from Enewetak Atoll, Marshall Islands (Crustacea: Decapoda: Pontoniinae).—Journal of Crustacean Biology 3: 644–654.

Bush, G. L. 1975. Modes of animal speciation.—Annual Review of Ecology and Systematics 6: 339–364.

Castro, P. 1982. Notes on symbiotic decapod crustaceans from Gorgona Island, Colombia, with a revision of the eastern Pacific species of *Trapezia* (Brachyura, Xanthidae), symbionts of scleractinian corals.—Anales del Instituto de Investigaciones Marinas de Punta de Bétin 12: 9–17.

Chassard-Bouchaud, C. 1965. L'adaptation chromatique chez les Natantia (crustacés décapodes).—Cahiers de Biologie Marine 6: 469–576.

Felsenstein, J. 1985. Phylogenies and the comparative method.—American Naturalist 125: 1–15.

Futuyma, D. J., and G. C. Mayer. 1980. Non-allopatric speciation in animals.—Systematic Zoology 29: 254–271.

Hedgecock, D., K. Nelson, J. Simons, and R. Shleser. 1977. Genic similarity of American and European species of the lobster *Homarus*.—Biological Bulletin 152: 41–50.

———, M. L. Tracey, and K. Nelson. 1982. Genetics.—*In:* L. G. Abele, ed., The biology of Crustacea, Vol. 2. Pp. 283–403. Academic Press, New York.

Henry, C. S. 1985. Sibling species, call differences, and speciation in green lacewings (Neuroptera: Chrysopidae: *Chrysoperla*).—Evolution 39: 965–984.

Huber, M. E. 1983. Ethology and population biology of *Trapezia*, a xanthid crab symbiotic with reef corals, with special reference to territoriality and speciation.—Ph.D. Thesis, University of California, San Diego, California.

———. 1985a. Allometric growths of the carapace of *Trapezia* (Brachyura, Xanthidae).—Journal of Crustacean Biology 5: 79–83.

———. 1985b. Population genetics of eight species of *Trapezia* (Brachyura: Xanthidae), symbionts of corals.—Marine Biology 85: 23–36.

Knowlton, N. 1980. Sexual selection and dimorphism in two demes of a symbiotic, pair-bonding snapping shrimp.—Evolution 34: 161–173.

———, and B. D. Keller. 1982. Symmetric fights as a measure of escalation potential in a symbiotic, territorial snapping shrimp.—Behavioral Ecology and Sociobiology 10: 289–292.

———, and ———. 1983. A new, sibling species of snapping shrimp associated with the Caribbean sea anemone *Bartholomea annulata*.—Bulletin of Marine Science 33: 353–362.

———, and ———. 1985. Two more sibling species of alpheid shrimps associated with the Caribbean sea anemones *Bartholomea annulata* and *Heteractis lucida*.—Bulletin of Marine Science 37: 893–904.

Lande, R. 1981. Models of speciation by sexual selection on polygenic traits.—Proceedings of the National Academy of Sciences 78: 3721–3725.

Lucas, J. S. 1970. Breeding experiments to distinguish two sibling species of *Halicarcinus* (Crustacea, Brachyura).—Journal of Zoology 160: 267–278.

Mayr, E. 1963. Animal species and evolution.—Harvard University Press, Cambridge. Pp. 1–797.
McKaye, K. R., T. Kocher, P. Reinthal, R. Harrison, and I. Kornfield. 1984. Genetic evidence for allopatric and sympatric differentiation among color morphs of a Lake Malawi cichlid fish.—Evolution 38: 215–219.
McLaughlin, P. A., G. T. Taylor, and M. L. Tracey. 1982. Systematic methods in research.—*In:* L. G. Abele, ed., The biology of Crustacea, Vol. 1. Pp. 29–63. Academic Press, New York.
Munsell, A. H. 1929. A color notation.—Firbin, Baltimore. Pp. 1–74.
Patton, J. L., and S. W. Sherwood. 1983. Chromosome evolution and speciation in rodents.—Annual Review of Ecology and Systematics 14: 139–158.
Patton, W. K. 1966. Decapod Crustacea commensal with Queensland branching corals.—Crustaceana 10: 271–295.
Rosenzweig, M. L. 1978. Competitive speciation.—Biological Journal of the Linnaean Society 10: 275–289.
Salmon, M., G. Hyatt, K. McCarthy, and J. D. Costlow, Jr. 1978. Display specificity and reproductive isolation in the fiddler crabs, *Uca panacea* and *U. pugilator.*—Zeitschrift für Tierpsychologie 48: 251–276.
———, S. D. Ferris, D. Johnston, G. Hyatt, and G. S. Whitt. 1979. Behavioral and biochemical evidence for species distinctiveness in the fiddler crabs, *Uca speciosa* and *U. spinicarpa.*—Evolution 33: 182–191.
Sneath, P. H. A., and R. R. Sokal. 1973. Numerical taxonomy.—W. H. Freeman, San Francisco. Pp. 1–573.
Templeton, A. R. 1981. Mechanisms of speciation–a population genetic approach.—Annual Review of Ecology and Systematics 12: 23–48.
Thorpe, J. P. 1982. The molecular clock hypothesis: biochemical evolution, genetic differentiation and systematics.—Annual Review of Ecology and Systematics 13: 139–168.
Turner, K., and T. A. Lyerla. 1980. Electrophoretic variation in sympatric mud crabs from North Inlet, South Carolina.—Biological Bulletin 159: 418–427.
von Hagen, H.-O. 1983. Visual and acoustic display in *Uca mordax* and *U. burgersi,* sibling species of neotropical fiddler crabs. I. Waving display.—Behaviour 83: 229–250.
———. 1984. Visual and acoustic display in *Uca mordax* and *U. burgersi,* sibling species of neotropical fiddler crabs. II. Vibration signals.—Behaviour 91: 204–228.
Wada, K. 1978. Two forms of *Macrophthalmus japonicus* de Haan (Crustacea: Brachyura).—Publications of the Seto Marine Biological Laboratory 24: 327–340.
———. 1984. Pair formation in the two forms of *Macrophthalmus japonicus* de Haan (Crustacea: Brachyura) at a co-occurring area.—Journal of Ethology 2: 7–10.
West-Eberhard, M. J. 1983. Sexual selection, social competition, and speciation.—Quarterly Review of Biology 58: 155–183.
Williams, A. B. 1983. The mud crab, *Panopeus herbstii,* s. l. Partition into six species (Decapoda: Xanthidae).—Fishery Bulletin, United States 81: 863–882.

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