
A COPEPODOLOGIST'S THOUGHTS ABOUT
PUNCTUATED EQUILIBRIA

BY

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An hypothesized evolutionary mechanism, punctuated equilibria, encompassing the concept of allopatric speciation, has been proposed by Eldredge & Gould (1972, see also Gould & Eldredge, 1977). This hypothesis identifies evolutionary change as speciation occurring during brief episodes between

Crustaceana 47 (2) 1984, E. J. Brill, Leiden

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long, evolutionarily static periods. Critical discussion of punctuated equilibria often focuses on its episodic aspect with attendant problems about the extent of phenotypic or genotypic change, and the time scale to be considered. A mechanism in which long periods of stasis are interrupted by brief episodes of speciation precludes significant evolutionary development of a species during its history. It is this static aspect of punctuated equilibria that seems most suspect. The problem is exemplified by the origin and development of a discrete phenotype within populations of *Cryptopecten vesiculosus* (Hayami, 1973). This event is dismissed, perhaps tautologically, by Gould & Eldredge (1977) because "The change has nothing to do with speciation; ---". It seems that punctuated equilibria must either reject the evolutionary significance of non-speciation events, including most genetic polymorphisms discussed for example by Ford (1975), or link the origin of these events to episodic speciation. If discrete, non-speciation events can be identified and judged significant to the evolution of a species, one challenge of punctuated equilibria clearly will be joined. Two simple phenomena from the biology of calanoid copepods further serve in illustration.

Speciation in marine calanoid copepods today is understood within the general speciation framework outlined by Mayr (1963), and articulated most clearly for calanoids by Fleminger (1975) and Fleminger & Hulsemann (1974, 1977). Populations of a species become geographically isolated through physiographic or hydrographic mechanisms. Subsequent biological isolation proceeds through the development of effective and efficient differences in reproduction among these populations, specifically mediated by accurate and precise mating behavior. Hybridization between subsequent sibling species is thus prevented.

The foundation for this concept from calanoid systematics dates from Steuer (1923), who suggested a morphological and biogeographical basis. Virtually similar and allopatric calanoids are assumed to have speciated recently. These groups often differ in the morphology of structures utilized in mating behavior (Blades & Youngbluth, 1980). Slight morphological differences in these secondary sex characters have been considered conclusive in separating species. The differences are believed to represent the morphological manifestation of efficient mating differences.

Precise and accurate spermatophore placement by males on females is generally understood to be one in a series of such differences, or mating barriers, ensuring reproductive isolation in calanoid copepods. Males of *Euchaeta norvegica* Boeck, 1872 exhibit an unusual, but not unique, behavior in their ability to place spermatophores, often in clusters, in one of three positions on the female's genital segment (Hopkins & Machin, 1977). Spermatophore placement then is precise but not accurate. The adaptive advantage of this behavior to the reproductive strategy of the animal is not completely understood. However, if speciation is mediated through the development of ac-

curate and precise mating barriers which ensure biological isolation in contemporary geographically isolated populations, a mechanism which includes inaccuracies of spermatophore placement during an episodic speciation event will be self-vitiating. Thus the origin of the behavior pattern permitting alternately-placed spermatophores could not occur during speciation.

The paradox can be resolved (Ferrari, 1978) by recognizing during mating a sequence of time ordered events, the barriers. Initially, no single barrier alone is prohibitive, but by functioning together in sequence, hybridization is excluded. Inaccuracies or imprecisions then may be introduced, subsequent to speciation, by preempting continued biological isolation in a restricted set of barriers from the initial sequence, and allowing inaccuracies or imprecisions with adaptive value in those barriers outside of the restricted set.

Calanoid copepods of the genus *Pleuromamma*, like all crustaceans, are basically bilaterally symmetrical animals comprised of a series of body segments, some of which bear serially homologous appendages. A few of these segments and appendages are, however, asymmetrical. As far as is known these are secondary sex characters. Their function is incompletely understood (Steuer, 1932), but homologous structures are used during mating behavior in related calanoids (Blades, 1977; Blades & Youngbluth, 1979, 1980; Hopkins et al., 1978). The positions of these asymmetrical characters, relative to one another, do not change. However, the alignment of the entire set of characters differs, in effect left or right, in animals of the same species. In several species incidences of left and right morphs are quite common. Efforts to separate left and right groups within a species into two cryptic species have failed on morphological grounds and because the frequency of morphs can differ markedly between sexes. Females of two species often exhibit left and right morphs while their males are virtually monomorphic. Ferrari (1984) suggested that species in the genus *Pleuromamma* exhibit the population phenomenon of dimorphic asymmetry. Dimorphic asymmetry has also been identified in *Clausocalanus furcatus* (Frost & Fleminger, 1968), another calanoid. That the origin of dimorphic asymmetry was an abrupt event, occurring within a generation, can be argued since the binary set of phenotypic outcomes (left or right) has always been exclusive and exhaustive. However, the origin of dimorphic asymmetry did not involve speciation.

As noted the origin of alternately-placed spermatophores and dimorphic asymmetry were not speciation phenomena. Whether they were significant phenomena in the evolutionary history of the animals is difficult to judge. I would argue they were significant to the biology of the animals since both altered a fundamental process, reproduction. And they were significant in another way. They affected primary and secondary sex characters. These are assumed to be important in the allopatric speciation of calanoids since their development and differentiation would mediate biological isolation among geographically isolate populations. The concept of allopatric speciation has

been incorporated, in a general way, in the punctuated equilibria hypothesis. Alternately-placed spermatophores represent a behavioral change and dimorphic asymmetry a morphological change along presumed pathways of alteration in future daughter species. Whether these phenomena can be considered exceptions which prove the rule of punctuated equilibria or which call the rule to question will depend on further survey and assessment of non-speciation evolutionary phenomena.

ACKNOWLEDGEMENTS

My thanks are offered to John Lundberg of Duke University, Carel von Vaupel Klein of the University of Leiden, and Porter Kier and Thomas Bowman of the Natural History Museum. While not in agreement with all conclusions drawn here, each provided thoughtful and helpful reviews of this manuscript.

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Received for publication 22 August 1983.

REVIEW

D. L. GREY, W. DALL & A. BAKER. A guide to the Australian Penaeid Prawns. 1983, Prawn Book Sales, Fisheries Division, Department of Primary Production, G.P.O. Box 4160, Darwin, Northern Territory 5794, Australia. 140 pp., 25 text-figs., 51 coloured plates. Price: A\$ 12.95 (in Australia), A\$ 14.95 (outside Australia, surface mail), A\$ 18.95 (air mail).

As the number of species of shrimps and prawns discovered to be of economic or potentially economic importance is steadily growing, the need for reliable guides for their identifications is more and more urgently felt. The above publication issued by the Northern Territory Government of Australia is a first class example of how such a guide should be produced. Of practically each of the 46 species dealt with, an excellent colour photograph is provided of a fresh specimen, furthermore a distribution map, a short account of the important morphological and colour characters, size, habitat and references; all this information is found on two facing pages, which makes consultation very easy. This treatment of the separate species is preceded by a general morphological account, with a glossary of the terms used, and a key to the species. The key is illustrated with simple line drawings of essential characters (like thelyca and petasmata) not shown on the colour photographs. Additional colour photographs show the variation in the colour of some of the species.

The excellent quality of both the illustrations and the text makes this guide a most useful tool for fishermen, amateur naturalists and scientists alike. Although its scope is restricted to N. Australia, the book will also be of interest in many other parts of the Indo-West Pacific area as several of the species have a wide range in that region.

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