

## MODES OF SPECIATION: MARINE INDO-WEST PACIFIC

*John C. Briggs*

### ABSTRACT

Within the Indo-West Pacific, the East Indies exhibits the greatest species richness in the marine world and may also be functioning as a center of evolutionary radiation. Both kinds of allopatric speciation, vicariance and dispersal, clearly take place. The parapatric mode of speciation occurs among planktonic organisms and along continuous shorelines. Judging from the biogeography of sibling species, sympatric (competitive) speciation is surprisingly common. It may occur in the majority of benthic invertebrates. Among the fishes, sibling patterns suggest that sympatric speciation is taking place in the East Indies and that newly formed species may be dispersing from that area. Studies of geographic patterns that are produced as the result of speciation can help elucidate the underlying evolutionary process.

*"The fossil record provides direct evidence that turnover rates have been higher in tropical settings than at high latitudes: the tropics are a cradle of species, genera, and even orders, and not simply a museum for biodiversity"* (Karl W. Flessa and David Jablonski. 1996. *The Geography of Evolutionary Turnovers*)

The world's greatest concentration of marine species occurs within a comparatively small triangle formed by the Philippines, the Malay Peninsula, and New Guinea. Almost every family of tropical organisms that occupies the continental shelf is represented by more species in this area than anywhere else in the world. Furthermore, considerable evidence supports the argument that the East Indies Triangle functions as a center of evolutionary radiation (Briggs, 1992). The apparently continuous production of dominant species suggests that it would be worthwhile to investigate the modes by which such species are produced.

The determination of the speciation modes that have led to the present level of diversity and phylogenetic attainment is dependent upon careful systematics together with accurate determination of biogeographic patterns. As Chesser and Zink (1994) have noted, the strongest evidence of geographic speciation mode should result from comparisons of sister species, which have undergone speciation more recently than other sister elements, and had relatively less time for dispersal to obscure the geographic pattern of speciation.

A commonly held view is that allopatric speciation is the only way (with rare exceptions) gene flow can be reduced to such a degree that conspecific populations might evolve reproductive barriers. This view has been developed and reinforced by prominent figures in evolutionary biology (Mayr, 1963; Futuyma and Mayer, 1980; Futuyma, 1986; Paterson, 1981). This view has been augmented by a group called vicariance advocates who advocate only one particular kind of allopatry. As a result, works that have attempted to demonstrate non-allopatric speciation have often been met with suspicion.

Recent investigations now show that other modes of speciation may be important in the East Indies and other parts of the marine environment. I will argue that allopatric, parapatric, and sympatric speciation are all detectable and that the latter could be of unprecedented importance. Within the allopatric mode, where speciating populations are separated by an extrinsic barrier, there are two types: (1) vicariance may take place when a new barrier arises to isolate parts of a formerly continuous population, and (2) speciation via dis-

persal may occur when propagules manage to overcome an existing barrier and succeed in colonizing a new territory.

#### ALLOPATRY

Examples of vicariance are often found where historic fluctuations in sea level have caused the making and breaking of land barriers. The occurrence of sibling pairs (geminate species) separated by the Malayan Archipelago has been noted by several authors (Greenfield, 1968; Allen, 1975; Fleminger, 1985; Woodland, 1990). A typical example is that provided by Springer and Williams (1994). They proposed that the present distributions of the sister species *Braniella interrupta* and *B. leopardus* (Blenniidae) (Fig. 1) are a reflection of separation that took place during the low sea stand of the most recent Pleistocene glaciation.

In his study of the distribution of neritic copepods in the East Indies area, Fleminger (1985) concluded that several vicariant speciation events had taken place due to the glacial-stage barrier between Southeast Asia and Australia. Oceanic continuity remained, but the narrowed gap between the two landmasses may have been affected by cool-water upwelling. As a result, a partial land barrier may have been augmented by a temperature block. In other parts of the Indo-West Pacific, land barriers were formed between New Guinea and Australia and across the mouth of the Red Sea. The appreciable endemism now found along the coast of northwestern Australia and in the Red Sea may be attributed to these blockages (Briggs, 1995).

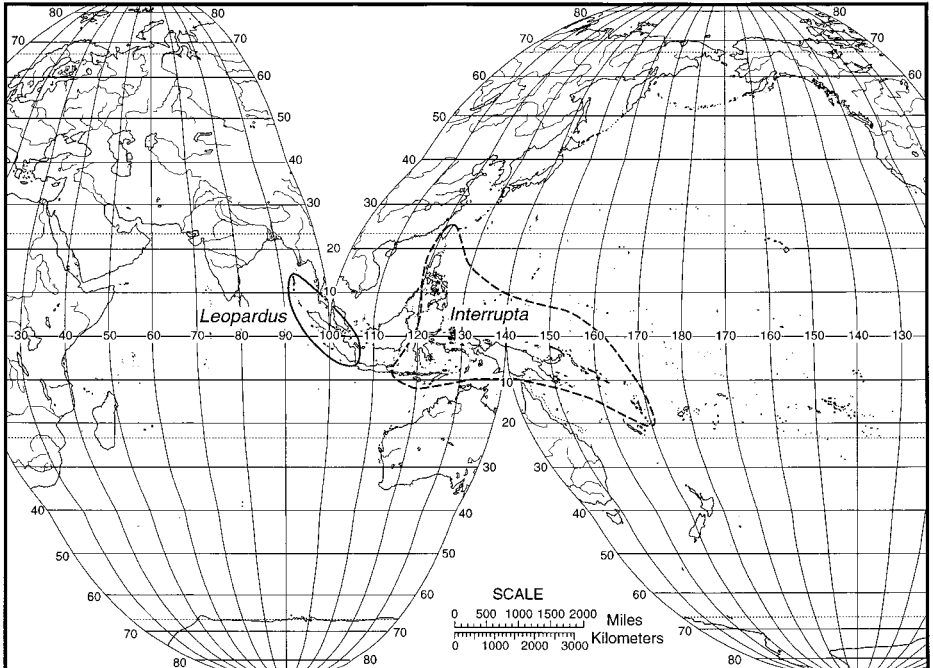


Figure 1. Distribution patterns of a sibling pair of blennioid fishes in the genus *Braniella* (Blenniidae). After Springer and Williams (1994).

Although vicariance has been an important impetus to speciation, dispersal has been no less so. The major part of the Western Pacific is underlain by the huge Pacific plate. As the Plate moved westward, it created a whole series of island arcs between New Zealand and the Aleutians. The plate also contains many sites of intraplate volcanism where island chains are created above hot spots or mantle plumes. The result of these tectonic activities is an enormous expanse of scattered islands and archipelagos that extend more than one-third of the way around the world. Islands so created are obligated to pick up their shallow marine (and terrestrial) biotas via dispersal.

#### PARAPATRY

Parapatric speciation takes place when two populations occupy essentially nonoverlapping areas but are in continuous contact along a mutual border with no extrinsic boundary to separate them. Oftentimes the border will be marked by a narrow hybrid zone. This kind of speciation is considered to be important in oceanic species where only a partial separation can occur (Pierrot-Bults and Van der Spoel, 1979). For example, a study of speciation in salps (Salpidae) suggests that a clinal parapatric speciation has taken place allowing populations to speciate while maintaining gene flow (DeVisser, 1985). Steps in the cline, associated with low population density, apparently enables related populations to accumulate genetic differences. The vicariant speciation of copepods in the East Indies described by Fleminger (1985) may have actually been parapatric in nature.

Although parapatric speciation has been traditionally associated with planktonic organisms, it may also be important in the benthic biota. In a review of sibling marine species Knowlton (1993) noted the occurrence of parapatric populations along continuous coastlines. Her data included 133 cases of sibling relationship representing 91 genera in nine phyla. In approximately 20% of the cases, parapatric distributions were identified. Almost all the species observed in this study were shallow-water macroinvertebrates. Many of the separated populations showed different depth preferences.

#### SYMPATRY

Recently, the process commonly known as sympatric speciation has been given a new name, "competitive speciation" (Rosenzweig, 1995). This new designation is appropriate since it refers to the natural condition under which the process takes place. That is, the absence of extrinsic barriers means that speciation has probably taken place in the presence of gene flow. Consequently, it may be observed that allopatric speciation depends on isolation opportunities while competitive speciation depends on ecological opportunities. How can ecological opportunities arise? There are well-documented cases of host switching among insects (Diehl and Bush, 1989; Bush, 1994) and some theoretical models support the feasibility of competitive speciation (Rice and Salt, 1990; Johnson et al., 1996; Kawecki, 1996). Coyne and Orr (1989) found that 46% of 119 pairs of sibling *Drosophila* species occurred sympatrically, a situation that suggests considerable competitive speciation.

For vertebrate animals, Carroll (1997) observed that sympatric (competitive) speciation may be possible but, few if any specific examples have been demonstrated. However, when Schlieuwen et al. (1994) investigated two volcanic lakes in the Cameroon, they found

endemic species of cichlid fishes that had arisen under competitive circumstances. The two lakes harbored nine and 11 species, respectively. Molecular data showed that each species flock was monophyletic and that they had evolved in each lake after a single colonization event. No microgeographic barriers existed since the habitats along the shorelines were uniform and free of physical obstructions.

Palumbi (1994) reviewed genetic divergence and reproductive isolation in the marine environment and observed that evidence for the action of selection in increasing reproductive isolation in sympatric populations is fragmentary. But Lazarus et al. (1995) examined fossil material which demonstrated competitive speciation in two large foraminiferan populations. The speciation process occurred over an interval of  $0.5 \pm 0.2$  million yrs. For contemporary populations without continuous fossil records, the detection of speciation mode is probably best determined by comparing the geographic patterns of closely related (sibling) species. This assumes that each new species will have had very little time to spread from its place of origin (Lynch, 1989; Chesser and Zink, 1994).

A survey of sibling species among the shallow-water marine invertebrates (Knowlton, 1993) suggests that competitive speciation may be very important. Of the 133 cases reviewed, the great majority demonstrated sympatry. If further research confirms this pattern, our concept of speciation in the sea will undergo a dramatic change.

A review of resource polymorphisms has provided a valuable insight into the mechanisms of population divergence and speciation (Smith and Skúlason, 1996). Such polymorphisms may be found among fishes, amphibians, and birds. Many have demonstrated genetic divergence and some have completed the speciation process (Fig. 2). The key seems to be the availability of underutilized resources requiring unique trophic specializations. An example among marine fishes is the genus *Hypoplectrus* (Serranidae). There

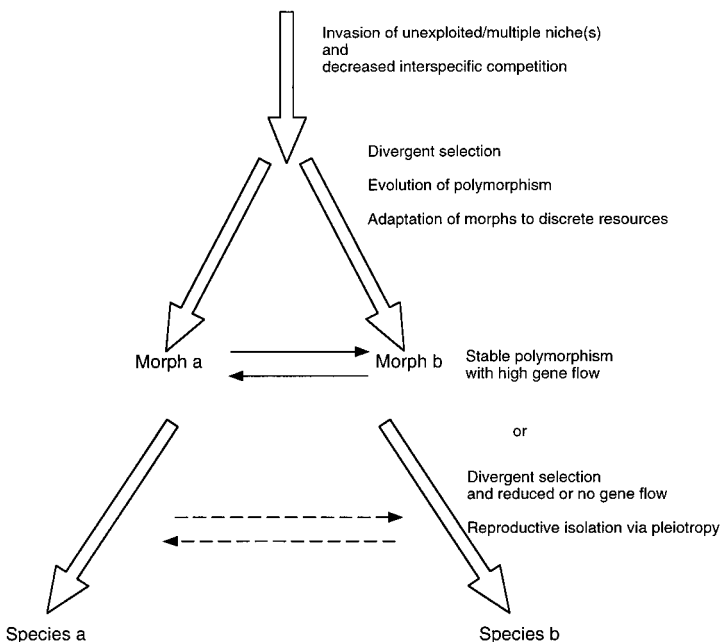


Figure 2. Possible steps and mechanisms leading to resource polymorphisms and speciation. After Smith and Skúlason (1996).

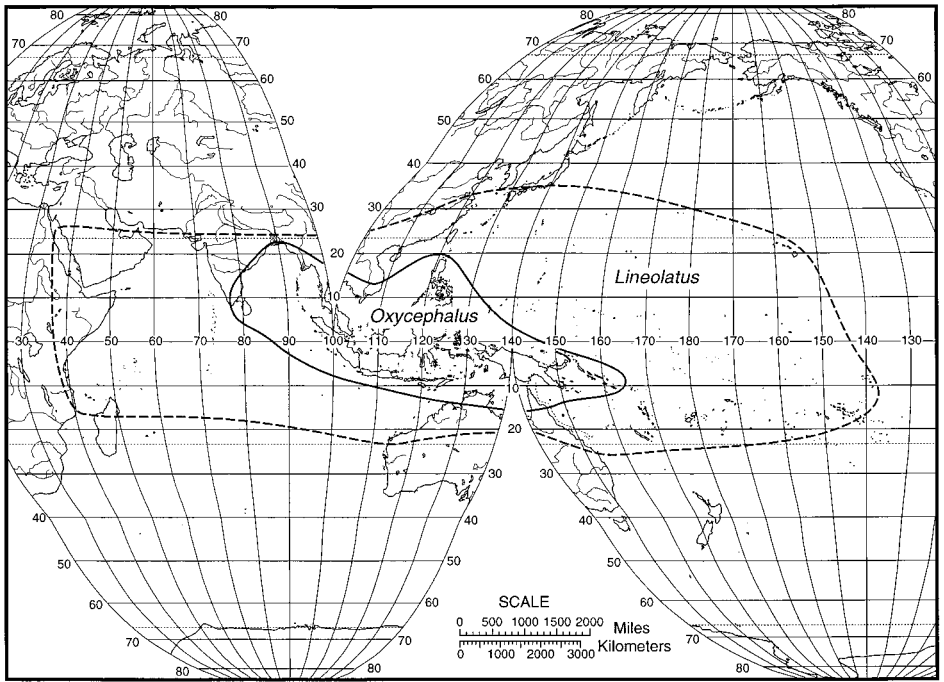


Figure 3. Distribution patterns of a sibling pair of butterflyfishes. After Burgess (1978) and Blum (1989).

are 12 morphotypes distinguished almost completely by color. Most are sympatric with as many as seven occurring on the same reef. There is very little mixed spawning and the morphotypes were determined to be a complex of incipient species (Fischer, 1980).

By taking advantage of some excellent systematic works on the fishes of the East Indies area, I have noted that one can detect indications of sympatric speciation (Briggs, 1995). The butterfly fishes of the family Chaetodontidae comprise a group of conspicuous, well-studied reef fishes (Burgess, 1978; Blum, 1989). Within this group, there are two pairs of sibling species that have sympatric distributions. *Chaetodon oxycephalus* occurs entirely within the range of its sibling *C. lineolatus* (Fig. 3) and *C. ocellicaudus* is confined within the range of *C. melannotus* (Fig. 4). In each case, the species with the smaller territory occurs primarily in the East Indies while its more widespread relative ranges broadly in the Indo-West Pacific. But other *Chaetodon* species groups may have a vicariant history (McMillan and Palumbi, 1995). In the family Pseudochromidae (Winterbottom, 1985) *Congrogadus hierichthys* occupies a restricted territory in the East Indies but is sympatric with and entirely within the range of its very close relative *C. subducens* (Fig. 5).

Even more remarkable is evidence showing that three sibling species have conjunctive ranges. Within the genus *Lutjanus* (Lutjanidae), there are three species that occur in both marine and freshwater habitats (Allen and Talbot, 1985; McDowell, 1988). One, *L. goldei*, has a restricted range along the south coast of New Guinea. It is sympatric with the more widely distributed *L. fuscescens*. These two occur within the range of the very widespread *L. argentimaculatus* (Fig. 6). In the pipefish (Syngnathidae) genus *Phoxocampus* (Dawson,

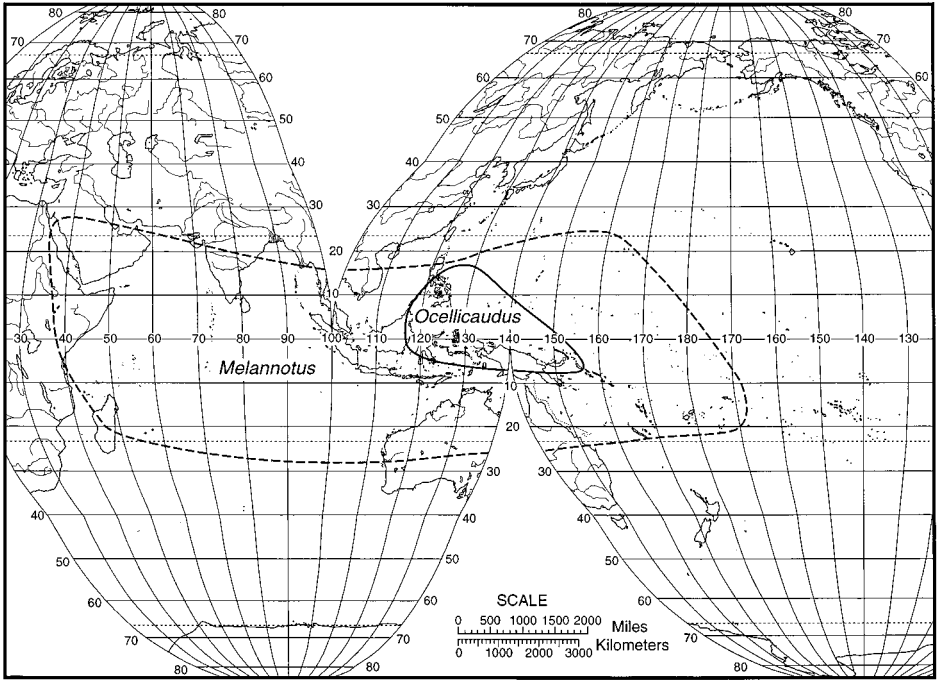


Figure 4. A second sibling pair of butterflyfishes. After Burgess (1978) and Blum (1989).

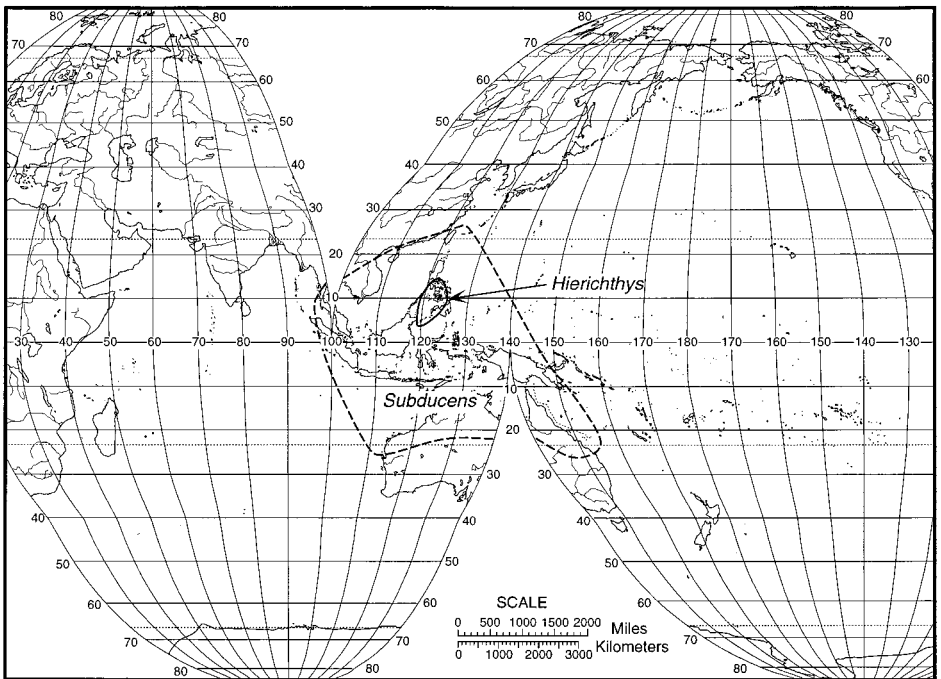


Figure 5. Distribution patterns of two closely related species in the family Pseudochromidae. After Winterbottom (1985).

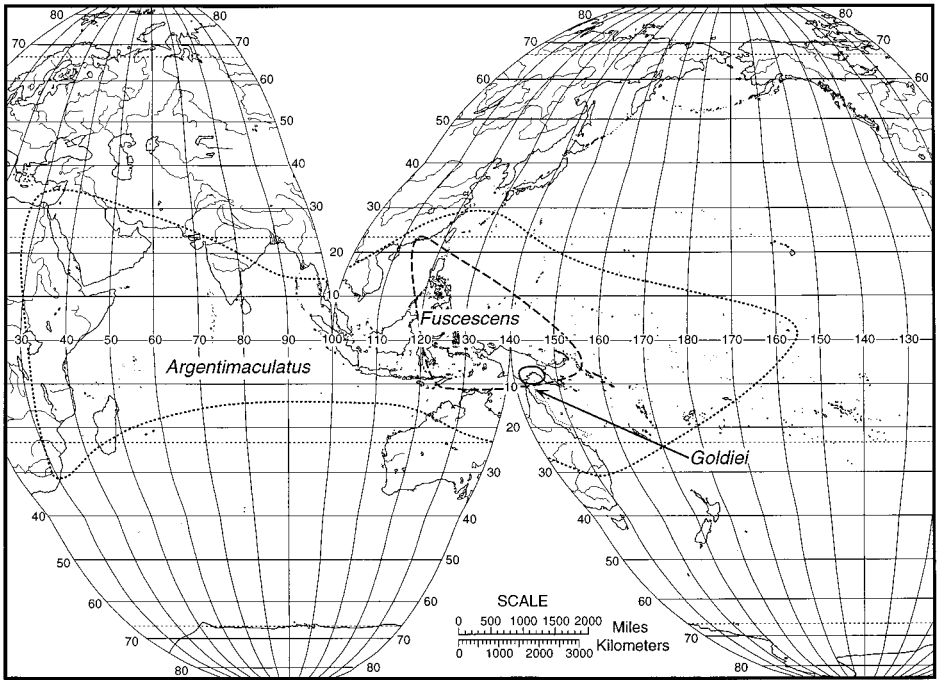


Figure 6. Distribution patterns of three closely related species in the genus *Lutjanus* (Lutjanidae). After Allen and Talbot (1985) and McDowell (1988).

1985), there are three known species. *P. tetrophthalmus* is found only in the East Indies and occurs entirely within the range of *P. diacanthus*. *P. belcheri* is very widespread and almost completely encompasses the ranges of its two sibling species (Fig. 7).

In each example of sibling sympatry, it may be seen that the most restricted member of the related group is confined primarily to the East Indies. In the two instances where three siblings are involved, the patterns are remarkably similar; one species has a very small East Indies range, the next occupies a larger portion of the area, and the third has become very widespread. There is the possibility that these are evolutionary patterns with the youngest sibling occupying the smallest area, the next eldest the intermediate size territory, and the oldest the larger. This hypothesis may be tested if one could use genetic research to determine the relative ages of each set of sibling species.

An obvious criticism of the foregoing sequence is that the patterns may represent species that are in the process of withdrawing toward the East Indies as they become older. In that view, the central populations would represent species that are declining toward extinction. However, there are important facts that argue against that interpretation: (1) systematic works on several animal groups have identified the East Indies as a center of origin with species being dispersed outward (Allen, 1975; Foin, 1976; Fricke, 1988). Other groups, well represented by fossil material, exhibit an increasing trend in average generic age from the East Indies outward (Newman, 1986; Roux, 1987; Veron, 1995). Also, a vicariant explanation to account for the sympatric occurrence of such sibling species does not appear to be possible in view of the apparent absence of barriers to gene flow.

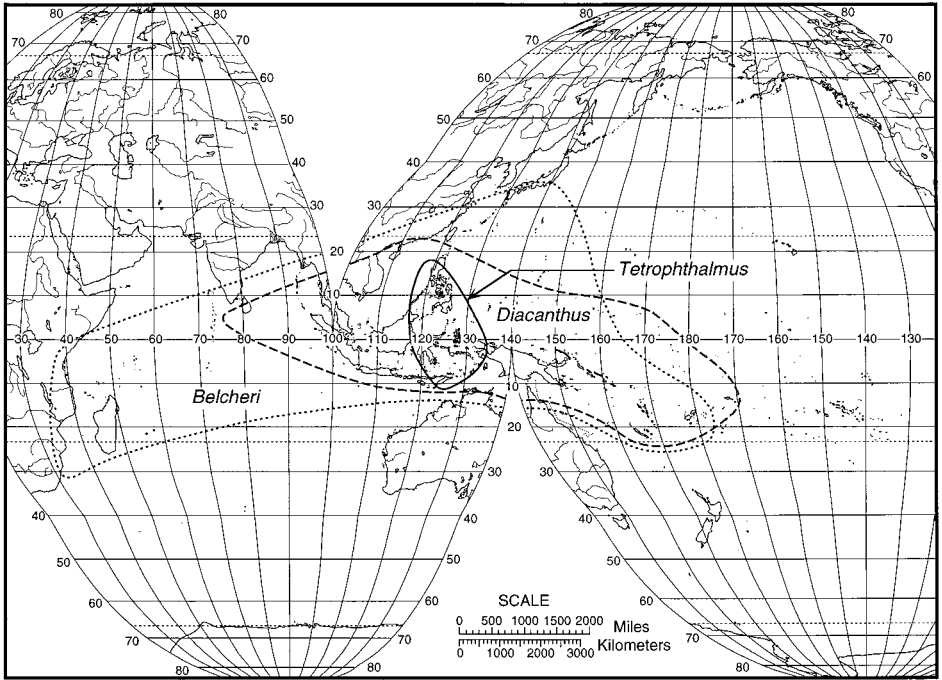


Figure 7. Distribution of the three known species in the genus *Phoxocampus* (Syngnathidae). After Dawson (1985).

More recently, works on the genetic structure of widespread Indo-West Pacific species have provided similar biogeographic data. The *Tridacna* clams show routes of gene exchange consistent with dispersal from the East Indies (Benzie and Williams, 1997). Data from mitochondrial DNA (mtDNA) in *Echinometra* sea urchins demonstrate a decreasing gradient in genetic diversity that parallels the drop in species diversity across the Pacific (Palumbi, 1997). An investigation of mtDNA sequences in shrimp belong to the genus *Penaeus* yielded data indicating an origin and maximum diversity in the IWP with an historic radiation to achieve its present circumtropical range (Baldwin et al., 1998). An mtDNA analysis of the olive ridley sea turtle (*Lepidochelys olivacea*) indicated the general East Indies area as the place of origin for its interoceanic radiation (Bowen et al., 1998). Allozyme studies appear to indicate a decreasing gradient of species and genetic diversity across the Pacific (Nichida and Lucas, 1988).

Species arising from small, isolated populations do not appear to be able to invade and replace a large parent population. If a barrier separating a peripheral group from its larger parent population is removed, it is usually the former that becomes extinct. For example, an examination of speciation in Cenozoic molluscs from the Turkana Basin in east Africa was conducted by Williamson (1981). He found that lacustrine regressions resulted in the isolation of small populations that proceeded to undergo rapid speciation. When lacustrine transgression eventually occurred, a reinvasion of ancestral species resulted in the extinction of the derived taxa. Likewise, the small, isolated populations on the periphery of the East Indies are unlikely to successfully invade toward the center. Although they are

capable of rapid speciation, they are subject to the debilitating effects of genetic drift and inbreeding depression.

In the case of the scleractinian corals, Veron (1995) has proposed that genetic races occur in a reticulate pattern governed by historic changes in ocean currents. As surface circulation strengthens, dispersion and hybridization increase. When circulation slows, populations become disjunct and endemism increases. This produces a net-like arrangement of evolutionary pathways. In this concept, there would be little distinction between central and peripheral speciation and no fundamental difference between allopatric and sympatric processes.

The idea of historic changes in genetic relationships being governed by ocean currents may be applicable to many species with planktonic larvae. However, as Veron (1995) has noted, the corals also demonstrate well-defined geographic patterns in diversity and age. The East Indies Triangle is the diversity center (genera and species) as well as being the location of the youngest genera (in average age). The Triangle appears to be a net source of diversity and the peripheral regions net sinks. These facts constitute support for the operation of the East Indies as a center of origin for successful species. There is an apparent tendency for successful species to originate in such centers while unsuccessful species derive from small peripheral populations.

Over the short term, successful evolution may be defined as that process which takes place when a new species expands from its place of origin and establishes itself in new territories. Unsuccessful evolution takes place when a new species remains more or less confined to its place of origin and apparently exists in an evolutionary trap. In the long term, successful evolution will lead to extended phyletic lines. The products of unsuccessful evolution may persist for long periods of time if they exist in locations that are protected from invasion by newer species (Briggs, 1996).

#### CONCLUSION

As the phylogenetic relationships and geographic patterns of sibling species become better known, they produce information that appears to be indicative of their speciation modes. Within the allopatric mode, one may find numerous examples of speciation resulting from vicariance and dispersal. Parapatric speciation is considered to be important among planktonic organisms and probably occurs among the benthic invertebrates. While competitive (sympatric) speciation has been demonstrated among insects and freshwater fishes, it has rarely been recognized in the marine environment.

Although competitive speciation may not be as common as the other modes, some sibling patterns produced by well-known species appear to reflect a competitive origin. The fact that this mode apparently takes place within the high diversity center of the Indo-West Pacific has considerable evolutionary significance. The East Indies Triangle is evidently a center of origin from which many successful species are dispersed. This suggests that species produced under competitive circumstances may have an evolutionary advantage.

A neglected area of biogeographic research is the examination of geographic patterns that are produced as the result of speciation. As species are formed and extend their ranges, and as others become scarce and finally extinct, they produce geographic pat-

terns. We should examine such patterns and attempt to interpret them, for they will help elucidate the underlying evolutionary process.

#### ACKNOWLEDGMENT

I wish to thank S. Gregory Tolley for his helpful suggestions. I am indebted to the Natural History Museum, University of Georgia, for logistic support.

#### LITERATURE CITED

- Allen, G. R. 1975a. Anemone fishes, 2nd ed. TFH Publications, Neptune City, New Jersey. 352 p.
- \_\_\_\_\_. 1975b. Damsel-fishes of the South Seas. TFH Publications, Neptune City, New Jersey. 237 p.
- \_\_\_\_\_. and F. H. Talbot. 1985. Review of the snappers of the genus *Lutjanus* (Pisces: Lutjanidae) from the Indo-Pacific, with description of a new species. *Indo-Pac. Fish.* 11: 1–87.
- Baldwin, J. D., A. L. Bass, B. W. Bowen and W. H. Clark, Jr. 1998. Molecular phylogeny and biogeography of the marine shrimp *Penaeus*. *Mol. Phylog. Evol.* [in press]
- Benzie, J. A. H. and S. T. Williams. 1997. Genetic structure of giant clam (*Tridacna maxima*) populations in the west Pacific is not consistent with dispersal by present-day ocean currents. *Evolution* 51: 768–783.
- Blum, S. D. 1989. Biogeography of the Chaetodontidae: an analysis of allopatry among closely related species. *Environ. Biol. Fishes* 25: 9–31.
- Bowen, B. W., A. M. Clark, F. A. Albreu-Grobois, A. Cheves, H. A. Reichart and R. J. Ferl. 1998. Global phylogeography of the ridley sea turtles (*Lepidochelys* spp.) as inferred from mitochondrial DNA sequences. *Genetica* 101: 179–189.
- Briggs, J. C. 1992. The marine East Indies: centre of origin? *Global Ecol. Biogeo. Ltrs.* 2: 149–156.
- \_\_\_\_\_. 1995. *Global biogeography*. Elsevier, Amsterdam. 452 p.
- \_\_\_\_\_. 1996. Biogeography and punctuated equilibria. *Biogeographica* 72: 151–156.
- Burgess, W. E. 1978. *Butterflyfishes of the world*. TFH Publications, Neptune City, New Jersey. 832 p.
- Bush, G. L. 1994. Sympatric speciation in animals—a new wine in old bottles. *Trends Ecol. Evol.* 9: 285–288.
- Carroll, R. L. 1997. *Patterns and processes of vertebrate evolution*. Cambridge Univ. Press, Cambridge, U.K. 448 p.
- Chesser, R. T. and R. M. Zink. 1994. Modes of speciation in birds. *Evolution* 48: 490–497.
- Coyne, J. A. and H. A. Orr. 1989. Patterns of speciation in *Drosophila*. *Evolution* 43: 362–381.
- Dawson, C. E. 1985. Indo-Pacific pipefishes (Red Sea to the Americas). *Gulf Coast Res. Lab., Ocean Springs, Mississippi*. 230 p.
- De Visser, J. 1985. Transition zones and salp speciation. Pages 266–269 in A. C. Pierrot-Bults, S. Van der Spoel, B. J. Zahuranec and R. K. Johnson, eds. *Pelagic biogeography*. Unesco, Paris.
- Diehl, S. R. and G. L. Bush. 1989. The role of habitat preference in adaptation and speciation. Pages 345–365 in D. Otte and J. A. Endler, eds. *Speciation and its consequences*. Sinauer Associates, Sunderland, Massachusetts.
- Fischer, E. A. (1980) Speciation in the hamlets (*Hypoplectrus*: Serranidae)—a continuing enigma. *Copeia* 1980: 649–659.
- Fleminger, A. 1985. The Pleistocene equatorial barrier between the Indian and Pacific oceans and a likely cause for Wallace's Line. Pages 79–84 in A. C. Pierrot-Bults, S. Van der Spoel, B. J. Zahuranec and R. K. Johnson, eds. *Pelagic biogeography*, Unesco, Paris.
- Foin, T. C. 1976. Plate tectonics and the biogeography of the Cypraeidae (Mollusca: Gastropoda). *J. Biogeogr.* 3: 19–34.

- Fricke, R. 1988. Systematic und historische zoogeographie der Callionymidae (Teleostei) des Indischen Ozeans, 2 vols. Doctoral Dissertation, Albert-Ludwigs-Universität, Freiburg im Breisgau, Germany. 612 p.
- Futuyma, D. J. 1986. The role of behavior in host-associated divergence in herbivorous insects. Pages 295–302 in M. D. Huettel, ed. *Evolutionary genetics of invertebrate behavior*. Plenum Press, New York.
- \_\_\_\_\_. and G. C. Mayer. 1980. Non-allopatric speciation in animals. *Syst. Zool.* 29: 254–271.
- Greenfield, D. W. 1968. The zoogeography of *Myripristis* (Pisces: Holocentridae). *Syst. Zool.* 17: 76–87.
- Johnson, P. A., et al. 1996. Conditions for sympatric speciation: a diploid model incorporating habitat fidelity and non-habitat assortive mating. *Evol. Ecol.* 10: 187–205.
- Kawecki, T. J. 1996. Sympatric speciation driven by beneficial mutations. *Proc. R. Soc. Lond., Ser. B.* 263: 1515–1520.
- Knowlton, N. 1993. Sibling species in the sea. *Ann. Rev. Ecol. Syst.* 24: 189–216.
- Lazarus, D., et al. 1995. Sympatric speciation and phyletic change in *Globorotalia truncatulinoides*. *Paleobiology* 21: 28–51.
- Lynch, J. D. 1989. The gauge of speciation: on the frequencies of modes of speciation. Pages 527–553 in D. Otte and J. A. Endter, eds. *Speciation and its consequences*. Sinauer Associates, Sunderland, Massachusetts.
- Mayr, E. 1963. *Animal species and their evolution*. Belknap Press, Cambridge, Massachusetts. 797 p.
- McDowell, R. M. 1988. Diadromy in fishes: migrations between freshwater and marine environments. Croom Helm, London. 308 p.
- McMillan, W.O. and S. R. Palumbi. 1995. Concordant evolutionary patterns among Indo-West Pacific butterflyfishes. *Proc. R. Soc. Lond., Ser. B.* 263: 229–236.
- Newman, W. A. 1986. Origin of the Hawaiian marine fauna: dispersal and vicariance as indicated by barnacles and other organisms. Pages 21–49 in R. H. Gore and K. L. Heck, eds. *Crustacean biogeography*. A. A. Balkema, Rotterdam.
- Nichida, M. and J. S. Lucas. 1988. Genetic differences between geographic populations of crown-of-thorns starfish throughout the Pacific region. *Mar. Biol.* 98: 359–368.
- Palumbi, S. R. 1994. Genetic divergence, reproductive isolation, and marine speciation. *Ann. Rev. Ecol. Syst.* 25: 547–572.
- \_\_\_\_\_. 1997. Molecular biogeography of the Pacific. *Coral Reefs* 16 (Suppl.): 547–552.
- Paterson, H. E. H. 1981. The continuing search for the unknown and unknowable: a critique of contemporary ideas on speciation. *Afr. J. Sci.* 77: 113–119.
- Pierrot-Bults, A. C. and S. Van der Spoel. 1979. Speciation in macrozooplankton. Pages 144–167 in S. Van der Spoel and A. C. Pierrot-Bults, eds. *Zoogeography and diversity of plankton*. John Wiley, New York.
- Rice, W. R. and G. W. Salt, G.W. 1990. The evolution of reproductive isolation as a correlated character under sympatric conditions: experimental evidence. *Evolution* 44: 1140–1152.
- Rosenzweig, M. L. 1995. *Species diversity in space and time*. Cambridge Univ. Press, Cambridge, U.K. 436 p.
- Roux, M. 1987. Evolutionary ecology and biogeography of recent stalked crinoids as a model for the fossil record. Pages 1–53 in M. Jangoux and J. M. Lawrence, eds. *Echinoderm studies*, vol. 2. A. A. Balkema, Rotterdam.
- Schliwen, U. K., D. Tautz and S. Pääbo. 1994. Sympatric speciation suggested by monophyly of crater lake cichlids. *Nature* 368: 629–632.
- Smith, T. B. and S. Skúlason. 1996. Evolutionary significance of resource polymorphisms in fishes, amphibians, and birds. *Ann. Rev. Ecol. Syst.* 27: 111–133.
- Springer, V. G. and J. T. Williams. 1994. The Indo-West Pacific blennioid fish genus *Istiblennius* reappraised: a revision of *Istiblennius*, *Blenniella*, and *Paralticus*, new genus. *Smithson. Contrib. Zool.* 565: 1–93.

- Veron, J. E. N. 1995. Corals in space and time: the biogeography and evolution of the Scleractinia. Cornell Univ. Press, Ithaca, New York. 321 p.
- Williamson, P. G. 1981. Paleontological documentation of speciation in Cenozoic molluscs from Turkana Basin. *Nature* 243: 437–443.
- Winterbottom, R. 1985. Revision and vicariance biogeography of the subfamily Congrogadinae (Pisces: Perciformes: Pseudochromidae). *Indo-Pac. Fish.* 9: 1–34.
- Woodland, D. J. 1990. Revision of the fish family Siganidae with descriptions of two new species and comments on distribution and ecology. *Indo-Pac. Fish.* 19: 1–36

DATE SUBMITTED: June 17, 1998.

DATE ACCEPTED: April 20, 1999.

ADDRESS: *Zoological Collections, Museum of Natural History, University of Georgia, Athens, Georgia 30602. Tel. 706-353-1945.*