BOOK REVIEWS

China to seal 30 decaying poison gas shells and three vats of mustard gas located by the Chinese authorities. The Japanese had already dispatched teams to China to check on possible soil contamination, but this is the first effort to neutralize some of the 2 million Japanese gas shells that reportedly remain buried in northeast China.

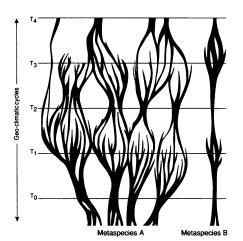
The physical apparatus of the factories of death was demolished by the Japanese 50 years ago. Regrettably, the legacy of psychological scars inflicted by the "certain foreign state" can never be eradicated from the pages of Sino-Japanese history.

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## **Evolution by Reticulation**

Corals in Space and Time. The Biogeography and Evolution of the Scleractinia. J. E. N. VERON. Comstock (Cornell University Press), Ithaca, NY, 1995. xiv 321 pp., illus. Paper, \$35 or £27.50.

Corals in Space and Time is a monumental synthesis of the evolution of corals in which the author challenges Charles Darwin head on. Veron argues that, instead of evolving dichotomously along discrete lineages as a result of natural selection as proposed by Darwin, coral species perpetually fuse (by hybridization) or separate (by isolation and genetic drift), giving rise to a reticulate pattern of evolution. Veron's theory of reticulate evolution initially grew out of his observation of the abundance of intergrades between species. He describes his early years of separating and classifying corals, in fact, as "a failure." In the last decade, three discoveries have bolstered Veron's theory with regard to corals. First, it has been established that about three-quarters of all coral species are spawners, releasing their gametes into the water column, where external fertilization takes place. The second discovery is the synchronous mass-spawning events on the Great Barrier Reef of Australia, where many dozens of coral species spawn (within a few days of each other) at the same time of the year, producing a rich soup of reproductive material that can lead to frequent hybridization. The third discovery is an increasing list of species that can produce viable hybrids at least at the F<sub>1</sub> generation. From all this Veron has concluded that coral intergrades are in fact hybrids, some viable but sterile, some viable and reproductive, some fusing back to the parent generation, some diverging, but to-



"Concept diagram of evolutionary changes in two metaspecies. Metaspecies A, a syngameon, is caught-up in palaeoclimatic cycles of reticulate evolution. Metaspecies B survives these cycles. Phylogenies have varying patterns of spatial separation. For A, high levels of genetic communication during periods of strong surface circulation (at times  $T_0$ ,  $T_2$  and  $T_4$ ) produce small numbers of well-defined species, while low levels of genetic communication during periods of weak circulation (at times  $T_1$  and  $T_3$ ) produce large numbers of ill-defined species complexes." [From Corals in Space and Time]

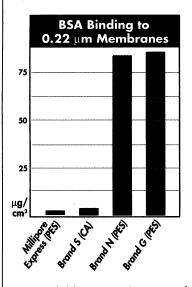
gether forming a species complex of races and subspecies—a large genetic pool of interconnected populations that he calls a syngameon. Such a species is not discrete; its boundaries are fuzzy, and it represents a continuum of variation. At opposite ends of the continuum species may appear different, but all varieties along the continuum are interfertile. The species complex may also include sterile hybrids, which can be ecological dominants, that is, species that may not themselves reproduce but that play a dominant role in the ecosystem and are continually reproduced over time by hybridizing parental populations.

The syngameon is an interconnected net of populations (races, subspecies, and species) that either converge or diverge in space and time depending on gene flow. Their connectivity in turn depends on the strength and direction of currents. Veron does not deny that natural selection is embedded within the process, but he sees connectivity, or the lack of it, as more important in species evolution. In this regard, this analysis is in agreement with neo-Darwinists Ernst Mayr, Niles Eldredge, and Stephen J. Gould. Veron sees ocean currents, a physical process, as being the dominant control over evolution in corals. He also invokes reticulate evolution to explain why biodiversity in corals in not higher. Hybridization and reproductive connectivity favor fusion and damp separation (speciation). Most coral reefs in the Indo-West-Pacific



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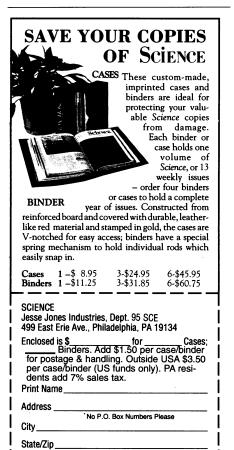
are characterized by less than 10 percent endemicity. This also helps to explain the very long average age (10 million years) of coral species in the fossil record.

Veron does not overlook the fact that low coral biodiversity can also be a consequence of low habitat diversity; reef-building corals occur only in the euphotic zone and in the tropics. Veron explains similarities in species composition as due to similarities in habitat. Reefs characterized by large differences in physical habitat though separated by a few miles may be more different than reefs with similar habitat on western and eastern coastlines of Australia, a separation of over 1000 miles. Herein may lie a limitation to Veron's argument. If corals need to retain genetic specialization (for example, habitat specificity), they must avoid hybridizing with species occupying very different but nearby habitats. Veron does not discuss this problem, but then he does not claim that reticulate evolution applies to all corals any more than it applies to all species in nature.

Thus Veron does not argue either-or regarding dichotomous or reticulate evolution; rather, he offers the latter as a significant process to explain the evolution of those species that can successfully hybridize. The hypothesis of reticulate evolution is not new regarding plants, but it has been given little consideration in animal systematics. Veron suggests that reticulate evolution may be a major mechanism in the evolution of many marine invertebrates (among them crustaceans, mollusks, polychaetes, and echinoderms) and some vertebrates, notably Amphibia, in which fertilization is external. This is the major contribution of the book, and it should usher in a plethora of new research to test the generality of the hypothesis. If it occurs broadly, reticulate evolution should wreak havoc on traditional cladistics. Ultimately, the overall importance of reticulate evolution may be proved or disproved by molecular genetics. Thus the book represents a challenge for future research.

Having focused on the positives, I would be remiss not to mention some shortcomings. Perhaps the most bothersome to me is Veron's use of the term "vicariance circulation" to explain both separation and connectivity. Clearly circulation (ocean currents) can cause both, but the term "vicariance" refers to separation only. Other bits of jargon, such as "connectivity ratchets" are distracting, although Veron's meaning is clear. The references in some chapters are rather spotty, and some typos need correcting, such as the latitude of Clipperton Atoll (10 degrees north, not south). The writing in places is somewhat nebulous, but this is more than offset by the numerous summaries of main points and conclusions. It may take a decade of research to verify reticulate evolution as a major evolutionary process. If it proves to be such, history could well place Veron's Corals in Space and Time on the shelf alongside the works of Darwin, Mayr, Eldredge, and Gould.

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## **Books Received**

Analysis of Biological Development. Klaus Kalthoff, McGraw-Hill, New York, 1995, xviii, 738 pp. + supplementary material. \$68.63.

The Botany of Mangroves. P. B. Tomlinson. Cambridge University Press, New York, 1995. xii, 419 pp., illus. Paper, \$29.95. Cambridge Tropical Biology. Reprint, 1986 ed.

Caring for Patients. A Critique of the Medical Model. Allen B. Barbour. Stanford University Press, Stanford, CA, 1995, xxx, 398 pp. \$45.

Crystal Chemistry of Condensed Phosphates. Durif. Plenum, New York, 1995. xvi, 408 pp., illus.

Empires of Time. Calenders, Clocks, and Cultures. Anthony F. Aveni. Kodansha Globe, New York, 1995. x, 371 pp., illus. Paper, \$16. Reprint, 1989 ed.

Encounters with Qi. Exploring Chinese Medicine. David Eisenberg, with Thomas Lee Wright. Norton, New