USE OF THE FOSSIL RECORD OF A CLADE OF MARINE BIVALVES (CARDIIDAE: FRAGINAE) IN INTERPRETING THE EVOLUTION OF HOST/PHOTOSYMBIONT SYSTEMS AND CASES OF ALLEGED GEMINATE SPECIATION.

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Geminate species are usually considered pairs of species that are each other's closest relative and separated by a geographic barrier. The classic example of the production of geminate species is the disruption of marine species ranges by the emergence of the isthmus of Panama.

The geminate species concept has been based only on data for living species. However, data only from Recent species cannot determine whether presumed geminates are each other's closest relatives. To break this circularity of the geminate concept, the fragine cardiid bivalves are used as a model system for the study of geminate speciation. Fragines are abundantly represented in living and fossil tropical faunas. Potential outgroups for the fragines are assessed and the phylogenetic history of the Fraginae is reconstructed. The results indicate that 1) nearly all pairs of alleged fragine geminates are not sister species, 2) the splitting of Atlantic and Pacific lineages of fragines took place over millions of years and occurred before the subaerial emergence of Panama, with divergence occurring first amongst deeper water taxa and last amongst shallower water taxa, and 3) for all lineages, speciation continued on either side of the isthmus after they were separated into Pacific and Atlantic sublineages by the emerging isthmus. Preservation of a geminate species concept should include the caveat that the species in question are each other's closest living relative.

The oldest fragines (species assigned to the extant taxa Papillicardium and Parvicardium) and tridacnines (species assigned to the extinct taxa Goniocardium, Avicularium and Byssocardium) are found in Lower Eocene rocks of Europe; the oldest tropical fragine and tridacnines are early Late Oligocene in age. Virtually all Recent tropical fragines (> 90% of fragine species) which have been anatomically examined have been found to harbor the photosymbiotic dinoflagellate alga Symbiodinium microadriaticum, the same alga found in hermatypic corals and all Recent giant clams (Cardiidae: Tridacninae). Data from studies of cardiid paleoecology undertaken in Florida, Jamaica and Panama are best explained by hypothesizing that fragines and tridacnines independently evolved the association with S. microadriaticum during the Oligocene when both cardiid clades invaded tropical waters.