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## WHAT METAZOAN PARASITES TELL US ABOUT THE EVOLUTION OF AMERICAN AND EUROPEAN EELS

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Two hypotheses have been forwarded to explain the divergence of American (*Anguilla rostrata*) and European (*Anguilla anguilla*) eels from a common ancestor. The “oceanic” hypothesis proposes that eels formerly inhabited either North America or Europe. Divergence occurred on the spawning grounds in the Sargasso Sea, with new oceanic currents arising during the Pleistocene carrying leptocephalid larvae to the new continent. The “vicariant” hypothesis proposes that an ancestral eel population inhabited the North Atlantic regions, including Greenland, Iceland, and Scandinavia. This population was forced southwards by the Pleistocene glaciation and separated into European and American components. Examination of the freshwater metazoan parasite fauna specific to eels on both continents forces rejection of the “oceanic” hypothesis. Six parasites specific to eels (*Gyrodactylus anguillae*, *Pseudodactylogyrus anguillae*, *Bothriocephalus claviceps*, *Proteocephalus macrocephalus*, *Daniconema anguillae*, *Paraquimperia tenerrima*) infect eels in freshwaters of both Europe and North America. This transcontinental distribution of freshwater parasites specific to eels is incompatible with an oceanic separation of eels on the spawning grounds, because adult eels die after spawning and leptocephalid larvae cannot acquire these parasites at sea. The disjunct distribution of these parasites implies that at one time their ranges were continuous, thus supporting the “vicariant” speciation hypothesis.

The American eel, *Anguilla rostrata* (LeSueur), and the European eel, *Anguilla anguilla* (L.), are sister species inhabiting separate continents. They differ only in the number of vertebrae, the frequency of certain enzymatic alleles, and the fre-

quency of several restriction endonucleases in the mtDNA genotype (Avisé et al. 1986, 1990). Although it has been established that these eels are distinct populations, some doubt exists as to whether they constitute distinct biological species (Williams and Koehn 1984). Although Anguillidae is an ancient family, the fossil record is virtually nonexistent (Cavender 1986). The earliest known *Anguilla* in North America dates from the late Pleistocene, while in Europe, to the Upper Miocene (Cavender 1986). These findings, together with the close relatedness of the sister-species *Anguilla rostrata* and *Anguilla anguilla*, suggest that the two species were recently separated. Both species grow in coastal, estuarine, and freshwater habitats, and then undergo a spawning migration to the southwestern Sargasso Sea, where they spawn in a largely overlapping area (McCleave et al. 1987). Leptocephalid larvae migrate to the continent of parental origin, partially by passive dispersal in oceanic currents. The nature of their sympatric spawning grounds has created difficulty in determining the origin of the two species. Two contrasting hypotheses have been forwarded recently to explain the divergence of these two anguilliforms from a common ancestral stock and to account for their present distributions (Avisé et al. 1990).

The “oceanic” hypothesis states that eels were native only to one side of the Atlantic, that is, Europe or North America (Avisé et al. 1990). During the Pleistocene epoch, changes in ocean currents occurred that carried some eel larvae from the spawning grounds in the Sargasso Sea to the new continent. These eels matured in the new habitat and returned to the spawning grounds. However, as they migrated from a new direction, that of the newly colonized continent,

these eels may have encountered suitable breeding grounds and commenced spawning away from the ancestral stock, establishing initial tendencies for assortative mating and a distinct spawning area. The oceanic currents may have persisted, leading to continued migrations to the new continent, selecting for behaviors adaptive to the new habitat, and promoting divergence of the two populations.

The "vicariant" hypothesis proposes that a single ancestral population existed across the North Atlantic, from Scandinavia to Greenland (Avisé et al. 1990). The Pleistocene glaciation rendered the northern regions uninhabitable and forced these fish to move southward, dividing the population between North America and Europe and leading to the separation of spawning grounds. The two distinct spawning areas may have produced larvae destined for the respective original continent of the parental generation. The subsequent retreat of sea ice and reemergence of suitable habitats led to the colonization of the northern latitudes by two distinct populations already separated by glaciation.

Scientists have been using parasite distributions for more than 100 yr to draw inferences about host dispersal and evolution, beginning with the work of von Ihering (1891). Metcalf (1920) and, more recently, Manter (1966, 1967) emphasized the importance of discontinuous distribution of parasites of the same or closely related hosts in determining ancient conditions and former continuity of the host species. Herein, we employ distributional data from freshwater parasites specific to eels in both North America and Europe to distinguish between the two hypotheses explaining the divergence of the two eels from a single ancestral population.

Eleven species of parasites specific to eels are found in European fresh waters. They include three monogeneans (*Gyrodactylus anguillae*, *Pseudodactylogyrus anguillae*, and *Pseudodactylogyrus bini*), two cestodes (*Bothriocephalus claviceps* and *Proteocephalus macrocephalus*), five nematodes (*Anguillicola crassus*, *Anguillicola novaezelandiae*, *Daniconema anguillae*, *Paraquimperia tenerrima*, and *Spinitectus inermis*), and one copepod (*Ergasilus gibbus*) (Malmberg 1970; Kennedy 1974; Koie 1988, 1991). Of these, all are indigenous to Europe with the exception of *Anguillicola crassus* and *Pseudodactylogyrus bini*, recently acquired from introduced Japanese eels, *Anguilla japonica*, and *Anguillicola novaezelandiae*, introduced via live New Zealand eels,

*Anguilla australis* (Koie 1991). All the cestodes and nematodes possess complex life cycles, whereas the monogeneans and copepod are transmitted directly.

Eight species of freshwater parasites are also specific to eels in North America. They include *Gyrodactylus anguillae*, *Bothriocephalus claviceps*, *Proteocephalus macrocephalus*, the nematode *Paraquimperia aditum*, the copepod *Ergasilus celestis*, the trematode *Crepidostomum brevivitellum* (Margolis and Arthur 1979; Crane and Eversole 1989), plus *Daniconema anguillae* and *Pseudodactylogyrus anguillae*, recently found in our collections from Atlantic Canada (Cone, unpubl. data).

The identity of *Paraquimperia aditum* has been questioned, and it is suggested that this is actually *Paraquimperia tenerrima* (Moravec 1966). Specimens from Nova Scotian eels are morphologically identical with *Paraquimperia tenerrima*, and we agree with Moravec that *Paraquimperia aditum* is synonymous with *Paraquimperia tenerrima* (Cone and Marcogliese, unpubl. data). Thus, six freshwater parasites specific to eels occur in both North America and Europe. Congeneric copepods also infect the two eels. The two species of *Ergasilus* are morphologically very similar, but *Ergasilus celestis* is confined to freshwater in North America (Kabata 1988), whereas *Ergasilus gibbus* occurs in fresh and brackish waters in Europe (Kabata 1979).

Nie and Kennedy (1991) questioned the contention of Koie (1991) and others that *Pseudodactylogyrus anguillae* was introduced with imported Japanese eels, because they found this monogenean on eels in areas of Britain where contamination from Japanese eels is unlikely. These authors speculate that *Pseudodactylogyrus anguillae* may actually be more widespread but went unobserved because of its small size. Our finding of this parasite in North America, where there has been no introduction of Japanese eels, supports the argument for a more cosmopolitan distribution of *Pseudodactylogyrus anguillae*.

With the exception of the cosmopolitan *Pseudodactylogyrus anguillae*, and the introduced *Pseudodactylogyrus bini*, *Anguillicola crassus*, and *Anguillicola novaezelandiae*, none of the parasites found in Atlantic eels occur in Pacific eels. Moreover, Pacific *Anguilla* spp. possess several parasites specific to them but not found in Atlantic eels (Manter 1955; Beumer et al. 1983). Among trematodes, at least three genera and six species are unique to Pacific eels. The distinct-

ness of the Atlantic and Pacific eel parasites suggests that divergence of the two Atlantic forms occurred independently of Pacific eels, and any association between eels from the two oceans predated the separation of the Atlantic species.

The transcontinental distributions of the six species of parasite in Atlantic eels are incompatible with an origin of the two eels derived from a single continental population either in Europe or North America, where larvae subsequently diverged on the spawning grounds because of oceanic currents ("oceanic" hypothesis). Because adult eels die after spawning, and newly hatched larvae and elvers cannot acquire freshwater parasites at sea, these host-specific, freshwater parasites could not have been introduced to the new continent by colonizing leptocephalids.

The disjunct distribution of the four parasites possessing different complex life cycles, *Bothriocephalus claviceps*, *Proteocephalus macrocephalus*, *Daniconema anguillae*, and *Paraquimperia tenerrima*, argues for the former continuous freshwater distribution of a single ancestral eel host. The ancestral eel population probably diverged into two groups allopatrically as a result of glaciation ("vicariant" hypothesis). Parasites with discontinuous distributions provide important evidence for the former continuity of a host species (Metcalf 1920; Manter 1966). Dispersal of these freshwater parasites could not occur across the Atlantic Ocean because of their strict host specificity and the inability of infective stages to survive extended transport in a marine environment. Through association by descent, parasite-host coevolution results from two processes, coaccommodation (mutual adaptation between host and parasite) and cospeciation (concomitant host and parasite speciation) (Brooks 1979). Furthermore, allopatric speciation can account for all observed patterns of host-parasite associations. However, Brooks (1979, pp. 300–301) further states "an allopatric speciation event is readily acceptable to explain the situation in which two sister-species of host harbor the same species of parasites wherein it is assumed that an isolation event led to host speciation but not parasite speciation." This situation appears applicable to the parasites of American and European eels, though some of the parasites may be undergoing speciation events but are not yet morphologically distinct.

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