

## Trans-equatorial connections between biotas in the temperate eastern Atlantic

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**Abstract.** Several marine genera and species occur in the shallow-water temperate biotas of Europe and southern Africa, but not in tropical West Africa. Studies of the fossil record show that these trans-equatorial distributions were achieved before the Late Pliocene rather than during glacial episodes of the Pleistocene. Species of North Pacific origin entered the northeastern Atlantic at the beginning of Middle Pliocene time, and many penetrated to warm-temperate coasts of the Mediterranean and northwestern Africa. The fact that no Pacific-derived shallow-water molluscs and only one Pacific-derived algal genus (*Laminaria*) reached southern Africa without human agency suggests that trans-equatorial interchange was infrequent after the opening of Bering Strait during the Middle Pliocene, about 3.5 million years ago. The West African tropical zone must have remained wide enough or warm enough from the Late Pliocene onward to have acted as an effective barrier in which temperate species were unable to survive even during glacial times.

### Introduction

The temperate marine biotas of Europe and southern Africa have many genera and species in common. In many cases, species or populations in tropical West Africa link these temperate representatives geographically, but other genera and species have disjunct distributions. Examples of disjunct taxa include the pelecypod species *Gari depressa* and *G. costulata* (von Cosel 1989), the pelecypod genus *Pecten* (Waller 1991), the opisthobranch gastropods *Retusa truncatula*, *Limacia clavigera*, and *Tritonia nilsodhneri* (Gosliner 1987), the limpet genera *Puncturella* and *Helcion*, the lobster genus *Homarus* (Holthuis 1974), and the kelp genus *Laminaria* (Kain 1979). Disjunctions such as these arise either because geographically intermediate populations have become extinct or because the tropical barrier was breached by long-distance dispersers. Glacial episodes during the Pleistocene have traditionally been blamed for most bipo-

lar and bitemperate disjunctions, including those in the eastern Atlantic (Hubbs 1952, Beu 1976, Gosliner 1987). At these times, the tropics were either cooler or latitudinally more restricted than they were before or since, or sites of cold-water upwelling suitable for the survival of temperate species in the tropical zone were more extensive or more widespread than today.

In order to understand the history of these disjunct distributions, it is necessary to establish when and how the trans-equatorial distributions were established, and when and how the northern and southern temperate populations came to be cut off from each other. In this paper, I shall review biogeographical and paleontological evidence pertaining to molluscs and algae to argue that the trans-equatorial distributions of temperate shallow-water taxa in the eastern Atlantic were achieved mainly before the Late Pliocene rather than during glacial episodes of the Pleistocene. Implications for the Pleistocene marine climate of tropical West Africa are also briefly explored.

Because the Neogene fossil record of southern Africa is almost entirely confined to strata of Late Miocene and younger age (Hendey 1981), the history of biogeographical connections between Europe and southern Africa is difficult to reconstruct. I shall employ two lines of evidence to constrain the times of origin of trans-equatorial distributions and of the temperate disjunctions. These are: (1) the known fossil record of disjunct taxa in Europe; and (2) the occurrence in South Africa of taxa known to have entered the North Atlantic from the North Pacific no earlier than Mid-Pliocene time.

### History of disjunct taxa

Consider first the disjunct native eastern Atlantic molluscan groups. The pelecypods *Gari depressa* and *G. costulata* are both known from Early Pliocene (Scaldisian) time onward in the North Sea Basin of Europe (Janssen et al. 1984). The subgenera to which they belong have existed in western Europe since at least the Oligocene

(Janssen 1979 a). If *G. depressa* and *G. costulata* arose in Europe, as the long history of their subgenera in Europe suggests, the trans-equatorial distribution of these species could have been established at any time from the Early Pliocene onward.

Evolutionary studies of fossil and living species of the scallop genus *Pecten* (Waller 1991) suggest that this genus arrived in the Mediterranean from the east during the Late Miocene. The South African species (*P. sulci-costatus*) appears to be more closely related to the western European *P. maximus* than to the Mediterranean *P. jacobaeus* (Waller 1991). Although *P. maximus* is known only from the Pleistocene onward, its forerunners are known in the North Sea Basin as early as the Early Pliocene. Neither the times of divergence nor the branching order of species are known with certainty, but invasion to South Africa by *Pecten* spp. cannot be ruled out for any time interval from the Late Miocene onward.

The opisthobranch *Retusa truncatula*, known in South Africa as far west as False Bay (Gosliner 1987), extends from the Late Miocene (Sylvian) to the Recent in western Europe (Hinsch 1977). The genus is known in Europe since at least Oligocene time (Janssen 1979 b). If *R. truncatula* had a North Atlantic origin, this species could have extended its range to South Africa as early as the Late Miocene.

All these disjunct molluscan taxa, then might have reached southern Africa from Europe at any time since the Late Miocene or Early Pliocene. We have no firm indications whether the trans-equatorial distributions were achieved by long-distance dispersal across a hostile tropical belt or by a slow southward invasion along the coast of West Africa followed by the disappearance of populations in what is now the tropical zone.

Direct evidence of the time of interchange between biotas of the northeastern Atlantic and southern Africa comes from de Muizon's (1982) phylogenetic studies of seals. The extinct Early Pliocene South African *Homiphoca capensis* is thought to have descended from an ancestor related to the Pliocene North Atlantic genus *Callophoca*. If this phylogenetic interpretation is correct, interchange leading to the establishment of *Homiphoca* would have been no later than the Early Pliocene.

A probable case of invasion in the opposite direction is the limpet genus *Helcion*. In Europe, this group is represented by *H. (Ansates) pellucidus*, a kelp-associated cool-temperate species whose earliest fossil record is from the Late Pliocene of Iceland (Gladenkov et al. 1980). There are three southern African species, all belonging to *Helcion* s.s., known from at least Late Miocene time onward. The interchange resulting in the establishment of *H. pellucidus* could not have occurred later than the Late Pliocene.

### Pacific elements in southern Africa

Events in the northern hemisphere have an important bearing on inferences about the time of origin of trans-equatorial distributions in the temperate eastern Atlantic. With the opening of Bering Strait during the Mid-

Pliocene, about 3.5 million years ago, a marine connection was established between the North Pacific and Arctic-Atlantic basins. Cold-adapted biotas in these two basins had been developing independently for the previous 30 to 40 million years (Marincovich et al. 1990). One biogeographical consequence of this new connection was the invasion of hundreds of marine species, including at least 261 molluscs, from the Pacific to the Atlantic (Vermeij 1991 and references therein). These invaders can be recognized on the basis of three criteria: stratigraphy (time of earliest occurrence of a given genus or species in the fossil record of the two basins), phylogeny (cladistic or molecular-evolutionary analysis of groups with representatives in the two basins), and biogeography (elimination of alternative geographical routes by an analysis of the geological or geographical distributions of groups in parts of the world other than the northern basins). Many of the invaders from the Pacific, or their immediate descendants, penetrated to the warm-temperate coasts of southwest Europe, the Mediterranean, and northwest Africa. Examples include the gastropods *Tectura testudinialis*, *Puncturella noachina*, *Littorina littorea*, *L. mariae*, *L. saxatilis*, *Buccinum undatum*, *B. humphreysianum*, *Neptunea* spp. *Nucella lapillus*, *Cryptonatica clausa*, and *Euspira pallida*; and the pelecypods *Chlamys islandica*, *Mytilus edulis*, *M. galloprovincialis*, *Mya* spp., *Macoma balthica*, *M. calcarea*, and *Panomya arctica* (see Vermeij 1991).

Applying my criteria for the recognition of Pacific-derived species, I find that at least 21 of the cold-adapted molluscs that have been reported from the Pleistocene of the western Mediterranean by Malatesta and Zarlenga (1986) have North Pacific origins. In their list of Holocene molluscs from the Canary Islands off northwest Africa, Talavera et al. (1978) include two species (*Amphissa acutecostata* and *Nucella lapillus*) that I infer to be Pacific-derived. Several of these species (including the species of *Mytilus*, *Littorina*, *Tectura*, *Mya*, *Macoma*, and *Panomya*) have planktonic dispersal stages. If the tropical barrier in West Africa was reduced or eliminated during cold intervals of the Late Pliocene and Pleistocene, some of these relatively warm-adapted Pacific-derived species should have been able to spread to temperate southern Africa. Analysis of the Late Pliocene to Recent faunas of southern Africa reveals that only four genera (*Mytilus*, *Littorina*, *Puncturella*, and *Nucella*) could be construed as invaders from the North Pacific. Below, I review each of these cases, and conclude that the South African representatives either were probably not derived from North Pacific ancestors or were brought to southern Africa through human agency.

The mussel genus *Mytilus* is a mainly northern-hemisphere group that until recently was unknown from southern Africa. In the northern hemisphere, *Mytilus* s. s. contains four species: *M. edulis* (North Atlantic), *M. galloprovincialis* (warm-temperate northeast Atlantic), *M. trossulus* (North Atlantic and North Pacific), and *M. coruscus* (northwestern Pacific) (see Kafanov 1987 and McDonald and Koehn 1988). According to Kafanov, *Mytilus* had a Tethyan origin during the Early Eocene, but the lineage giving rise to the four species mentioned

above originated in the North Pacific during the Late Eocene. When Bering Strait opened, *Mytilus* entered the North Atlantic. Electrophoretic evidence (Varvio et al. 1988) suggests that *M. edulis* arose from *M. trossulus*, and that *M. galloprovincialis* is a southern offshoot from the *edulis* stock. It is possible that the original Tethyan *Mytilus* persisted in the Mediterranean regions throughout the Neogene, and that the Pleistocene and Recent *M. galloprovincialis* is derived from this purported stock rather than from the Pacific-derived *trossulus-edulis* group; but there is no paleontological evidence in support of this scenario (Kafanov 1987). Several southern-hemisphere populations related to or conspecific with *M. edulis* are known from the southern hemisphere (southern South America, southwest Australia, New Zealand, and Kerguelen Island). The Kerguelen population, known as *M. edulis desolationis*, has been distinct since at least the Late Pliocene (Blot et al. 1988). The only *Mytilus* that has been reported from southern Africa is *M. galloprovincialis* (see Grant and Cherry 1985). An electrophoretic study (Grant and Cherry 1985) strongly suggests that the mussels are recently introduced from Europe or the Mediterranean area. This species has also been introduced to Japan, California, and perhaps Australia (McDonald and Koehn 1988). There is no evidence that *M. edulis* ever reached South Africa, either from the North Atlantic or from South America. The occurrence of ultimately Pacific-derived *Mytilus* in South Africa is, therefore, most likely attributable to human agency rather than to natural invasion.

*Littorina (Neritrema) saxatilis* is the only representative in South Africa of the subgenus *Neritrema*, which Reid (1990) has shown on cladistic evidence to have a North Pacific origin. Studies of electrophoretic polymorphism in the two known South African populations of this otherwise North Atlantic species suggest that, although divergence has occurred relative to European populations, this divergence has been recent (Knight et al. 1987). In the absence of compelling evidence to the contrary, and given that *L. saxatilis* is represented in South Africa by only two isolated populations of the salt-marsh morph of the species, the most plausible hypothesis is that this species was recently introduced by humans to South Africa from Europe (Knight et al. 1987).

The keyhole limpet genus *Puncturella* is represented in South Africa by a number of species, several of which appear to be very close to the North Atlantic and North Pacific *P. noachina* (see Herbert and Kilburn 1986). The latter species is known from Pliocene time onward in Europe, and probably invaded from the North Pacific, where the genus extends back to the Eocene. Although it is possible that the South African species of *Puncturella* are derived from northern-hemisphere stocks, the fact that the genus is well represented throughout the cool southern hemisphere suggests that *Puncturella* may have a long history there. Unfortunately, there is no fossil record of *Puncturella* in southern Africa, but elsewhere in the southern hemisphere the genus is known from the Duntroonian (Late Oligocene to earliest Miocene) of New Zealand (Beu and Maxwell 1990). In summary, a

northern origin for South African *Puncturella* is plausible, but other explanations of its history cannot be ruled out.

Several predatory gastropods in southern Africa have been assigned to the muricid genus *Nucella*, all other species of which occur in the North Atlantic and North Pacific. In the North Pacific, the genus extends back to the Early Miocene of California and Japan. The earliest North Atlantic representatives are from the Mid-Pliocene (Scaldisian) of Belgium and England. The South African species most similar to the living North Atlantic *N. lapillus* is *N. dubia*. One interpretation is that the latter species is derived from a northern-hemisphere *Nucella*, but the fact that *N. dubia* occurs in Upper Miocene strata at Langebaanweg in South Africa (Hendey 1981) makes this very unlikely. Work in progress suggests that, although *Nucella* in South Africa is anatomically very similar to northern members of the genus (S. Kool personal communication, April 1991), the pattern of spiral sculpture in the southern African species differs from that in the northern forms. *Nucella* is anatomically very similar to a number of southern-hemisphere muricids (S. Kool personal communication). It is therefore possible that the whole *Nucella* complex of genera originated in or came to the southern hemisphere early in the Neogene or the Paleogene, and that *Nucella* spread to the North Pacific by Early Miocene time. The possibility remains that one or more South African species of *Nucella* invaded the northeastern Atlantic, where they could have given rise to *N. lapillus* or the Pliocene *N. tetragona*. Phylogenetic analysis in progress may shed further light on this possibility. Early forms of *N. lapillus* in Europe, however, do not closely resemble *N. dubia*, and are much more similar in shape and sculpture to several North Pacific species. *N. tetragona* has some sculptural similarities with the South African Pliocene *N. praecingulata* and the Recent *N. squamosa*. If there is an evolutionary link between the latter two South African species and the European *N. tetragona*, it would imply an early to Mid-Pliocene dispersal event.

In groups other than molluscs, the only plausible genus with North Pacific origins in South Africa is the kelp *Laminaria*. Two species of this otherwise northern-hemisphere genus occur in southern Africa, namely *L. shinzii* (apparently restricted to Walvis Bay) and *L. pallida*, which is found also at New Amsterdam and St. Paul Islands in the southern Indian Ocean (Kain 1979). *L. pallida* is very similar to the Mediterranean *L. ochroleuca* (Kain 1979). Estes and Steinberg (1988) have marshalled evidence in favor of the view that *Laminaria* and all other kelp genera originated during the Neogene in the North Pacific. With the opening of Bering Strait, several stocks of *Laminaria* invaded the Arctic-Atlantic basin. Although several kelps invaded the southern hemisphere in the Pacific (e.g. *Macrocystis*, *Ecklonia*, and *Lessonia*), *Laminaria* is the only one likely to have done so in the Atlantic. This dispersal was most likely along the West African coast some time after the Early Pliocene. Estes and Steinberg (1988), citing two reported occurrences of *Laminaria* in subtropical deep waters off Brazil (Kain 1979), thought that the dispersal route of *Laminaria* was

along the western side of the Atlantic. However, the similarity of *L. pallida* to the Eastern Atlantic *L. ochroleuca* strongly suggests to me that *Laminaria* dispersed along the African coast. Regardless of its route, *Laminaria* is not known today from tropical West Africa, and represents the only plausible example of a shallow-water taxon of North Pacific origin in the temperate southern African biota known to me.

### Discussion and conclusions

Most of the biogeographical evidence reviewed above indicates that contact between the temperate biotas of Europe and southern Africa occurred before or during the Pliocene. If interchange had been possible during the Late Pliocene and Pleistocene, at least some of the two dozen or more molluscan species of North Pacific origin that had penetrated the warm-temperate zone of the eastern Atlantic would have extended their range to southern Africa. Although Pleistocene interchange cannot be excluded for some of the molluscs with present-day disjunct bitemperate distributions in the eastern Atlantic, a Mid-Pliocene or earlier interchange via long-distance dispersal is possible in all cases. The divergence of the seal *Homiphoca* from *Callophoca* was Early Pliocene at the latest and must have followed dispersal of the ancestral form from north to south. The only taxon of North Pacific origin in southern Africa appears to be *Laminaria*, which could not have arrived earlier than the mid-Pliocene. Based on this evidence, I conclude that interchange between Europe and southern Africa was most likely during the Early Pliocene. If it continued through the Late Pliocene and Pleistocene, it must have involved only a very small number of species.

The use of North Pacific invaders to constrain the time of interchange between temperate biotas in the eastern Atlantic might be seen by some skeptics as inappropriate. It could be argued that no species that invaded the North Pacific from the North Atlantic via the Arctic was a participant in the trans-equatorial interchange in the temperate eastern Pacific, despite the observation that many native North Pacific taxa clearly did enter temperate South America during the Pliocene and Pleistocene, well after the opening of Bering Strait. This line of argument can be countered by two observations. First, the number of North Pacific species of North Atlantic origin is small (about 34, according to the compilation of molluscs by Vermeij 1991). Second, most invaders from the North Atlantic did not extend to the warm-temperate zone in the northeastern Pacific and would therefore have been unlikely candidates for trans-equatorial invasion. By contrast, many invaders from the Pacific to the Atlantic do or did range into the warm-temperate zone in the Atlantic. Thus, whereas many European species of Pacific origin would have been geographically and climatically in a position to extend to temperate South Africa given a narrower or cooler tropical belt, Atlantic invaders to the Pacific were too few and geographically too far removed to have had the same opportunity in the eastern Pacific to extend to the southern hemisphere.

For similar reasons, western South American taxa that invaded the North Pacific are unrepresented in biotas of the North Atlantic, and no species of South African origin in the North Atlantic is known from the North Pacific. These trans-equatorial invaders were generally warm-temperate species for which the Arctic may have presented an insuperable cold barrier.

It is unclear why the Early Pliocene should have been a time favorable to interchange between the northern and southern temperate biotas in the eastern Atlantic. Studies of the faunal succession at Langebaanweg, about 120 km north of Capetown, led Hendey (1981) and Olson (1984) to postulate that the Early Pliocene was markedly cooler than was the preceding interval of the Late Miocene. However, the strata considered by these authors to represent Early Pliocene time may in fact prove to be of Late Pliocene age (Kensley and Pether 1986), and the strata earlier interpreted to be of Late Miocene age may instead chronicle the Early Pliocene. If this newer interpretation stands, the Early Pliocene would have been warm, as it was in the North Sea Basin and elsewhere in temperate Europe, whereas the Late Pliocene was much cooler, as it also was in Europe; It is odd, therefore, that interchange involving temperate species would have occurred during the relatively warm interval of the Early Pliocene.

One possible explanation is that the strength of the equatorward eastern-boundary currents increased during the Early Pliocene. The currents involved are the northward-flowing Benguela Current along the west coast of southern Africa, and the southward-flowing Canary Current in northwestern Africa. That upwelling conditions (and therefore the Benguela Current) existed in southern Africa is suggested by phosphorite deposits in the Langebaanweg succession (Hendey 1981). One reason for an increase in the intensity of Atlantic circulation was the shoaling and ultimate closure of the Central American seaway during the Pliocene. The Gulf Stream in the North Atlantic increased in velocity as the seaway closed (Kaneps 1979), and quite possibly this increase affected other currents in the Atlantic as well (Berggren and Hollister 1977). If the eastern boundary currents did strengthen, trans-equatorial dispersal of temperate species might have become more likely. This entire scenario must, however, be regarded as speculative. Much remains to be learned about the climatic and oceanographical history of the eastern Atlantic.

In his review of trans-equatorial interchange in the eastern Pacific, Lindberg (1991) identified a number of temperate taxa that evidently extended their ranges north or south during the early Pleistocene. His findings therefore imply that Pleistocene interchange may have been more extensive across the equator in the eastern Pacific than in the eastern Atlantic.

It may be no accident that the only definitely Pacific-derived invader via the North Atlantic to southern Africa is an alga. In the eastern Pacific, the proportion of disjunctly distributed seaweeds in the marine flora of temperate western South America is higher (7.1%) than that of molluscs (< 5%) (Santelices 1980, Lindberg 1991). Algae such as kelps may disperse more readily than do marine animals.

The disjunct temperate taxa discussed here are chiefly shallow-water forms that, with the possible exception of *Puncturella*, could not traverse the tropical zone in deep cold water. Numerous genera and families that occur in relatively shallow waters at high latitudes live at greater depths in the tropics (see e.g. Hubbs 1952). These tropically submerged taxa probably achieved their bipolar distributions much earlier than the shallow-water taxa considered in this paper.

The timing of north-south interchange in the eastern Atlantic and eastern Pacific bears on interpretations of marine conditions in West Africa and western tropical America. If the Late Pliocene and Pleistocene were generally unfavorable to long-distance trans-equatorial dispersal of shallow-water species between southern Africa and Europe, as argued above, then West Africa's tropical belt must have remained warm enough or wide enough to act as an effective warm-water barrier even during the glacial intervals of the last three million years. This interpretation is consistent with the observation that tropical West Africa serves as a major refuge for warm-water taxa that, during the Pliocene, also occurred in either the Mediterranean or the tropical western Atlantic (Vermeij 1986). The eastern Pacific tropics also provide refuge for species whose Miocene and Pliocene distributions were broader (Vermeij 1986). Although the latitudinal extent of the tropical marine belt is similar in the eastern Atlantic and eastern Pacific (about 30 degrees of latitude), there may have been more "stepping stones" in the form of sites of persistent cool-water upwelling in the eastern Pacific that permitted more trans-equatorial dispersal in the eastern Pacific (Lindberg 1991) than in the eastern Atlantic. Perhaps the climatic variations associated with the El Niño-Southern Oscillation cycles, which are far greater in the eastern Pacific than in the Atlantic, have exacerbated this difference. Upwelling varies greatly in extent and intensity from year to year, and sometimes has been strong enough to cause widespread mortality of eastern Pacific reef corals (Glynn et al. 1983). Trans-equatorial dispersal may be easier at times of unusually intense upwelling than at times when cold-water upwelling fails, as during El Niño years. Although there is upwelling along the coast of tropical West Africa as well, the kind of oceanographic variation among years that is characteristic of the eastern Pacific does not seem to affect the eastern Atlantic as much.

Speculative as the arguments in this paper are, they show that a knowledge of history of biotas and climates can contribute to the resolution of biogeographical problems. Further phylogenetic, paleontological, and stratigraphic work is certain to provide additional insights into the origins of bipolar distributions and other biogeographical patterns.

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