

Abstract.—The phylogeny and historical biogeography of hakes (*Merluccius*) are reexamined using a cladistic analysis of Inada's (1981) osteological data. One of the 188 most parsimonious trees (cladograms), which also has the lowest (best) *F* value, is congruent with the scheme of evolution proposed by Ho (1974) for the hake-specific copepod parasites. Offshore hake *M. albidus* is the sister group of all other extant hakes. Silver hake *M. bilinearis* is the sister group of the three eastern Pacific hakes: Chilean hake *M. gayi*, Panamanian hake *M. angustimanus*, and Pacific hake *M. productus*. The five Eastern Atlantic species, European hake *M. merluccius*, Senegalese hake *M. senegalensis*, Benguelan hake *M. polli*, shallow-water cape hake *M. capensis*, and deep-water cape hake *M. paradoxus*, are monophyletic and constitute the sister group that forms a trichotomy with Argentine hake *M. hubbsi* and New Zealand hake *M. australis*. The biogeography inferred from the most parsimonious phylogenetic hypothesis of hakes differs from the views given by both Inada (1981) and Kabata and Ho (1981). The ancestral hake in the eastern seaboard of North America diverged into two stocks. Subsequently, one of them vicariated into a northern and a southern population. The southern population moved southward first and then separated into three stocks, with one of them moving eastward and crossing the Atlantic in the region of low latitudes. One of the two remaining stocks moved further southward and entered the Pacific through the Drake Passage. After further divergence, a descendant stock of the northern population off the coast of North America also moved southward; it did not enter the south Atlantic, but, instead, moved into the Pacific over the submerged Panamanian Isthmus. Some geologic events are discussed for their possible effects in the formation of the present pattern of hake distribution.

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Phylogeny and Biogeography of Hakes (*Merluccius*; Teleostei): A Cladistic Analysis

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In 1981, two views on the historical biogeography of hake were proposed: one by T. Inada and the other jointly by Z. Kabata and J.S. Ho. Although inferred from different sets of biological information, ichthyological vs. parasitological, the two views are remarkably alike in most major points. Both views (Fig. 1) suggest that the hakes originated in the eastern North Atlantic and dispersed southward via two routes: one along the west coast of Europe and the other along the east coast of North America. These authors also arrived at the same conclusion that hakes entered the Pacific over the submerged Panamanian Isthmus. The major discrepancy between the two views lies in their accounts of the origin and dispersal of Argentine hake *Merluccius hubbsi*.

Using the coevolutionary relationships between hakes and their copepod parasites, Kabata and Ho (1981) suggested that the Argentine hake was derived from the western North Atlantic stock because it shares the subspecies of copepod parasite *Neobrachiella insidiosa lageniformes* with the silver hake *M. bilinearis* occurring off the east coast of North America. However, in contrast, Inada (1981) proposed that the Argentine hake was derived from an eastern South Pacific stock that rounded Cape Horn to reach Argentina. The Pacific origin of Argentine hake was first proposed by Szidat (1955, 1961), but Ho (1974) questioned its validity based on his studies on the copepod parasites of European hake *M. merluccius*, silver hake *M. bilinearis*, Chile-

an hake *M. gayi*, and shallow-water cape hake *M. capensis*. Contrary to the conclusion of Kabata and Ho (1981), Ho (1974) speculated that hakes originated in the western North Atlantic.

Recently, Fernandez (1985) studied the parasites of a population of New Zealand hake occurring at Guafo Island, Chile (lat. 43°36'S, long. 74°43'W), and corroborated the view of Kabata and Ho on hake biogeography. Since her study methods are the same as that of Kabata and Ho (1981), the above-mentioned disagreement between ichthyologist and parasitologist on the origin and dispersal of Argentine hake remains unresolved. A third method of investigation is needed.

Cladistic analysis is a systematic method that attempts to discover genealogical (phylogenetic) relationships of taxa (Hennig 1966, Wiley 1981). Since a detailed phylogenetic hypothesis for a group of organisms can and should serve as a basis for inferring the biogeographic history (Hennig 1966, Brundin 1966, Nelson and Platnick 1981, Humphries and Parenti 1986), I have used this approach to reexamine the phylogenetic relationships and biogeography of hakes. This paper reports my results.

Character analysis

In his revision of *Merluccius* Rafinesque, Inada (1981) recognized 12 species of hake (Table 1) and provided detailed redescription of each species, including measurements of 28

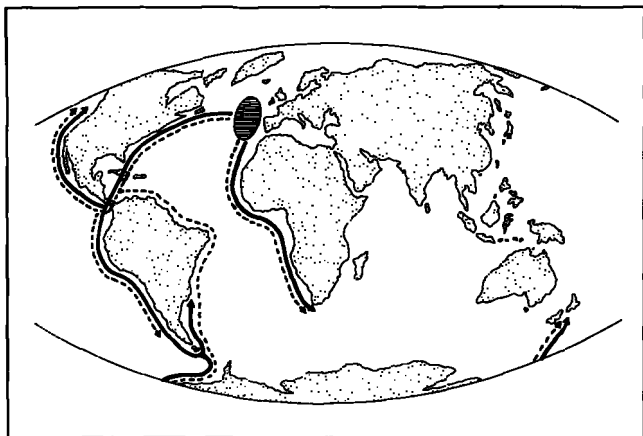


Figure 1

Distribution and movements of hakes as proposed by Inada (1981) (→) and Kabata and Ho (1981) (---→).

body parts and counts for nine meristic characters. Moreover, he added osteological information for 14 groups of bones, and discussed the distribution, biology, and fishery of all the species recognized. It is the most complete revision ever published on the genus *Merluccius*.

The morphological differences and diagnostic characters of the 12 species of hake were succinctly listed by Inada (1981, tables 37 and 38). Because quantitative variables are difficult to analyze cladistically (Pimentel and Riggins 1987), data in table 37 of Inada (1981) were not included in the present analysis. Thus, only the osteological information summarized in his table 38 was used.

Steindachneria is a problematical gadiform genus that has been treated as a merlucciid or as a monotypic family with uncertain affinities. Recently, Fahay (1989) presented evidence from ontogenetic and osteological grounds to support the removal of the genus from the Merlucciidae. Nevertheless, in his report on the systematics of Merlucciidae, Inada (1989) concluded that the family contains four genera in two subfamilies, Steindachneriinae (*Steindachneria*) and Merlucciinae (*Lyconus*, *Macruronus*, *Merluccius*). This treatment is in line with Nolf and Steurbaut's (1989) result based on analysis of otolith features. Therefore, I included *Steindachneria* in my analysis of outgroup genera to determine the sister group of *Merluccius*.

The osteological information given in Inada's (1989) Table 1 was used in my search for outgroup genera. Lotinae was selected as the outgroup to polarize the character states of the four merlucciid genera, because both the works of Dunn (1989) and Nolf and Steurbaut (1989) indicate that it is the nearest sister group of Merlucciidae. Since six of the thirteen enumerated characters in table 1 of Inada (1989: 199) show no dif-

Table 1

Extant species of hakes (*Merluccius*) recognized by Inada (1981), and their distribution.

Species	Common name	Distribution
<i>merluccius</i>	European hake	Europe, western North Africa
<i>senegalensis</i>	Senegalese hake	Western north Africa
<i>polli</i>	Benguelan hake	Mauritania to Angola
<i>capensis</i>	shallow-water hake	Angola to South Africa
<i>paradoxus</i>	deep-water cape hake	Nambia, South Africa
<i>bilinearis</i>	silver hake	Atlantic coast of North America
<i>albidus</i>	offshore hake	Western Atlantic, Gulf of Mexico, Caribbean
<i>productus</i>	Pacific hake	Pacific coast of North America
<i>angustimanus</i>	Panamanian hake	Baja California to Columbia
<i>gayi</i>	Chilean hake	Peru, northern Chile
<i>hubbsi</i>	Argentine hake	Argentina
<i>australis</i>	New Zealand hake	Southern Argentina, southern Chile, New Zealand

ferences in their states among the five genera under consideration, they were excluded from the present analysis. The BRANCH AND BOUND algorithm from the phylogenetic computer package PAUP (version 2.4.1, David L. Swofford, III. State Nat. Hist. Surv., Urbana 61820), which guarantees the finding of all the most parsimonious trees, was used in this analysis. Two trees were obtained, both with a consistency index of 0.667. The one with the lower F value (= 0.174) is selected and reproduced in Figure 2. Unexpectedly, it shows that *Merluccius* is a sister group of the rest of the merlucciid genera. This disagrees with the phylogeny proposed by Inada (1989) and Okamura (1989).

According to the outgroup procedure as proposed by Maddison et al. (1984), all three genera—*Steindachneria*, *Macruronus*, and *Lyconus*—were included in the analysis of the "outgroup node" for polarization of character states of the hake. Dr. Tadashi Inada (Tohoku Reg. Fish. Res. Lab., Same, Hachinohe 031, Japan, pers. commun., Dec. 1988) has kindly provided osteological information for these three genera. Appendix 1 gives the coding of osteological characters (Inada 1981) for the hake species, and Appendix 2 shows the matrix of the character states in the twelve extant species of hakes. A new species of hake, *Merluccius hernandezii*, has been reported from the Gulf of California (Mathews 1985) since revision of Inada. However, it is not included in the present analysis due to the lack of osteological information.

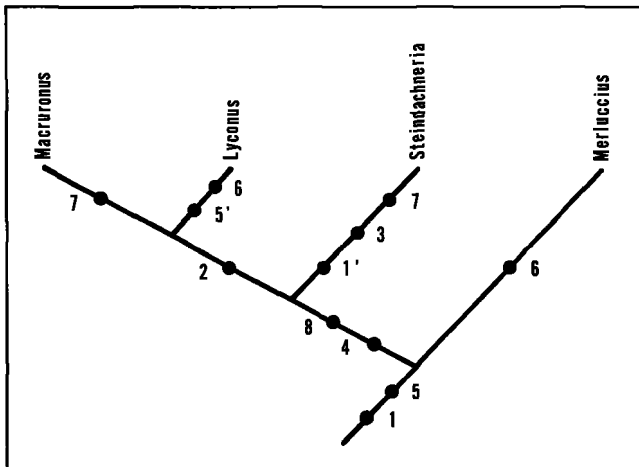


Figure 2

Cladogram showing hypothesized relationships of the merlucciid genera. Character codes: 1 = V-shaped crest on skull present; 1' = V-shaped crest on skull absent; 2 = foramen for trigemino-fascialis nerve present; 3 = shape of anterior parasphenoid vertical; 4 = upper window on suspensorium closed; 5 = two dorsal fins; 5' = one dorsal fin; 6 = one pseudospine in dorsal fin; 7 = two pseudospines in dorsal fin; 8 = caudal fin tapering.

Phylogeny

An unusually large number of trees (cladograms) were obtained, 188 in total, all with a consistency index of 0.522. The *F* value of these most parsimonious trees ranges from 0.277 to 0.482. However, there is only one tree with the lowest (best) *F* value, reproduced in Figure 3. Since the development of host specificity in parasites is the result of coevolution between the host and its parasite, an hypothesis of the host phylogeny should also apply to the phylogeny of its specific parasite. In other words, host-specific parasites can be useful to corroborate host phylogeny.

Brooks et al. (1986) suggested that the lower the *F*-ratio (= *F* value), the greater is the degree of historical constraint on the data. In this regard, the tree with the lowest *F* value (Fig. 3) should exhibit the highest degree of congruence with the parasite data set. To check this congruency, a parasite summary cladogram needs to be constructed. Figure 4 is such a cladogram, generated by replacing the hake species on the cladogram with each of their respective subspecies of *Neobrachiella insidiosa*, a host-specific copepod parasite of hakes. Since *Chondracanthus palpifer* Wilson was recently found by Villalba and Fernandez (1985) to parasitize not only *Merluccius* but also another merlucciid (*Macruronus magellanicus* Lönnberg) in Chilean waters, it can no longer be treated as a *Merluccius*-specific parasite as previously proposed. Accordingly, only the three subspecies of *Neobrachiella insidiosa* are considered.

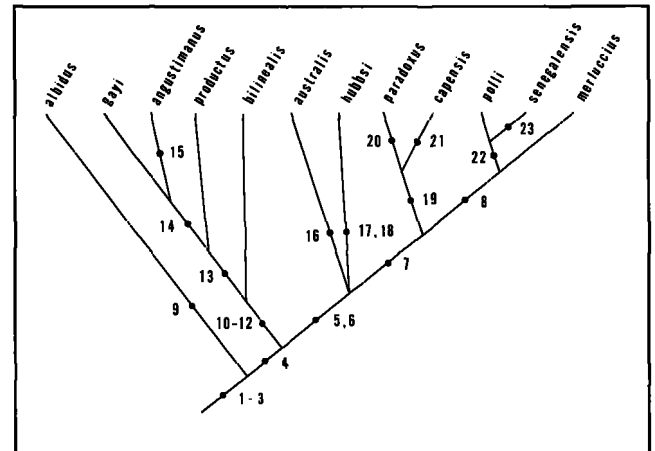


Figure 3

Cladogram showing hypothesized relationships among species of *Merluccius*. For character codes 1-23, see Appendix 1.

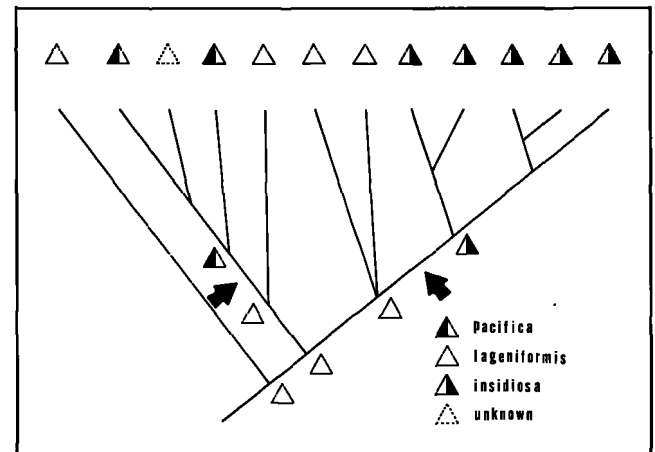


Figure 4

Parasite summary cladogram showing relationships among subspecies of *Neobrachiella insidiosa* inferred from hypothesized relationships among species of hake (*Merluccius*). Arrows indicate the changes (evolution) of parasites.

As in Figure 4, the result agrees, indicating that the hake-specific *Neobrachiella insidiosa* had changed (evolved) from *N. insidiosa lageniformis* (western Atlantic form) to *N. insidiosa insidiosa* (eastern Atlantic form) on one hand, and from the western Atlantic form (original form) to *N. insidiosa pacifica* (Pacific form) on the other. This scheme of evolution for *Neobrachiella insidiosa* contradicts the one proposed by Kabata and Ho (1981) but, nevertheless, agrees with the hake-parasite evolution proposed by Ho (1974). The phylogenetic hypothesis predicts a Pacific form of *N. insidiosa*, but it is yet to be found in *M. angustimanus*. The discovery of *N. insidiosa pacifica* on the Panamanian hake would strongly support the cladogram shown in Figure 3.

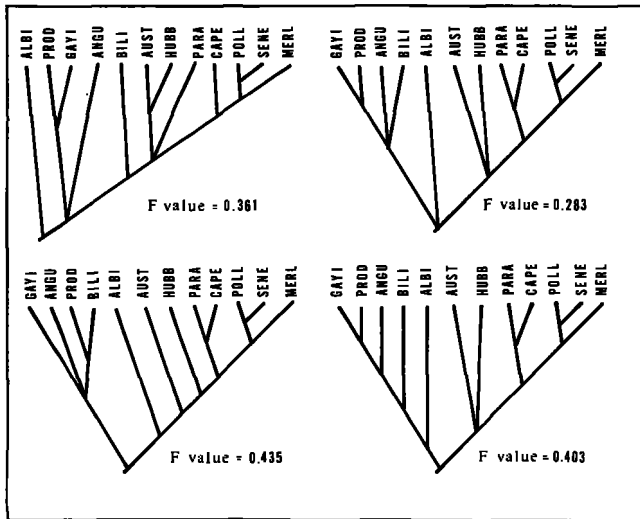


Figure 5

Examples of some most parsimonious cladograms of hakes (*Merluccius*). All have 23 steps and a consistency index of 0.522. Abbreviation of species names: ALBI = *albidus*; ANGU = *angustimanus*; AUST = *australis*; BILLI = *bilinearis*; CAPE = *capensis*; HUBB = *hubbsi*; MERL = *merluccius*; PARA = *paradoxus*; POLL = *polli*; PROD = *productus*; SENE = *senegalensis*.

With currently available information, the tree in Figure 3 is considered to be the better hypothesis than the other existing hypotheses of hake phylogeny. Admittedly, it has a high ratio of homoplasy (17/23 or 73.9%). Such frequent homoplasy is somewhat undesirable in a cladistic analysis. Nevertheless, using different sets of characters (number of gill-rakers, vertebrae, and fin rays), Inada (1981) identified five groups in his key to the species of *Merluccius*, with four species (*australis*, *bilinearis*, *hubbsi*, *polli*) in two groups, two species (*gayi*, *senegalensis*) in three groups, and one species (*capensis*) in four groups. This repeated sharing of many characters (high frequency of homoplasy) seems to be the norm in *Merluccius*.

Close examination of each of the 188 most parsimonious trees revealed that European hake *M. merluccius*, Senegalese hake *M. senegalensis*, Benguelan hake *M. polli*, shallow-water cape hake *M. capensis*, deep-water cape hake *M. paradoxus*, Argentine hake *M. hubbsi*, and New Zealand hake *M. australis* are always included in a monophyletic group. However, relationships among the three eastern Pacific hakes—Chilean hake *M. gayi*, Panamanian hake *M. angustimanus*, and Pacific hake *M. productus*—and the two western North Atlantic species—silver hake *M. bilinearis* and offshore hake *M. albidus* are not as consistent. Some representative trees are reproduced in Figure 5 for comparison. Offshore hake (ALBI, Fig. 5) appears to occupy the most plesiomorphic node in almost all cases. This is an

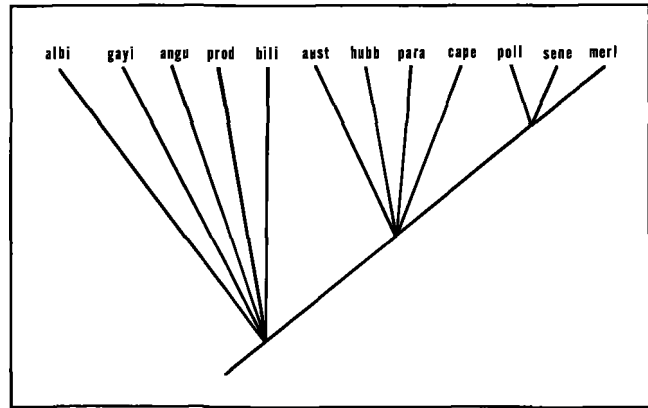


Figure 6

Strict consensus tree of hakes showing information common to the 188 equally parsimonious trees. For abbreviation of species names, see Figure 5.

indication that offshore hake is the extant species closest to the ancestral form.

The strict consensus tree in Figure 6 was obtained using the CONTREE algorithm contained in the PAUP program. It summarizes the point of agreement in all 188 equally parsimonious trees. Remarkably, the monophyletic relationships of the seven species of hakes occurring off the coasts of Europe, Africa, and eastern South America are also supported by this consensus tree.

Biogeography

According to the principle of vicariance biogeography (Nelson and Platnick 1981, Humphries and Parenti 1986), the pattern of spatial distribution attained by the hakes can be deduced from the phylogenetic hypothesis. The area summary cladogram in Figure 7 illustrates how the present pattern of hake distribution was attained. According to the progression rule of Hennig (1966), it implies that the ancestral hake, residing in the western North Atlantic, diverged into two lineages. One gave rise to the modern offshore hake (ALBI, Fig. 7), and the other formed the species A, which is the ancestor of all the remaining extant hake species. Species A vicariated into two populations: the northern population (C, Fig. 7) whose descendants later occupied the Pacific Ocean, and the southern population (B, Fig. 7), whose descendants gave rise to all the hakes in the western South Atlantic and entire eastern Atlantic.

I interpret the cladogram to mean that (1) hake originated in the western North Atlantic, (2) migrated southward and then eastward in the Atlantic, and (3) entered the Pacific in two ways, over the submerged

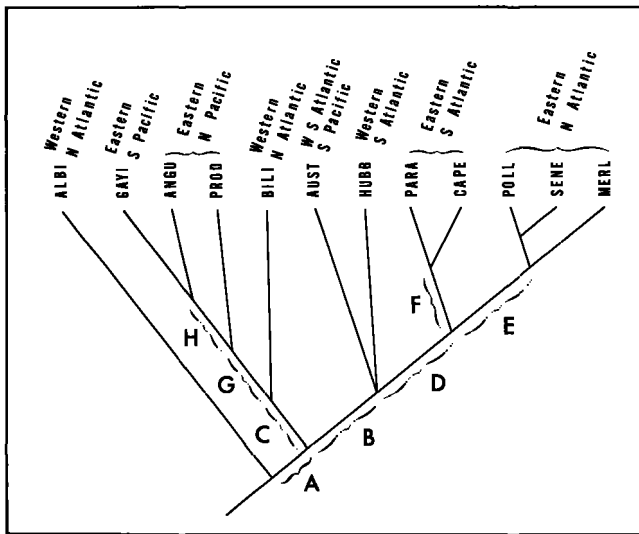


Figure 7

Area summary cladogram of hakes (*Merluccius*) with ancestral species (A-H). For abbreviation of species names see Figure 5.

Panamanian Isthmus and through the Drake Passage. Assertion (1) agrees with the proposal of Ho (1974) concluded from a work on host-specific copepod parasites of hake, but it contradicts Inada (1981) and Kabata and Ho (1981) who suggested otherwise. Assertion (3) is roughly the same as those suggested by Inada (1981) and Kabata and Ho (1981), differing only in the details. However, the 2nd assertion is a new discovery; this track has never been proposed.

Inada (1981) speculated that hakes had migrated out of the western Atlantic only once, when they dispersed to the southern hemisphere during the Pliocene over the submerged Panamanian Isthmus. He believed that the hakes could not have migrated to the South Atlantic along the coast of Brazil because the low salinity in the estuarine area of the Amazon River would have acted as a natural barrier to their dispersal. However, the Amazon River estuary was not an effective deterrent to hake dispersal in the early Tertiary. In work on the coevolution between freshwater stingrays and helminth parasites, Brooks et al. (1981) concluded that the Amazon Basin became a separate eastward-flowing entity in the Miocene. Moreover, Damuth and Kumar (1975) reported that the Brazilian plate developed a geosyncline downfold when the Andes began to fold up in the Pliocene, and, as the result of this lowering of the eastern side of the plate, the water from the landlocked sea (of the Pre-Amazonas) started to flow eastwards to the Atlantic. Therefore, during and prior to the Miocene the salinity in this area could not have been as low as it was in the Pliocene and the ancestral hakes could have migrated to the South Atlantic along the coast of Brazil. If true, migration

pathways of hake would be different from those proposed by Inada.

Both the works of Inada (1981) and Kabata and Ho (1981) indicated that European hake *M. merluccius* occur in the region of the North Atlantic inhabited by the original stock (Fig. 1). However, the phylogenetic hypothesis (Fig. 3) implies that European hake is the most derived species among the eastern Atlantic hakes, and, consequently, could not be the one occupying the original habitat (Hennig 1966, Wiley 1981).

Before discussing further the biogeography of hake inferred from the phylogenetic hypothesis given in Figure 7, some points about the nature of the movement and range expansion of hake need to be explained.

Hakes of the genus *Merluccius* are coastal inhabitants occurring in the waters above the continental shelf and slope. Most species exhibit a seasonal on-shore-offshore bathymetric migration correlated with water temperature. Adults and juveniles move inshore during the spring. When winter cooling occurs on the shelf, they migrate to warmer waters on the continental edge and slope (Grinols and Tillman 1970). Additionally, the silver hake and Pacific hake apparently undertake a latitudinal migration (Bailey et al. 1982, Leim and Scott 1966, Nelson 1969). During the fall they move southward and then return to more northerly waters during the late spring. Clearly, paleotemperature changes in the ocean could be one of the factors in altering the limits of the distribution of hake in the past: they expanded onto the continental shelf or slope of lower latitudes when there was a cooling trend, and retreated to the waters of higher latitudes when the cooling trend subsided.

The copepod parasite *Neobrachiella insidiosa lageniformes* has been recorded from widely separated species of hake, e.g., the silver hake off the coast of Florida and the New Zealand hake in the western South Pacific (Kabata and Ho 1981). Since this parasite is found mostly on the adult hake, rarely on juveniles and never on the larvae, the dispersal of this parasite from North America to New Zealand via the South American coast must have been effected by the adults. Besides, this parasite belongs to the family Lernaeopodidae which is noted for a brief stage of free-living during development. It is logical to assume that adult hakes, not larvae, are responsible for extending their range.

The offshore hake *M. albidus*, primarily an inhabitant off the U.S. east coast and in the Gulf of Mexico and Caribbean (Inada 1981), does not share its clade with any extant hake (Fig. 7). The distributional ranges of its ancestor must have waxed and waned like other ancestral hakes with the changes of ocean temperature and sea level. However, it is very likely that this stock of hake stayed mostly in the Gulf of Mexico and

Caribbean for most of the time since its evolution in the Eocene.

Geologic events that cause fragmentation of the contiguous, ancestral distribution are considered the major means of distributional pattern formation (Nelson and Platnick 1981). Although not all vicariant events are identifiable at present, those known geologic events that could have produced the present pattern of hake distribution are explored below.

Range expansion and vicariance of species B

The closeness between fossil members of the genera *Palaogadus* and *Merluccius* has led Fedotov and Bannikov (1988) to speculate that hake originated from a species related to *Palaogadus intergerinus* in the Middle Miocene. However, since fossil records indicate the minimum age, the discovery of fossil *Merluccius inferus* from the Tethys area of the Soviet Union in the Middle Oligocene deposit may not necessarily signify that *Merluccius* originated in the Middle Oligocene. The genus could have made its appearance much earlier. It is unclear when the hakes living on the western North Atlantic seaboard (off North America) diverged into two stocks, but species B must have expanded its range southward and moved into the continental shelves of low latitudes in the late Eocene (about 40 million years ago [MA]), an age characterized by a major decrease in annual temperature (Frakes 1979, Wolfe and Poore 1982). According to Savin et al. (1975), equatorial temperatures may have been as low as 20°C throughout the Oligocene (35–25 MA); consequently, species B most likely migrated into Brazilian waters during this long cooling period.

In his discussions on Caribbean biogeography, Rosen (1975, 1978, 1985) concluded that there was an isthmian land bridge between North and South America in the late Cretaceous or early Cenozoic. A similar intercontinental link was also suggested by Savage (1966, 1982), Axelrod (1975), and White (1986) in their biogeographic studies on the herpetofauna, plants, and silverside fishes, respectively. Alternatively, recent geologic reports suggested that this isthmian link was most developed sometime in the Eocene (Coney 1982, Pindell and Dewey 1982). In that case during their southward range expansion, hakes of the species B would have been prevented from entering the Pacific.

The area cladogram (Fig. 7) obtained from the adopted phylogenetic hypothesis (Fig. 3) indicates that species D had expanded across the Atlantic Ocean to become the common ancestor of hakes in the eastern Atlantic. The occurrence of such range expansion would invoke a geologic event with a shallow-water (<200 m) connection between South America and Africa, because, from the parasitological point of view,

it is the demersal adult hakes (and not the planktonic larvae) that are responsible for this range expansion. Since the fossil hake *Merluccius inferus* is known from the middle Oligocene deposit in Europe (Svetovidov 1940), this eastward crossing of the Atlantic must have occurred in the early Tertiary. However, no such extension of continental shelf in the Tertiary has been proposed by geologists, except Vail et al. (1977) who recognized five major lowstands in the Tertiary (Mid-Paleocene, Early-Mid Eocene, middle Late Oligocene, Late Miocene, and Late Pliocene-Early Pleistocene). According to them, during these lowstands the sea level fell below the edge of the continental shelf in most regions; thus, the eastward expansion of species D across the Atlantic Ocean in the low latitudes was possible. After reaching the eastern Atlantic, it spread north and south along the coast of Africa.

In the Early Miocene between 22 and 20 MA, the prolonged cooling trend initiated in the late Eocene was reversed (Haq 1982). Temperatures in low latitudes rose to modern values and might have exceeded 30°C in some areas. This change in global climate, even if it did not affect the adult hakes because of their preference for deep water (Grinols and Tillman 1970), could have effectively prevented hatching of their eggs (normally at 11–14°C) and the normal growth of their epipelagic larvae (found usually at 40–60 m); thus, the hakes were prevented from occupying waters of low latitudes. This unusual warming of the tropical waters can be viewed as a vicariance event that split species D into a northern segment which later developed into another ancestral form (species E, Fig. 7), and a southern segment representing the common ancestor (species F, Fig. 7) of the shallow-water and deep-water cape hake. Species E must have invaded again the waters of low latitudes during another cooling, which started in early Middle Miocene (about 15 MA) when a major enlargement of the East Antarctic ice-sheet developed (Savin 1977, Woodruff et al. 1981). This would account for the presence of Benguelan hake *M. polli*, one of the descendants of species E, in the tropical waters of the eastern Atlantic. However, further divergence of species E is unclear given the present knowledge of geologic history.

The ancestor of New Zealand hake *M. australis* is a sister group of species D. It must have occupied the continental shelf off Argentina when the latter crossed the Atlantic. The extinct hake *Merluccius fimbriatus*, known from the Miocene deposit in Victoria, Australia (Stinton 1958), may be a descendant of this stock since the Drake Passage had remained open since the Oligocene, between 29 and 28 MA (Haq 1984). According to Inada (1981), there are two distinct populations of New Zealand hake: the New Zealand population living in New Zealand waters, and the Patagonian

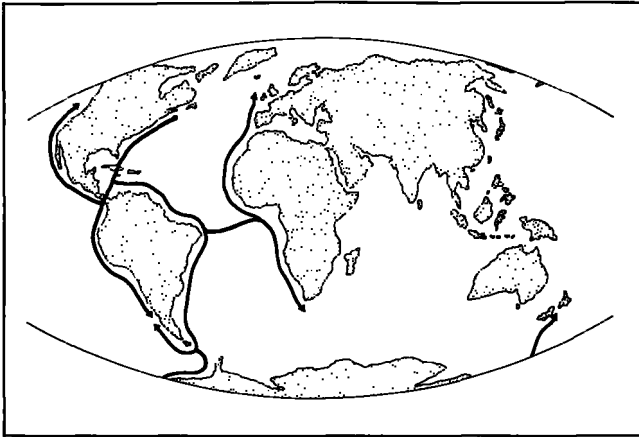


Figure 8

Dispersal routes of hakes inferred from the area summary cladogram in Figure 7.

population living on both sides of the southern part of South America south of 40°S. Interestingly, both populations, in spite of being distantly separated by the Pacific, carry the same species of copepod parasite—*Neobrachiella insidiosa lageniformes*—on their gills (Kabata and Ho 1981), a clear indication that the New Zealand population must have originated from the hakes in South American waters.

Range expansion and vicariance of species C

According to the proposed history of the relative motion of the plates in the Gulf of Mexico/Caribbean region, Pindell and Dewey (1982) concluded that the large-scale eastward migration of the Caribbean plate started in the Oligocene (about 36 MA) and eventually placed the Greater Antilles in their present positions. It is assumed that species C, as in species B, expanded southward prior to the initiation of this Caribbean plate movement. However, being a northern population, it did not reach as far south into the South Atlantic as Species B. Instead, it expanded into the Pacific when the Panamanian seaway was opened in the Oligocene.

As with the hake in the eastern Atlantic, species C was prevented from inhabiting the waters of low latitudes when the climate warmed in the Early Miocene. By this restriction, species C was divided into an Atlantic population, which eventually gave rise to silver hake *M. bilinearis* and a Pacific population (species G, Fig. 7) which became the ancestor of the three eastern Pacific species. The fossil remains of the Pacific hake *M. productus* are common in the Pliocene deposit of California (Fitch 1969, Fitch and Reimer 1967, Zinsmeister 1970), indicating that the divergence of species G into species H and Pacific hake (*M. productus* or its immediate ancestor) took place either in Miocene or Pliocene.

Species H was very likely confined to the North Pacific off the coast of Mexico until the Pliocene when the Panamanian isthmus was reestablished at about 3 MA (Haq 1984). Panamanian hake *M. angustimanus* is found from Baja California to Colombia, but not in the Caribbean; therefore, species H must have moved southward after closing of the Panamanian seaways. The vicariance event responsible for the separation of species H into Panamanian hake and Chilean hake is unclear, but the influence of the Ice Ages during the late Pliocene and Pleistocene may have played a role.

Conclusion

The phylogenetic hypothesis of hake (Fig. 3) presented here is the most parsimonious scheme derived from the cladistic analysis of the osteological data of Inada (1981). It is congruent with the scheme of evolution proposed by Ho (1974) for the hake-specific copepod parasites. This is a testable model; it can be corroborated by including more anatomical data (e.g., musculature), ontogeny, karyology, DNA sequences, and allozymes. Parasitological information from protozoans, helminths, and crustaceans can also provide further corroboration, particularly when hake-specific parasites are found among them.

The vicariance model proposed for the hake biogeography is based on the adopted most-parsimonious tree that shows congruence with the available parasitological information. The inferred pattern of biogeography, particularly the track across the Atlantic in the low latitudes (Fig. 8), is yet to be reported for demersal fishes. However, it should be mentioned that Van der Spoel and Heyman (1983) considered that the planktonic faunas of the Panama Passage and South American inland sea as ancestral to all eastern Atlantic distant neritic taxa, and proposed a similar eastward dispersal.

The ranges of ancestral hake waxed and waned with the fall and rise of paleoceanographic temperatures in the Tertiary, dispersed during the cooling periods and fragmented by the development of warming trends. Development of major lowstands in sea level is also viewed as an effective vicariant event. This model can be tested with additional details of the plate-tectonic models and paleoceanographic-climatic history. Works on other marine life with similar distributions would test the validity of the three inferred general tracks.

Both the phylogenetic hypothesis and biogeographic model differ from current views, but they are viewed as the better explanation of available data. They are presented here as a working model subject to modification as more exact information becomes available.

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Appendix 1

Coding of osteological characters for the hake species (Imada 1981).

Character	States of character (code)
Gill raker length	0: short 1: medium (10)(19)(23) 2: long (11)(20)
Size of teeth on jaws	0: small (22) 1: large (4)
Hyomandibular intermuscular process length	0: none 1: short (1)(21) 2: long (5)
Postcleithrum head	0: large (7) 1: medium (2)(14) 2: small (9)(12)(16)
Urohyal	0: thin 1: thick (17)
Cleithrum groove	0: none 1: deep (3)(15) 2: shallow (13)(18)
Infraorbital foramen width	0: wide 1: medium (6) 2: narrow (8)

Appendix 2

Matrix of character states in the twelve extant species of hakes.

Character	Species											
	1	2	3	4	5	6	7	8	9	10	11	12
Gill raker length	0	1	0	1	2	2	0	2	2	2	0	0
Size of teeth on jaws	1	0	0	1	1	1	0	0	0	0	1	1
Hyomandibular intermuscular process length	2	2	2	1	2	1	1	1	1	1	2	2
Postcleithrum head	0	0	0	0	0	2	2	2	1	1	1	2
Urohyal	0	0	0	0	0	0	0	0	0	0	1	0
Cleithrum groove	1	1	1	1	1	1	1	2	1	2	2	1
Infraorbital foramen width	2	2	2	1	1	0	0	0	0	0	1	1
1 <i>merluccius</i>	4 <i>capensis</i>	7 <i>albidus</i>	10 <i>gayi</i>									
2 <i>senegalensis</i>	5 <i>paradoxus</i>	8 <i>productus</i>	11 <i>hubbsi</i>									
3 <i>polli</i>	6 <i>bilinearis</i>	9 <i>angustimanus</i>	12 <i>australis</i>									