

ADAPTIVE RADIATION OF WHALES:
IS CONSTITUTIVE HETEROCHROMATIN
AN INTRINSIC ISOLATING MECHANISM?

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ABSTRACT: Because cetacean populations are vagile, panmictic, and resource-limited, competition in sympatry, and hence disruptive selection, may have had a more important role in speciation than geographic isolation. The unique quantity and distribution of C-heterochromatin in cetacean chromosomes are proposed as an intrinsic isolating mechanism which permitted coadaptation of genetic linkages by reducing the probability of chiasmata in segments of euchromatin adjacent to C-heterochromatin. Resultant polymorphism was favored because it reduced intraspecific competition. Driven by disruptive selection, the heterochromatin increased in effect and quantity. Therefore, increasingly specialized interactions of phenotype and environment eventually favored homozygosity and the development of prezygotic isolating mechanisms. Because this process is selectively directed, hence rapid, and requires neither spatial isolation nor macromutations, the model is a plausible alternative to strict allopatric speciation in whales.

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INTRODUCTION

The cosmopolitan distribution of many whales, their extreme mobility, and the scarcity of clear geographic barriers in the world ocean appear to reduce the effectiveness of isolation as a factor in cetacean evolution. Wright (1931) showed that in large, freely interbreeding populations, gene frequencies approach equilibrium and there is no evolution in the absence of environmental change. I postulate that in whales excessive gene flow was a factor impeding adaptive diversification, thus selectively favoring the reduction of recombination at meiosis. The exceptional quantity, distribution, and heteromorphism of constitutive (C-) heterochromatin in cetaceans are proposed to be an intrinsic isolating mechanism which permits the establishment of discontinuous variation in panmictic populations by reducing recombination between appropriate homologous segments of chromosomes at meiosis (John and Miklos 1979). I propose that enhancement of the distinction between competing morphs, and concomitant amplification of the quantity of C-heterochromatin, are driven by disruptive selection. Because ancestral cetaceans were presumably resource-limited and because unexploited adaptive space was available, disruptive selection would have been particularly significant in partitioning new adaptive zones.

Several models (Maynard Smith 1966; Dickinson and Antonovics 1973) and experiments (Thoday and Gibson 1962) affirm the theoretical possibility of sympatric speciation based on disruptive selection. Rosenzweig (1978) and Pimm (1979) showed how competition within a species can lead to an increase in phenotypic variation and then to disruptive selection. Their model predicts change analogous to character displacement. At carrying capacity an average phenotype cannot compete successfully with similar but divergently specialized phenotypes. The new forms depress the fitness of the original by continued competition for the predominant resource, causing disruptive selection. Here I argue that disruptive selection was more crucial than geographic isolation in cetacean evolution.

Direct evidence of the rate of gene flow within cetacean species is scant. Re-

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cently several cases of site-specific behavior have been documented in whales but these observations do not apply to the behavior of subadults in populations at, or near, carrying capacity; dispersal would presumably be more important to such animals. Management biologists recognize particular stocks of whales but such units may not be genetically discrete. Indeed the International Whaling Commission has delimited quotas in the Southern Ocean simply along lines of longitude. Whales are usually hunted, and hence managed, at high latitudes on their feeding grounds but at lower latitudes feeding stocks may intermingle and distributions may be less restricted by resources. The recognition of some discrete stocks may be a rationale for continuing to hunt whales in areas where depletion of a more widespread population is not yet evidenced (e.g. Arnason 1981). Intraspecific discontinuities certainly exist but the fact that most species of these largely cold-water animals occur in both hemispheres suggests that even equatorial waters permit dispersal on an evolutionary time scale (Davies 1963).

Cetaceans as K-selected generalists

Estes (1979) argued that marine mammal populations should not be limited by predation or disturbance. Cetacean calves are born in the water and must be large and precocial to cope with high thermal costs. High energy investment per offspring restricts reproductive rate, which in turn restricts the range of tolerable mortality rates. Marine mammals limited primarily by predation or disturbance would not be able to compensate adequately for a high and varying mortality. Rorqual populations depressed by commercial exploitation exhibit increased rates of pregnancy and decreased age at sexual maturity (Gambell 1973). This suggests that rorquals are normally limited by competition for resources, hence the observed responses when populations are reduced. The large size of the early archaeocetes (Kellogg 1928) suggests that cetaceans have occupied high trophic positions, and therefore been resource-limited, throughout their history.

Specialization in whales, in spite of their being resource-limited and sharing broadly overlapping distributions, is incomplete in that most species opportunistically exploit the niches of similar taxa. Confamilial cetacean species often congregate on aggregations of prey. Gaskin (1976) described odontocetes as generally opportunistic. There is much overlap in the prey of mysticete species. Drastic reduction of antarctic blue and fin whale populations increased the pregnancy rate of relatively unexploited sei whales, presumably due to reduction of interspecific competition for Antarctic krill, *Euphausia superba* (Gambell 1973). Sergeant (1978) described some cetacean distributions as limited at high latitude by temperature tolerances and at low latitude by competition from related species.

I conclude that cetaceans maintain opportunistic, overlapping adaption to the predominant resources of their environment; this contrasts with the general concept of K-selected organisms as specialists (Wilson 1975, p.100). Diffuse competition (MacArthur 1972) interconnects the resource base of the various forms and could be the basis for competitive speciation (Rosenzweig 1978).

Conservative genetic features in whales

Cetaceans are so divergent in anatomy that the common ancestry of the toothed whales and baleen whales has been controversial (Van Valen 1968; Gaskin 1976). A similar karyotype is shared by most living cetaceans in spite of a diverse array of ancient taxa. Arnason (1969) and Duffield-Kulu (1972) proposed a monophyletic origin for odontocetes and mysticetes, based on the profound similarity of their chromosomes; this is supported by homologous satellite DNAs (Arnason, Purdom and Jones 1982; Arnason 1982a) and similar chromosome banding in species of each suborder (Duffield 1977; Arnason 1982b). The fossil record indicates that the latest period in which odontocetes and mysticetes could have diverged is the late Eocene (Simpson 1945). The basic cetacean karyotype has been conserved at least since that time.

Representatives of the eight extant families of Cetacea (Rice 1977) have been

studied cytogenetically. Of these, only the sperm whales, Physeter and Kogia, have chromosomes that cannot be clearly related to a common $2n=44$ cetacean karyotype (Arnason and Benirschke 1973). Beaked whales (Ziphiidae) share a diploid number of 42 with the physeterids but their chromosomes are still clearly related to the general cetacean karyotype (Arnason et al. 1977). Although the ziphiids and physeterids are related at the superfamilial level, Arnason et al. (1977) were not able to relate the $2n=42$ karyotypes of the two families. Among the mysticetes, only the balaenids, in the one species studied, have a reduced diploid number of 42. As in the Ziphiidae, this is the result of a single fusion event (Jarrell 1979). Intrafamilial variation in chromosomes seems minimal. A study of banded chromosomes (Arnason, Lutley and Sandholt 1980) indicates that the reportedly unique $2n=44$ karyotype of the killer whale, Orcinus (Duffield-Kulu 1972; 1977), differs from that of other delphinids primarily by additional C-heterochromatin.

The harem-forming social structure of Physeter may have promoted their exceptional chromosomal evolution (Duffield 1977). Small, discrete breeding units are defended and relatively few males contribute gametes to successive generations. Such endogamy could promote the fixation of chromosomal mutations (Wilson et al. 1975; Bush et al. 1977). Thus the karyotypes of sperm whales may have evolved in a manner consistent with models related to small demes.

Though not well studied, differences in allozymes between related cetaceans appear to be minimal. Sharp (1975) studied hemoglobins from eleven delphinids and concluded that "the morphological differentiation of these species as compared to their molecular evolution is dramatic."

A noncentromeric satellite DNA from each of the two cetacean suborders cross-hybridizes according to relatively strict criteria (Arnason, Purdom and Jones 1982). This satellite and another localized near the centromeres yield virtually identical melting curves in homo- and heterologous hybridizations of DNA and complementary RNA from three species of Balaenoptera; the ancestral sequences of the two DNA satellites appear to have been conserved since the appearance of the genus in the lower Pliocene (Arnason, Purdom and Jones 1978).

Differentiation in whales apparently has involved neither extensive chromosomal rearrangement, change in structural genes, nor change in the composition of satellite DNAs. This conservatism may relate to the few generations involved in the radiation of these long-lived and slowly reproducing animals. Alternatively, coadaptation of linked alleles as a means of adaptive divergence might occur without marked change in these parameters.

Heterochromatin

The term C-heterochromatin, as used here, refers to constitutive, as opposed to facultative (Brown 1966), material containing highly repeated (or satellite) DNA and staining as chromosomal C-bands. This material is not transcribed into mRNA but can alter the location of chiasmata at meiosis (Yamamoto and Miklos 1978; Miklos and John 1979; John and Miklos 1979). Heterochromatic polymorphisms, which are ubiquitous in many organisms, consist of apparently continuous variations in the quantity of C-heterochromatin at specific sites (Yamamoto and Miklos 1978; Verma and Dosik 1980). Inheritance of these heteromorphisms is Mendelian but spontaneous rearrangement occurs in man (Verma and Dosik 1980). Miklos, Willcocks and Baverstock (1980) reviewed the literature relating heterochromatin to speciation. They concluded that the proposed functions of heterochromatin are specious. In particular, they stated that heterochromatic differences in chromosome structure are not barriers to interfertility.

The size and distribution of segments of C-heterochromatin are singularly labile features of cetacean genomes; intraspecific heteromorphism is pronounced (Arnason et al. 1980). This is demonstrated by C-bands, which make up about 25% of the total length of mysticete chromosomes and 10 to 15% of odontocete chromosomes (Arnason 1974a). Most eukaryotes have C-heterochromatin associated with the centromeres but

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