pearance of eastward flow at the surface. This has been observed previously during April through September, when the trade winds weaken [K. Wyrtki *et al.*, *Science* **211**, 22 (1981)].

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9. We thank W. Austin, the crew of the R.V. *Machias*, and the technicians who made possible the longtime series of current measurements. The work was funded primarily by the National Science Foundation, with additional support from the National Oceanic and Atmospheric Administration and the State of Hawaii. This is contribution No. 1435 from the Hawaii Institute of Geophysics.

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Onshore-Offshore Patterns in the Evolution of Phanerozoic Shelf Communities

Abstract. *Cluster analysis of Cambrian-Ordovician marine benthic communities and community-trophic analysis of Late Cretaceous shelf faunas indicate that major ecological innovations appeared in nearshore environments and then expanded outward across the shelf at the expense of older community types. This onshore-innovation, offshore-archaic evolutionary pattern is surprising in light of the generally higher species turnover rates of offshore clades. This pattern probably results from differential extinction rates of onshore as compared to offshore clades, or from differential origination rates of new ecological associations or evolutionary novelties in nearshore environments.*

The broad outlines of the Phanerozoic history of skeletonized marine animals are now reasonably well known (*1*). However, comparatively little is known about how changes in global diversity relate to local environments (*2*). In light of this situation, we have analyzed marine faunal changes within environmental gradients for two pivotal intervals of the Phanerozoic: the Cambrian and Ordovician periods in the early Paleozoic and the Late Cretaceous Epoch at the end of the Mesozoic. The Cambro-Ordovician interval encompassed the origination of all three of the great "Evolutionary Faunas" that compose the Phanerozoic marine fossil record (*3*), with the appearance of the first shelly fauna (the "Cambrian Fauna") in the Early Cambrian, the rapid expansion of the more complex and diverse "Paleozoic Fauna" in the early and middle Ordovician, and, finally, the rise of early members of the modern fauna in the mid-to-late Ordovician. The Late Cretaceous interval, some 340 million years later, included a major reorganization of communities within the Modern Fauna, with the Mesozoic marine revolution bringing diversification of durophagous predators and infaunal bioturbators, decline of epifaunal suspension feeders, and increase in both global and local species richness (*1*, *4*). Our analyses of the faunal changes within an environmental framework during both intervals indicate that the major new community types appeared first in nearshore settings and then expanded into offshore settings, despite higher rates of species-level evolution in the offshore habitats.

For the Cambro-Ordovician interval, a Q-mode cluster analysis was performed on 102 animal communities with well-documented macrofaunas [tabulated in (*5*)]. These communities, as illustrated in Fig. 1, were selected to give broad coverage of all marine environments from nearshore to continental slope and deep basin over the whole of the 140-million-year interval (*6*). The communities were clustered (*7*) in order to see what environments had similar ordinal–level faunas and therefore to determine where and when major faunal changes were occurring along the shelf-slope gradient. The analysis revealed four primary clusters of communities, represented by the patterned boxes in Fig. 1. The oldest two clusters correspond to the Cambrian Fauna (*3*) and are differentiated only by the dominant trilobite orders. The last appearance of the second Cambrian Fauna cluster is markedly time-transgressive, so that this grouping encompasses all shelf and slope localities in the Middle and Upper Cambrian, but then becomes restricted to progressively more offshore environments through the Ordovician—a pattern of faunal replacement first recognized by Berry (*8*). The third cluster corresponds to the Paleozoic Fauna, extending across the shelf after its initial diversification near the shoreline in the early Ordovician. Finally, a fourth primary cluster occurs in nearshore environments in the late Ordovician; this group represents the first appearance of the Modern Fauna in a distinct environmental association (*2*, p. 11; *9*). Thus, by the end of the Ordovician, the three major evolutionary faunas of the Phanerozoic oceans were arrayed in distinct community associations across the continental shelf and slope: the remnants of the Cambrian Fauna on the slope, the Paleozoic Fauna on the mid- to outer shelf, and the early members of the Modern Fauna on the inner shelf.

A parallel onshore-offshore pattern of faunal change was found in the distribution of adaptive types (as opposed to higher taxonomic groups) within the Modern Fauna over the course of the post-Paleozoic (Fig. 2). Late in the Cretaceous (Santonian-Maestrichtian) of the Gulf and Atlantic Coastal Plain and the Western Interior Provinces of North America, nearshore assemblages were dominated largely by infaunal suspension-feeders, whereas more fine-grained or midshelf assemblages (or both) were trophically mixed, containing a large complement of deposit feeders; these results correspond well to environmental patterns in modern marine benthos (*4*, *10*, *11*). Unlike their modern counterparts, however, Late Cretaceous mid-to-outer shelf and slope assemblages were still dominated numerically by immobile epifaunal suspension feeders (*10*, *12*), the prevalent adaptive type across much of the Paleozoic and earlier Mesozoic shelf (*10*, *13*, *14*). These Late Cretaceous epifaunal dominants on soft substrata include pycnodont and exogyrine oysters, inoceramid bivalves, articulate brachiopods, and cyclostome and cheilostome bryozoans (*10*). In contrast, in offshore settings today immobile epifauna occur almost exclusively on hard substrata or on firm, coarse sediments that are either relict or maintained by current action (*10*, *11*). Soft, offshore muds today are dominated by deposit feeders and carnivores, and lack the epifaunal suspension-feeding mode of life so prevalent in the Paleozoic and in certain Mesozoic habitats.

Several alternative evolutionary dynamics could have given rise to the onshore-offshore patterns of faunal change documented here. The patterns cannot be driven simply by differential speciation rates, because origination rates at low taxonomic levels actually tend to be higher offshore than onshore in both the Paleozoic (*15*) and post-Paleozoic (*16*). Two alternative mechanisms are:

1) *Differential extinction*. The greater extinction-resistance of nearshore clades (*16*) increases both the probability that nearshore innovations persist long

enough to diversify and the total number of speciation events within a clade over its lifetime (*17, 18*).

2) *Differential origination.* Although speciation rates are lower onshore, the temporal and spatial heterogeneity of nearshore environments may be conducive to the production of evolutionary novelties or new ecological associations (*19*); new community types could then expand across the shelf in the wake of attritional extinction of offshore taxa (*20*).

Both of these hypotheses are testable with detailed data on rates of origination and extinction of clades within their paleoenvironmental context. Whatever the underlying mechanism, the data summarized here indicate that major evolutionary ecologic changes were not accomplished entirely by random species replacement throughout the marine environment. Rather, they occurred by outward expansion of evolutionary innovations and new community types from a nearshore evolutionary crucible into more conservative offshore habitats.

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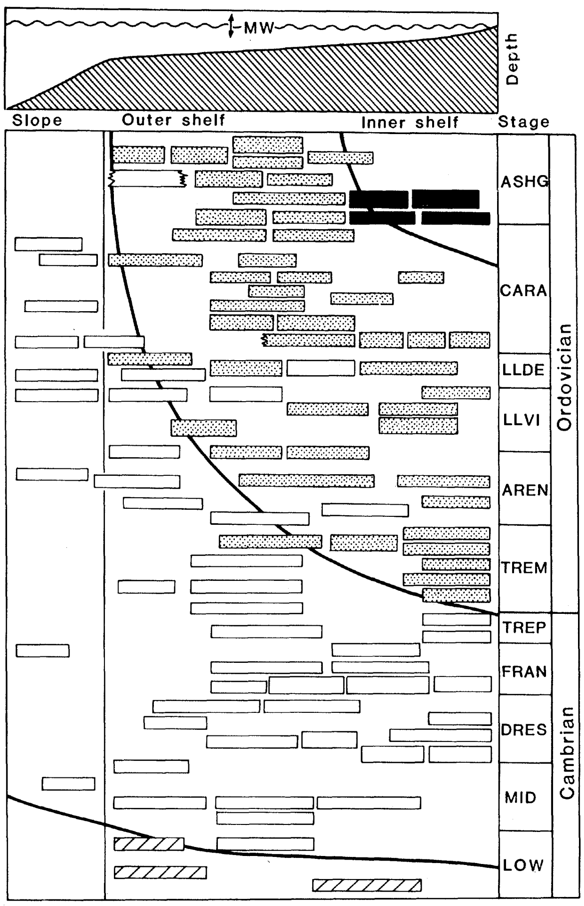

Fig. 1. Time-environment diagram showing the distribution of four primary clusters of Cambro-Ordovician fossil communities. Each box in the diagram represents a single community; the vertical position shows the age of the community; the horizontal position shows its approximate environmental range. Cluster membership of each community is indicated by patterning (diagonal ruling, Lower Cambrian shelf cluster unified by the joint possession of redlichiid trilobites, hyolithids, and inarticulate brachiopods; blank, Middle Cambrian to lower Ordovician shelf and Ordovician slope cluster unified by the joint possession of diverse ptychopariid trilobites and lingulid and acrotretid brachiopods; stippling, Ordovician shelf cluster unified by diverse orthid brachiopods, archeogastropods, trepostome and cryptostome bryozoans, crinoids, and some ptychopariid trilobites; solid black, Upper Ordovician inner shelf cluster distinguished by the dominance of bivalves, especially modiomorphoids, nuculoids, and pterioids). Cluster boundaries are strongly time-transgressive, indicating that major faunal associations originate in the nearshore environments and spread across the shelf. Stages from bottom to top are as follows: Lower, Middle, Dresbachian, Franconian, Trempealeauan, Tremadocian, Arenigian, Llanvirnian, Llandeilian, Caradocian, and Ashgillian.

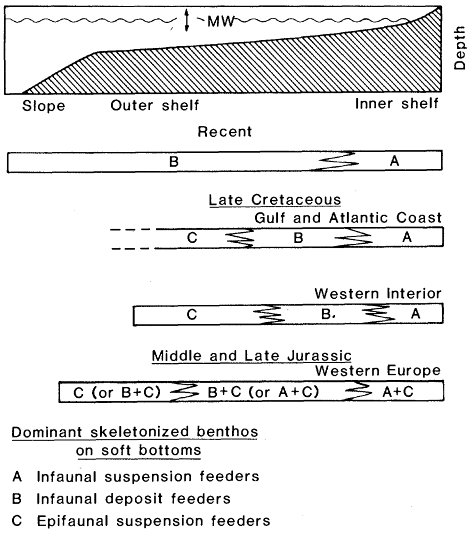

Fig. 2. Generalized macrofaunal adaptive types in generalized shelf transects in two Late Cretaceous provinces, and for comparative purposes, Recent and Middle-Late Jurassic. For the Cretaceous transects, note prevalence of immobile epifaunal suspension-feeders in soft-bottom offshore settings, reminiscent of Paleozoic and earlier Mesozoic shelf communities; in modern seas such habitats are occupied predominantly by small-bodied deposit feeders, again suggesting an onshore-new, offshore-archaic pattern of replacement for major benthic ecologic groupings. Predominant Late Cretaceous epifaunal taxa in the Gulf and Atlantic Province include gryphaeid oysters and, locally, articulate brachiopods and inoceramids, and in the Western Interior Province, inoceramid bivalves and an assortment of their epibionts.

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18. In addition to background extinctions, mass extinctions could also contribute to the pattern, especially if marine habitats are differentially affected.
19. The incessant local extinctions and recolonizations in frequently disturbed nearshore habitats may promote the origin of major new community types through repeated sorting and recombining of new and established species (*5*). Alternatively, the evolutionary novelties themselves may arise preferentially nearshore because new isolates in those habitats are commonly small and drawn from panmictic populations, and are thus more likely to undergo genetic revolutions or transiliences that could produce rapid shifts in morphology or physiology than the more frequent speciation events in offshore environments [see D. Jablonski and R. A. Lutz, *Biol. Rev. Phil. Soc.* **58**, 21 (1983); J. W. Valentine and D. Jablonski, in *Evolution, Time and Space: The Emergence of the Biosphere*, R. W. Sims, J. H. Price, P. E. S. Whalley, Eds. (Academic Press, New York, 1983); A. R. Templeton, *Evolution* **34**, 719 (1980); E. Mayr, *ibid.* **36**, 1119 (1982); but see B. Charlesworth, R. Lande, M. Slatkin, *ibid.* p. 474].
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Productive Infection and Cell-Free Transmission of Human T-Cell Leukemia Virus in a Nonlymphoid Cell Line

Abstract. *Human T-cell leukemia virus (HTLV), American PL isolate, was transmitted by cocultivation and by cell-free filtrates to a nonlymphoid human osteogenic sarcoma (HOS) cell line, designated HOS/PL, but not to nine other lines bearing receptors for HTLV. HOS and HOS/PL cells are not dependent on interleukin-2 and do not express interleukin-2 receptors that are recognized by anti-Tac monoclonal antibody. HTLV released by the Japanese MT2 cell line was also transmitted to HOS cells. The infected HOS cells release substantial titers of progeny HTLV which is antigenically indistinguishable from parental virus and is able to transform T cells.*

Human T-cell leukemia virus (HTLV) is a C-type RNA tumor virus associated with a mature form of adult T-cell leukemia-lymphoma (ATLL). HTLV was first isolated and characterized from patients in the United States (*1*) and later in Japan (*2*), and in patients of West Indian origin (*3*) and in Israel (*4*). Human umbilical cord lymphocytes and peripheral blood lymphocytes cocultivated with HTLV-releasing lymphoma cells become infected and transformed in vitro (*4, 5*). Transformation of simian and rabbit peripheral blood T cells by HTLV has also been reported (*6*). Several of the T-cell lines transformed in vitro produce larger quantities of HTLV particles than the original tumor lines.

We have recently demonstrated that cocultivation of HTLV-producing cells with a variety of human and animal nonlymphoid cell types induces cell fusion, leading to the formation of large, multinucleated syncytia as a result of HTLV expression (*7*). These observations indicate that HTLV interacts with the surface of a number of cell types. Further studies with vesicular stomatitis virus (VSV) pseudotypes bearing the envelope glycoproteins of HTLV showed that there is a broad range of cells susceptible to pseudotype infection (*8*). Thus the expression of HTLV receptors is not restricted to lymphoid cells, because many cell types derived from diverse mammalian species are permissive for HTLV adsorption and penetration.

In this report we describe the productive infection of a nonlymphoid human cell line by American and Japanese strains of HTLV. Furthermore, we show that cell-free transmission of HTLV is achieved in this line.

Permissivity of HOS cells to HTLV replication. Five human and five animal cell lines known to have receptors for HTLV (*8*) were cocultivated with HTLV-producing C91/PL T cells. The human cells were 7605L embryonic lung fibroblasts, HOS osteogenic sarcoma cells, RD rhabdomyosarcoma cells, HeLa cervical carcinoma cells, and EJ bladder carcinoma cells. Animal cells were Vero African green monkey kidney cells, Fcf2th canine thymus murine sarcoma virus (MSV)–transformed S$^+$L$^-$ cells, feline CCC MSV-transformed S$^+$L$^-$ cells, CCL64 mink lung cells, and XC Rous sarcoma virus (RSV)–induced rat sarcoma cells. In the first set of experiments HTLV-producing cells were not x-irradiated but during serial passage the lymphoma cells were soon lost from the adherent cultures. The cells were maintained in Dulbecco-modified Eagle's medium with 5 to 10 percent fetal calf serum and were passaged for 5 months.

Although each of the ten cell types cocultivated with HTLV-producing cells was susceptible to HTLV penetration and eight were susceptible to HTLV-induced cell fusion, only one cell type, the HOS cell line (*9*), was permissive for HTLV replication. During the first 2 weeks of cocultivation, cell fusion occurred among the HOS cells, but with the loss of C91/PL cells on passage, the

Table 1. Virus production, syncytium induction, pseudotype formation, and antigen expression by HOS/PL cells.

Cell line	Reverse trans-ciptase*	Syn-cytium induc-tion†	VSV (HTLV) pseudo-type titer‡	Percentage of cells immunofluorescent: HTLV antigens§ ATLL	Percentage of cells immunofluorescent: HTLV antigens§ p19	Percentage of cells immunofluorescent: T-cell marker¶	Percentage of cells immunofluorescent: IL-2 recep-tor ‖
C91/PL	16361	+++	3×10^3	87	89	72	85
HOS/PL	18890	++++	5×10^4	98	82	0	0
HOS	926	−	$< 10^1$	0	0	0	0

*Assay of viral RNA-directed DNA polymerase, expressed as the counts per minute of [^{3}H]TMP incorporated during incubation for 60 minutes at 37°C (*7*). †XC indicator cells were cocultivated with test cells for 18 hours and examined for syncytia (*7*). The results are expressed as the percentage of nuclei contained within syncytia: −, no syncytia; +++, 30 to 50 percent; ++++, > 50 percent. ‡Plaque-forming units per milliliter of vesicular stomatitis virus (VSV) with envelope antigens specific to HTLV (*8*). §Indirect immunofluorescence on fixed cells using serum from an antibody-positive ATLL patient (*7*) and monoclonal antibody to p19 (*10*). ¶Indirect immunofluorescence with UCHT1 monoclonal antibody (*12*) on live cells. ‖ Indirect immunofluorescence with anti-Tac monoclonal antibody (*14*) on live and fixed cells.