als, leading to a strong increase in T_c with decreasing volume. Simply doubling the overlap from 1 to 2% is predicted to increase T_c from 17 to 30 K. Clearly, our experimental observation of a strong decrease in T_c with pressure is at odds with this theory.

Chakravarty and Kivelson (*11*) have argued that the C_{60} molecule's electronic structure, specifically the partially filled π-electron system, can in itself provide an effective attractive interaction for the electrons, favoring even occupancy of the C_{60} molecules, that is, electron pairing. In the limit where the overlap between C_{60} molecules is weak compared to the pairing energy, a positive pressure dependence is predicted for T_c in opposition to the results presented here. For the reverse situation, overlap comparable to or larger than the pairing energy, then one recovers an essentially BCS-type dependence of T_c on the change in density of states or bandwidths, that is, decreasing T_c under pressure.

Taking the simplest possibility, that superconductivity in K_3C_{60} follows the BCS form, then a strong pressure dependence would develop as follows. In BCS, $T_c \propto \omega \exp(-1/\lambda)$, where ω is a characteristic phonon frequency and λ is the electron-phonon coupling parameter that is linearly proportional to the density of electronic states at the Fermi energy, $N(E_F)$, and inversely proportional to ω^2. Because of the exponential dependence, we expect $\lambda(p)$ to dominate. Recently, we have suggested, on the basis of the measured London penetration depth (*7*) that the structure in the density of states $N(\varepsilon)$ near E_F is unusually narrow, around 600 K wide. Pressure is expected to increase ω and broaden the density of states at E_F, thereby reducing $N(E_F)$, and a relatively strong decrease in T_c could result. Whether this simple model can explain the magnitude of dT_c/dp remains an open question.

The same arguments might be used to explain the higher T_c observed in Rb_xC_{60} (*6, 8*) whose superconducting phase composition and structure remain unknown. Because the Rb^+ ion is larger than K^+, it would likely decrease the density of C_{60} packing, resulting in a narrowing of the band and a further enhancement of the density-of-states at E_F. Further work in progress on the Rb_xC_{60} system to determine the composition, structure, and pressure dependence will answer these questions (*24*).

Note added in proof: Our preliminary measurements on a T_c = 30 K Rb:C_{60} sample show an even larger rate of decrease $dT_c/dp = -1.0$ K kbar^{-1} (*25*).

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26. Work at Los Alamos National Laboratory was performed under the auspices of the U.S. Department of Energy. S. J. Anz and F. Ettl produced and separated the molecular carbon samples used in this research. Funding has been provided by the NSF grants (R.L.W. and F.N.D., and to R.B.K.) and by the David and Lucille Packard Foundation (R.L.W. and R.B.K.). For stimulating discussions, the authors thank S. Chakravarty and S. Kivelson.

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Environmental Patterns in the Origins of Higher Taxa: The Post-Paleozoic Fossil Record

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Of the 26 well-preserved orders of benthic marine invertebrates that have originated since the beginning of the Mesozoic, 20 first appear in onshore environments. This distribution differs significantly from that shown by well-preserved genera and families, and by the 16 poorly preserved orders. These discordances suggest that the pattern of preferential onshore origination is not an artifact of preservation or collection and that the origin of higher taxa cannot be regarded as a simple extrapolation of rates and patterns at lower levels. The onshore environment fosters production or enhances survivorship of species that initiate lineages tending to accumulate suites of derived characters and that thus are ultimately afforded high taxonomic rank.

HIGHER TAXA HAVE NOT ARISEN randomly in space and time. For example, most of the skeletonized invertebrate phyla and classes originated in the Early Paleozoic radiations (*1*). Recently, environmental trends have also been recognized, with a variety of Paleozoic (*2*) and post-Paleozoic (*3–6*) marine taxa evidently originating in onshore settings and spreading across the continental shelf; further, a number of taxa today restricted to the outer shelf, slope, or abyssal environment have fossil records suggesting a more onshore distribution earlier in their histories (*3, 7*). Here we test the generality of this pattern with a survey of the environment of first appearance for all known post-Paleozoic benthic marine invertebrate orders. Our results corroborate the environmental bias in originations: 77% of the well-preserved orders first appear in relatively disturbed, onshore environments. This pattern contrasts significantly with the more even pattern seen for first appearances of orders with poor preservation potential and for first appearances of genera within the well-preserved orders. The first disparity suggests that the environmental pattern in well-preserved orders is not an artifact of the stratigraphic record, and the second suggests that major evolutionary novelties arise differently from novelties at the genus level.

As currently recognized, 42 orders of marine benthic invertebrates have originated since the beginning of the Mesozoic. Of these, 16 have skeletons that are too lightly calcified (for example, the notaspidean gastropods) or too readily disarticulated (for example, the eight seastar orders) to yield a reliable record of the time or environment of first occurrences, and these are treated separately from the remaining 26 orders (*8*) (Fig. 1). In the absence of a complete phylogenetic analysis of skeletonized invertebrates, we use ordinal origination as a rough proxy for the origin of important evolutionary novelties, including those giving rise to new body plans (*4, 5, 9*). We are testing for differences across hierarchical levels, not validity of a particular taxonomy, and where

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taxonomy is controversial we have chosen the alternatives that least favor our conclusions (*10*). Some of the orders used here are almost certainly paraphyletic, but this is not a problem because we are essentially tabulating first occurrences of derived characters that mark the origins of groups, rather than tracking their subsequent histories (that is, even successive paraphyletic groups have definable points of origin).

Environments of first occurrence were inferred from sedimentary and stratigraphic features of the rocks containing the oldest known species of each order, and occurrences were placed within a five-division, generalized shelf transect based entirely on environmental energy levels (*4*). These subdivisions are virtually identical to those used by Sepkoski (*11*) and Miller (*3*), except that their environments two and three are combined into our inner shelf category. Where numbers of first occurrences per environment are too low for reliable statistics, we group the nearshore and inner shelf environments into an onshore category (above normal storm wave base) and the middle shelf, outer shelf, and slope–deep basin into an offshore category (below normal storm wave base).

Onshore first appearances are significantly more frequent for the well-preserved orders than the poorly preserved orders [$P < 0.025$, G test using a simple onshore-offshore dichotomy (*12*)] (Fig. 1). Given that first appearances of poorly preserved orders are probably dictated more by the vagaries of preservation and sampling than by ecological preferences or evolutionary processes (*13, 14*), we can treat their distribution as a null hypothesis for environmental patterns of post-Paleozoic originations. The significant contrast with the pattern for well-preserved orders leads us to reject the null hypothesis and accept the onshore peak as biologically meaningful. Pooling all the localities ($n = 599$) or species records ($n = 2227$) in our best documented groups (isocrinid crinoids, cheilostome bryozoans, tellinacean bivalves, salenioid echinoids) (*4–6*) to estimate sampling intensities across environments also yields a frequency distribution significantly different from the environmental distribution of well-preserved orders ($P < 0.025$ for localities, $P < 0.005$ for records). Confirmatory work, such as time-specific and order-by-order tests with taphonomic control taxa, which have similar preservation characteristics to the particular target taxon (*4*), would strengthen the argument, but our results strongly suggest that there is more signal than noise in the well-preserved category. Previous work on taphonomic controls suggests that environmental coverage is sparsest in the early and middle Triassic (*4*); differences are still significant when data from this interval are excluded ($P < 0.05$, G test).

The first appearances of genera [and thus presumably species (*15*)] also differ significantly from the environmental pattern seen for well-preserved orders (Fig. 2). Grouping data for the four orders of level-bottom stalked crinoids (*16*), the 41 generic originations show a distinct mode in the middle shelf, again different from the overall ordinal pattern ($P < 0.001$, G test using the onshore-offshore dichotomy; $P < 0.01$, Kolmogorov-Smirnov test on frequency distributions in Fig. 2; excluding early and middle Triassic data, $P < 0.001$ and $P < 0.005$, respectively). Combined with comparable analyses of tellinacean bivalve families (*5*), cheilostome bryozoan novelties (*5*), and salenioid echinoid genera (*17*), the crinoid data suggest that the origins at or below the family level more closely conform to the bathymetric diversity gradient of their particular higher taxon than to a particular suite of environments: environments richest in species, genera, and families are generally the sites of more origination at those levels. This discordance across taxonomic levels provides support for hierarchical views of evolution (*9, 18*): ordinal origination patterns could not have been predicted by a smooth extrapolation for lower levels.

We are not arguing for a theory of evolutionary saltation, in which each order appears with all derived characters in place. Recent hummingbirds and geese do not resemble theropod dinosaurs as closely as *Archaeopteryx* does, but *Archaeopteryx* (and presumably its immediate precursors) had novelties that laid the foundation for the later diversification of the avian clade; similar claims might be made for early members of these invertebrate groups. We also do not claim that ordinal rank per se has an objective reality, comparable across all phyla. The discordant behavior of taxa treated as genera and orders suggest, however, that origin of new body plans, with the potential to diversify and accumulate additional derived characters, is governed by factors different from those that determine origination of species that simply produce more species or new genera. The origin of groups that are assigned high taxonomic rank evidently tends to be habitat-dependent, whereas the origin of families and lower taxa tends to be diversity-dependent.

Causal mechanisms for these differences

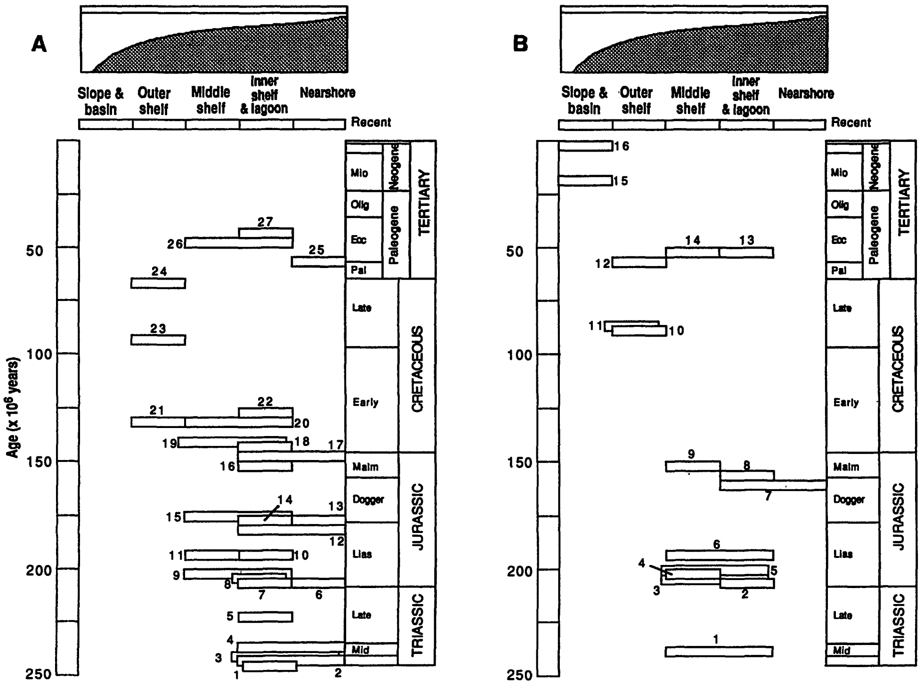

Fig. 1. Environments of first appearance for well-preserved and poorly preserved marine invertebrate orders. (**A**) Well-preserved orders; 1, Encrinida; 2, Isocrinida; 3, Scleractinia; 4, Millericrinida; 5, Lychniscosida; 6, Phymosomatoida; 7, Pedinoida; 8, Hemicidaroida; 9, Pygasteroida; 10, Holectypoida; 11, Cyrtocrinida; 12, Superorder Microstomata [see (*10*)]; 13, Salenioida (=Calycina); 14, Disasteroida; 15, Cassiduloida; 16, Milleporina; 17, Cheilostomata; 18, Holasteroida; 19, Spatangoida; 20, Temnopleuroida; 21, Neogastropoda; 22, Helioporacea (=Coenothecalia); 23, Bourgueticrinida [see (*10*)]; 24, Stylasterina; 25, Clypeasteroida; 26, Oligopygoida; and 27, Echinoida. (**B**) Poorly preserved orders: 1, Trichasteropsida; 2, Forcipulatida; 3, Comatulida; 4, Notomyoida; 5, Valvatida; 6, Velatida; 7, Paxillosida; 8, Anaspidea; 9, Micropygoida; 10, Echinothurioida; 11, Diadematoida; 12, Spinulosida; 13, Sacoglossa (=Ascoglossa); 14, Notaspidea; 15, Brisingida; and 16, Stolonifera.

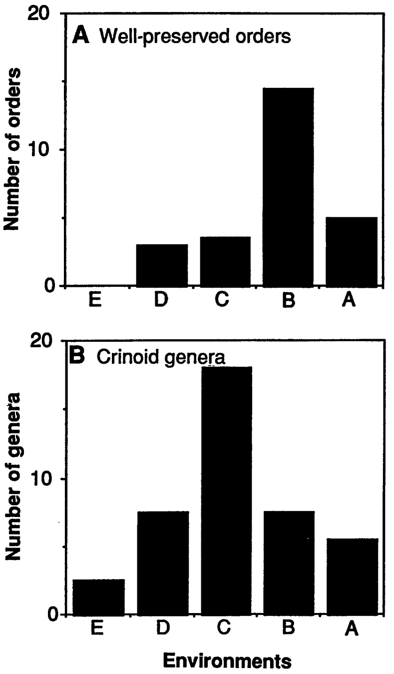

Fig. 2. Environmental frequency distributions of (**A**) well-preserved orders and (**B**) stalked crinoid genera. Environments: A, nearshore; B, inner shelf; C, middle shelf; D, outer shelf; E, slope and deep basin [see (*4*) for criteria]. First occurrences that could only be resolved to two environments (due to ambiguities in stratigraphic placement or paleoenvironmental information, or to multiple occurrences) were scored as 0.5 in each environment.

are a matter of considerable debate (*3–5*, *19*), and the expansion across the shelf shown by many taxa should perhaps be treated as a separate issue (although marine taxa that originate onshore can expand in only one direction, of course) (*20*). Different mechanisms may even be required for patterns in the post-Ordovician Paleozoic [when global and within-habitat diversity was in approximate steady state (*11*)] and in the post-Paleozoic [when diversity was increasing exponentially, checked only briefly by mass extinctions (*21*)]. Some hypotheses have been eliminated (*5*), but the differential origination pattern might still be set by increased novelty production in more variable, more frequently disturbed onshore habitats, or by preferential survival of early representatives in extinction-resistant onshore species (*6*). In any event, the results presented here suggest that environmental variables cannot be ignored when constructing macroevolutionary theories.

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10. For example, the crinoid order Bourgueticrinida might be subsumed within Isocrinida [M. J. Simms, in *Echinoderm Phylogeny and Evolutionary Biology*, C. R. C. Paul and A. B. Smith, Eds. (Clarendon, Oxford, 1988), pp. 269–284]; to do so eliminates an offshore origination in Fig. 1A. The echinoid superorder Microstomata begins with primitive taxa bearing novelties related to an important functional shift to deposit-feeding, but not formally assignable to the presently recognized orders [see Jablonski and Bottjer (*6*)]; to use this superorder instead of the first occurrence of its oldest formally recognized order, the Cassiduloida, would further increase the proportion of onshore ordinal originations.
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13. Regarding preservational factors, see, for example, D. M. Raup, *Bull. Carnegie Mus. Nat. Hist.* **13**, 85 (1979); taphonomy section of D. E. G. Briggs and P. K. Crowther, Eds., *Palaeobiology: A Synthesis* (Blackwell, Oxford, 1990), pp. 213–303.
14. At least two-thirds of the extant poor-preservation taxa occur in inner shelf depths today [S. P. Parker, Ed., *Synopsis and Classification of Living Organisms* (McGraw-Hill, New York, 1982)], thus excluding ecological constraints as a reason for the absence of a strong onshore peak in their first occurrences.
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