

tion. Displacements of 1 cm have been detected for artificial targets^{24,25} and the ultimate precision of the technique is at the millimetre level²⁶. For this shallow earthquake, the range changes measured by radar agree extremely well with both the field observations at the fault and the dislocation model in the intermediate and far fields. The detailed features of the radar fringes near the fault require more sophisticated modelling. For deeper earthquakes associated with little or no surface rupture, radar interferometry will become a powerful tool for measuring surface displacement in the intermediate and far fields. Unlike surveying techniques, there is no need to install ground stations before the earthquake. To ensure a pre-earthquake observation, one needs only to archive radar images of the potentially seismogenic area each time the satellite passes over it, as ERS-1 currently does once every 35 days. □

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The tropics as a source of evolutionary novelty through geological time

David Jablonski

Department of the Geophysical Sciences, University of Chicago, 5734 South Ellis Avenue, Chicago, Illinois 60637, USA

SPATIAL and temporal variations in biological diversity can be shaped by a variety of dynamical interactions between origination and extinction^{1–3}. For this reason, the evolutionary basis of the latitudinal diversity gradient—with the tropics extraordinarily rich in species, higher taxa and evolutionary novelties—has been much debated^{4–8}. High origination rates with the tropics operating as a diversity pump^{8–11}, low extinction rates with the tropics operating as a diversity accumulator^{12–15}, or some combination of the two^{16–18}, have all been proposed to explain the wealth of higher taxa and morphological variety in low latitudes. Few historical data have been available, however, to test directly whether the tropics are 'a cradle or a museum'^{15,19}. A new palaeontological analysis of post-Palaeozoic marine orders shows significantly more first appearances in tropical waters, whether defined latitudinally or biogeographically, than expected from sampling alone. This provides direct evidence that tropical regions have been a major source of evolutionary novelty, and not simply a refuge that accumulated diversity owing to low extinction rates.

Forty-two orders of benthic marine invertebrates have appeared since the beginning of the Mesozoic^{20,22}, and the age, environment, and location of the oldest known members are documented²⁰. These data are difficult to evaluate, however, because palaeontological sampling is severely biased geographically, with maximum density in north temperate latitudes^{23–25}. First occurrences of the 26 orders considered to have good preservation potential²⁰ were restored to their original palaeolatitudes, grouped in 10° belts (Fig. 1a), and compared to two null hypotheses that quantify different aspects of sampling bias:

H₀₁: Observed first appearances are determined primarily by preservational factors. This distribution (Fig. 1c) was based on the first occurrences of orders whose members are only lightly mineralized or easily disarticulate into seldom identified fragments. These records of poorly preserved orders are probably

dictated more by vagaries of sampling and preservation than by true biogeographic history, and thus provide one measure of the distribution or discovery rate of deposits yielding especially rich biotas²⁰.

H₀₂: Observed first appearances are determined primarily by sampling intensity. This distribution (Fig. 1d) was based on all published records of echinoid species (excluding isolated spines) from the beginning of the Triassic to the Bajocian Stage of the Middle Jurassic, an interval that encompasses over half of the ordinal originations²⁶. Echinoids are relatively common post-Palaeozoic fossils that have attracted considerable palaeontological attention over the past 200 yr, so that the geographic pattern of their individual records provides a general measure of sampling intensity across latitude. Because many of the well-preserved orders²⁰ are in Phylum Echinodermata, echinoids are probably a more appropriate taphonomic control²⁰ than molluscs or other taxa.

First occurrences of the well preserved orders (Fig. 1a, b) are significantly more frequent in tropical seas relative to either of the null hypotheses (Fig. 1c, d). The Early Triassic is especially poorly sampled and poorly understood biogeographically^{20,27}, but results remain significant even when originations in this interval are excluded.

Adjustment of the well preserved ordinal occurrences using H₀₁ and H₀₂ datasets (Fig. 1e, f) gives a general picture of how far the well preserved orders diverge from null expectations. These can only be very approximate corrections but serve to illustrate, for example, that so few poorly preserved orders and species records occur at 0–20° palaeolatitude that even the low number of well preserved orders appearing there exceeds that expected from sampling. More generally, the relatively wide distribution of first occurrences in Fig. 1a and 1b, despite the massive sampling biases revealed in Fig. 1c and 1d, suggests that improved sampling would shift even more ordinal originations into tropical regions. Also, because comparisons are made within each 10° band, the decrease in global surface area with increasing latitude is factored out as a potential bias.

The distribution of reefs and other indicators of tropical conditions has oscillated continually over geological time^{28,29}, so that first occurrences might better be calibrated not to absolute palaeolatitude but to the contemporaneous limits of tropical biotas. Such a biogeographic calibration yields results comparable to the palaeolatitudinal tests (Fig. 2): well preserved orders first occur in tropical settings significantly more frequently than

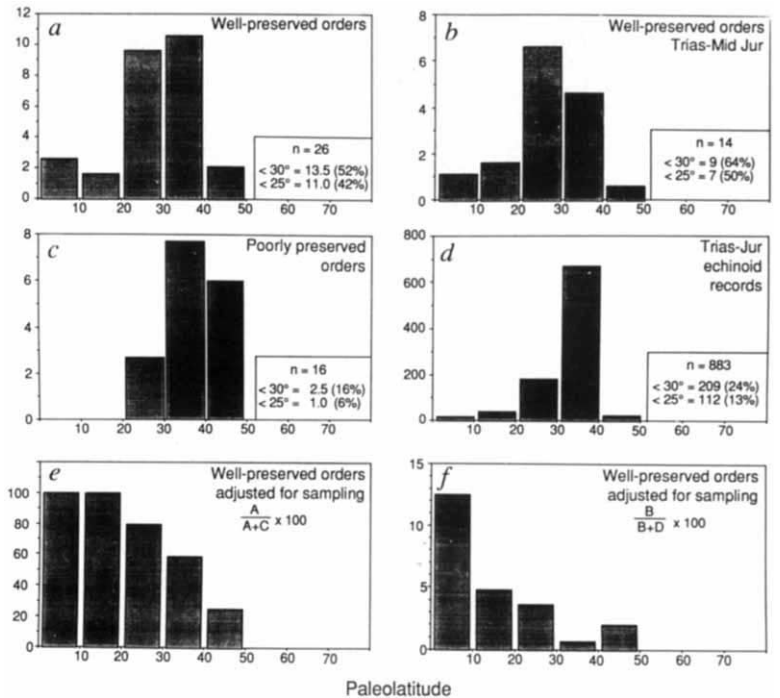
FIG. 1 First occurrences of post-Palaeozoic marine benthic invertebrate orders, grouped in 10° palaeolatitude belts (N and S plotted on same axis). At this level of resolution (probably the most robust given uncertainties in palaeogeographic reconstructions) the limits of the tropics fall within the 20–30° belt. Use of 5° resolution, with the tropics in the 20–25° belt, does not significantly change the results. Degrees palaeolatitude calculated for the appropriate 5-Myr interval using computer software developed by D. B. Rowley for the Palaeogeographic Atlas Project, University of Chicago. *a*, Well preserved orders, Triassic–Recent; *b*, Triassic–Mid Jurassic (through Bajocian Stage) well preserved orders; *c*, poorly preserved orders, Triassic–Recent (H_01 , significantly different from *a*, $P < 0.01$, Kolmogorov–Smirnov test on frequency distributions, and $P < 0.001$; G test using either 25° or 30° N and S as an approximate tropical–nontropical boundary); *d*, Triassic–Bajocian echinoid records, calculated as the number of localities from which each species is recorded (H_02 , significantly different from *b*, $P < 0.025$, Kolmogorov–Smirnov test; $P < 0.005$, G test as above); *e*, well preserved orders from *a*, adjusted for preservation and sampling using the distribution of poorly preserved orders in *c*; *f*, Triassic–Bajocian well preserved orders in *b*, adjusted for sampling using the distribution of echinoid records in *d*. This adjustment procedure effectively factors out potential sampling artefacts arising from the decreasing area of each belt with increasing latitude: well preserved orders are assessed relative to the total number of records within each belt for the H_0 datasets. Despite the larger total area of tropical regions, they are more poorly sampled, so that the proportion of well preserved orders originating in tropical seas is greater than expected. As noted in the text, this does not rule out area differences as a potential biological mechanism for the latitudinal pattern. Orders appearing simultaneously in two adjacent latitudinal belts are scored as 0.5 in each; these are starred and listed here in the lower of the two latitudinal bands. Well preserved orders: 0–10°, Pedinoidea, Oligopygoida* (contemporaneous records not in adjacent belt but in 21–30°), Clypeasteroidea; 11–20°, Isocrinida*, Pygasteroidea; 21–30°, Milleporina*, Scleractinia, Cheilostomata, Encrinida, Millericrinida, Hemicidaroida, Phymosomatoida, Holoctypoida, Holasteroidea*, Spatangoida*; 31–40°, Lychniscosida, Helioporacea, Neogastropoda*, Cyrtocrinida*, Bourgueticrinida, Temnopleuroidea, Salenioida (= Calycina), Echinoida, Cassiduloida, Disasteroidea; 41–50°, Stylasterina. Poorly preserved orders: 21–30°, Trichasteropsida, Valvat-

ida, Paxillosida*; 31–40°, Stolonifera, Micropygoida, Anaspidea, Notaspidea, Forcipulatida, Notomyoidea, Velatida; 41–50°, Sacoglossa (= Ascoglossa), Comatulida, Echinothurioida, Diadematoida, Brisingida, Spinulosida. The patterns shown here are robust to alternative taxonomies. They are strengthened if the echinoid superorder Microstomata is used in addition to or instead of Order Cassiduloida²¹; if the crinoid order Bourgueticrinida is subsumed within the Isocrinida³⁰; or if the crinoid family Holocrinidae is considered a stem group to all articulate crinoids rather than part of Order Isocrinida³⁰, with Isocrinida then starting with the mid-Triassic *Laevigatocrinus laevigatus* (Münster) and *Isocrinus tyrolensis* (Laube)³⁰. Inclusion of possible occurrences of two additional poorly preserved orders in the Late Cretaceous of northern Europe²⁰, namely isolated spicules attributed to Homoscleromorpha (Porifera) and borings attributed to Ascothoracica (Arthropoda), would also reinforce the results.

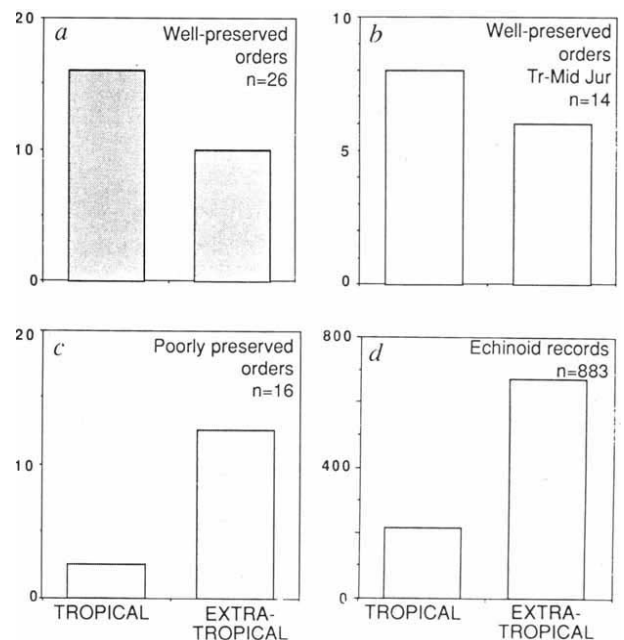
expected from poorly preserved orders (62% and 22%, respectively, $P < 0.005$, G test), or from echinoid records (57% of Triassic–Bajocian ordinal records versus 24% of echinoids, $P < 0.01$, G test). Again, differences remain significant when the Early Triassic data are excluded.

Whether defined palaeolatitudinally or biogeographically, tropical seas have produced more new orders than expected from sampling bias alone. This does not mean that all taxa have tropical origins: the rich molluscan fossil record may indicate a truly extratropical origin for the Order Neogastropoda^{20,30}, and many individual families and genera clearly originated in high latitudes¹⁶. Nor do these results require that ordinal rank *per se* has objective reality across all phyla, or that orders originate with all derived characters in place^{20,21}. They do suggest, however, that novel body plans with the potential to accumulate further derived characters—thereby defining groups likely to be accorded ordinal status—originate most frequently in tropical species.

FIG. 2 First occurrences of orders in tropical and extra-tropical seas, as defined biogeographically on the basis of contemporaneous distributions of tropical indicators such as abundant dasycladalean algae^{39,40} and large benthic foraminifera^{41–43} (to avoid circularity, macroinvertebrate indicators were not used). *a*, Well preserved orders, Triassic–Recent; *b*, poorly preserved orders, Triassic–Recent; *c*, Triassic–Bajocian well preserved orders; *d*, Triassic–Bajocian echinoid records.



ida, Paxillosida*; 31–40°, Stolonifera, Micropygoida, Anaspidea, Notaspidea, Forcipulatida, Notomyoidea, Velatida; 41–50°, Sacoglossa (= Ascoglossa), Comatulida, Echinothurioida, Diadematoida, Brisingida, Spinulosida. The patterns shown here are robust to alternative taxonomies. They are strengthened if the echinoid superorder Microstomata is used in addition to or instead of Order Cassiduloida²¹; if the crinoid order Bourgueticrinida is subsumed within the Isocrinida³⁰; or if the crinoid family Holocrinidae is considered a stem group to all articulate crinoids rather than part of Order Isocrinida³⁰, with Isocrinida then starting with the mid-Triassic *Laevigatocrinus laevigatus* (Münster) and *Isocrinus tyrolensis* (Laube)³⁰. Inclusion of possible occurrences of two additional poorly preserved orders in the Late Cretaceous of northern Europe²⁰, namely isolated spicules attributed to Homoscleromorpha (Porifera) and borings attributed to Ascothoracica (Arthropoda), would also reinforce the results.



Several mechanisms, not necessarily mutually exclusive, might explain the observed pattern. (1) The great species richness of the tropics, both within communities and summed over the immense total area^{5,17,31}, may provide so many evolutionary experiments that the overall probability of ordinal origination is inevitably higher there². Such probabilistic explanations are undermined, however, by bathymetric and temporal disparities between species richness and ordinal origination in the fossil record: orders tend to arise onshore regardless of bathymetric patterns at lower levels²⁰, and tend to appear in the early Palaeozoic and early Mesozoic in advance of prolonged diversity increases and plateaus at lower levels^{6,26,32}. Alternatively, tropical carbonate platforms, which can build out to the shelf edge and thus usurp middle and outer shelf habitats^{33,34}, may bias the tropics on a per-km-of-coastline basis in favour of the shallow-water settings that evidently give rise to most new orders²⁰. (2) The complexity, resource spectrum, or favourableness^{1,11} of the tropics, all variously invoked to explain species richness patterns, may actually confer a higher per species rate of ordinal origination. This seems less likely than the first set of hypotheses because it is unclear why tropical environments should favour greater disparity per speciation event or produce species with greater 'evolutionary potential'. Such arguments focus on background extinction and origination, however, and the tropics are much less stable over geological timescales than previously thought³⁵⁻³⁷. Rebounds of the global marine biota after extinction events are twice as likely to produce new orders than are background processes²⁶, and the potential evolutionary consequences of such upheavals in the tropics, repeatedly disrupting and reassembling these rich communities, are poorly understood. Whatever the ultimate causal mechanism, the present analysis adds a new geographical dimension to the growing evidence^{20,38} that evolutionary novelties do not originate randomly in time and space. □

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Stratification of ON and OFF ganglion cell dendrites depends on glutamate-mediated afferent activity in the developing retina

Stefan R. Bodnarenko & Leo M. Chalupa

Department of Psychology and the Center for Neuroscience, University of California, Davis, California 95616-0657, USA

A FUNDAMENTAL attribute of the vertebrate visual system is the segregation of ON and OFF pathways signalling increments and decrements of light¹⁻⁴. In the mature retina, dendrites of ON- and OFF-centre retinal ganglion cells (RGCs) stratify in different sublaminae of the inner plexiform layer (IPL), and are differentially innervated by two types of bipolar cells which depolarize and hyperpolarize on exposure to light⁵⁻¹⁰. This stratification of ON and OFF RGCs is achieved by the gradual restriction of their dendrites which ramify throughout the IPL early in development¹¹⁻¹⁴. The factors underlying this regressive event are unknown. Dendritic stratification occurs around the time that bipolar cells form synapses in the IPL^{15,16}, which raises the possibility that synaptic activity is involved in this process. Here we test this hypothesis by treating the developing cat retina with the glutamate analogue 2-amino-4-phosphonobutyric acid (APB), which hyperpolarizes ON cone bipolar and rod bipolar cells, thereby preventing their release of glutamate¹⁷⁻¹⁹. We report that intraocular injection of APB during the period when dendritic stratification normally occurs prevents the formation of structurally segregated ON and OFF retinal pathways. These results provide evidence that glutamate-mediated afferent activity regulates the remodelling of RGC dendrites during development.

The central region of the cat retina contains the highest density of beta cells which can be readily identified on the basis of soma size and dendritic morphology²⁰. As can be seen in Fig. 1a, the primary dendrites of these neurons stratify either proximal (ON-centre) or distal (OFF-centre) to the soma. In newborn animals, and in those treated with APB, the dendritic morphology of many of these neurons is strikingly different, such that the primary dendrites are multistratified, ramifying both proximal and distal to the soma (Fig. 1b and c).

We first determined the incidence of multistratified ganglion cells in postnatal-day-2 (P2) retinae, the age at which APB injections were initiated. Previous studies have suggested that stratification of cat retinal ganglion cells begins in the central retina before birth and is completed at the periphery several weeks later¹⁶. At P2 a substantial proportion of the dendrites of ganglion cells in the central retina (42.7% of 389 cells) were still multistratified (Fig. 1c). These data provide a baseline for comparing the incidence of multistratified cells in normal and APB-treated retinae of older animals.

We next examined dendritic morphology of beta cells in APB-treated and control retinae. This revealed that the proportion of multistratified cells normally decreases quite markedly by P8, with a gradual reduction occurring during the next 5 days. At