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ORIGINS OF MARINE PATTERNS OF BIODIVERSITY: SOME CORRELATES AND APPLICATIONS

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Abstract: Marine shelf diversity patterns correlate with macroecological features of basic importance that may play causal roles in macroevolution. We have investigated the global diversity pattern of living Bivalvia, which is dominated by the latitudinal diversity gradient (LDG), maintained by high tropical origination rates. Generic-level lineages expand poleward, chiefly through speciation, so that species richness within provinces and globally is positively correlated with generic geographical ranges. A gradient in diversity accommodation progressively lowers both immigration and speciation rates in higher latitudes. The LDG correlates with seasonality of trophic resources but not with area; tropical provinces are not diverse because they are large but because they are tropical. A similar dynamic evidently underlays Jurassic and Carboniferous LDGs. Larval developmental modes correlate with the LDG and thus with resource seasonality, with tropical dominance of planktotrophs offset by increasing nonplanktotrophy to poleward. The acquisition of planktotrophy in several early Palaeozoic clades indicates a change in macroecological relationships during Cambrian and Ordovician radiations.

Key words: biogeography, Bivalvia, Brachiopoda, latitudinal diversity gradient, Neogene, provincial biodiversity.

MANY of the factors responsible for major biodiversity patterns are still unresolved, and thus macroecological and evolutionary theory cannot yet reliably predict the patterns that should result from given environmental situations. However, a significant and growing body of data permits correlation of environmental conditions and trends with biotic ones and contains evidence of causal processes. Here, we review marine biodiversity patterns at shelf depths in modern seas and briefly evaluate the dynamics that seem to be largely responsible for producing them, based chiefly on Neogene data. Our data are drawn largely from molluscs, partly from gastropods but mostly from bivalves, which we use as a model system (see Krug *et al.* 2009*a*). The diversity patterns of these molluscan groups are generally concordant with each other and with those of other major clades and of the living marine fauna as a whole at the scales of provinces and climate zones (e.g. Bellwood and Hughes 2001; Briggs 2007; Reaka *et al.* 2008). We concentrate on the latitudinal diversity gradient (LDG) and ask whether patterns described deeper in time can be interpreted by the dynamics underlying Neogene patterns, and thus whether factors correlated with the LDG have had macroevolutionary consequences.

GLOBAL AND PROVINCIAL BIODIVERSITY PATTERNS

As a general principle, the standing species diversity of an ecological unit (e.g. the global ocean, a climate zone, a marine province, a local region and a local biotope) is determined by the rate of species origination, extinction, immigration and emigration associated with that unit. At the global level, diversity is controlled by origination and extinction alone, and at the local levels, evidence is available only for local introductions or extirpations; while at the intermediate levels, all factors must be taken into account.

Global patterns

The global marine biodiversity pattern is dominated by the LDG (Text-fig. 1A–C; and see Roy *et al.* 1998). For bivalves, the dynamics of the LDG during the Neogene are fairly clear (Jablonski *et al.* 2006; Krug *et al.* 2009*a*; data are best from the Upper Miocene to Recent times). Both species and lineages at the generic level originate at highest rates in lower latitudes, and in general, peak

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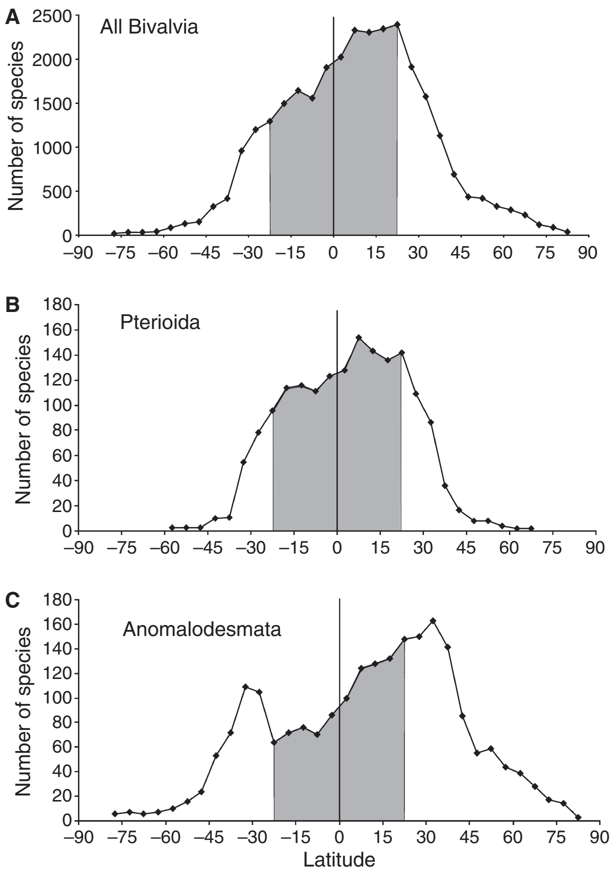


TEXT-FIG. 1. Latitudinal diversity gradients for present-day marine bivalve species. A, Marine bivalves as a group. B, Order Pterioida. C, Anomalodesmata, a 'contrarian' clade lacking a diversity maximum in the tropics. Shaded areas mark the general position of the tropics, between 25°N and S latitude, although this boundary varies significantly among oceans and through time.

diversities correspond with peak origination rates, and lower diversities, as at the poles, with lower origination rates (Jablonski *et al.* 2006; Krug *et al.* 2007, 2009*a*). A taxonomically broader Phanerozoic analysis using coarser time bins also found higher per-taxon originates rates in the tropics (Kiessling *et al.* 2010).

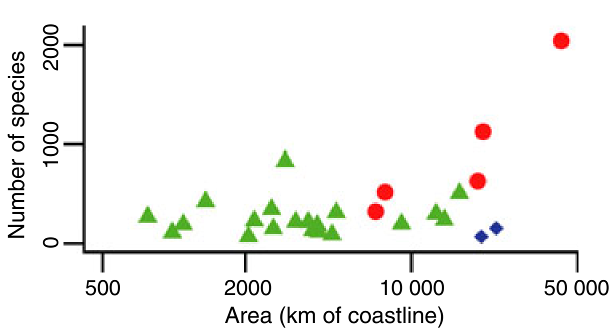
Today, the median age of generic lineages of bivalves increases monotonically from the tropics (youngest) to the poles (oldest) (Jablonski *et al.* 2006). Estimated Neogene extinction rates, available for the Northern Hemisphere show a different trend, being low in the tropics, significantly higher in the temperate zone and lower again in polar waters, and thus do not correlate with the age gradient (Valentine *et al.* 2008). High tropical extinction rates across the Phanerozoic have been reported (Kiessling *et al.* 2010), but those data appear to be dominated by obligate reef dwellers such as corals, sponges, and larger foraminifera, – taxa prone to extinction when reef structures are degraded – and more work is needed on the sampling density of other clades in tropical vs. extratropical habitats. During Neogene times, physical environmental factors (surface temperatures, for example, and the many factors they entrain) are most variable in temperate latitudes, seasonally and on ecological and evolutionary time scales, which may drive the elevated extinction rates (see Jannson 2003 for a Pleistocene example). Over time, many tropical lineages expand into higher latitudes (an out-of-the-tropics scenario), perhaps aided by the 'openings' created by the higher extinction rates in the temperate zones, and this is largely a one-way street; little or no movement from temperate zones into the tropics has been detected (Jablonski *et al.* 2006). Further, few lineages that show tropical originations have withdrawn from the tropics. Of the 113 bivalve genera recorded as originating in the Late Miocene–Pleistocene tropics (Jablonski *et al.* 2006), 72 expanded into higher latitudes, but only two vacated the tropics (Jablonski In press).

Although many bivalve genera are exclusively or mainly tropical, about three quarters of bivalve genera in both temperate and polar zones have tropical representatives (Krug *et al.* 2008). Expansions from the tropics are not random: genera with the highest speciation rates have been the chief invaders of more poleward zones (Krug *et al.* 2008), suggesting that these range expansions at the clade level are commonly accomplished via speciation. A hypothesis that satisfies these data proposes a latitudinal gradient in diversity-dependent factors (Valentine 1972, 1973) that progressively restricts diversity towards the poles, with incumbent faunas that are already exploiting those factors tending to preclude invasion or origin of new species (Walker and Valentine 1984), thus progressively damping both origination and immigration rates poleward of the tropics (Valentine *et al.* 2008).

The two most obvious diversity-dependent factors are trophic resources and living space as defined or at least influenced by habitat heterogeneity. Living space as simple area does not appear to regulate diversity patterns in the sea, while primary productivity displays a strong latitudinal gradient in seasonality that does tend to parallel biodiversity (Valentine 2009). We suggest that the very low productivity of high-latitude winters imposes a characteristic set of biological consequences. For example, compared with low-latitude faunas, more high-latitude species tend to be generalists and thus live in more habitats and feed on broader ranges of food items, a strategy for survival that requires a broad resource base, and that therefore limits the environmental capacity to accommodate species (see Valentine 1983; for recent experimental support see Compton *et al.* 2007 (marine) and Nava *et al.* 2008 (terrestrial); and for a more competition-based view that also emphasizes stability and quantity of resources, see Vermeij 2005). Reproductive modes in higher-latitude molluscs tend to nonplanktotrophic development or brooding with a parental supply of yolk or other nutriments – a developmental strategy that lowers fecundity but raises juvenile survival in a trophically unstable environment – whereas in the tropics planktotrophic development is far more common, with larvae feeding in the plankton, a dependable trophic resource in an environment of low trophic seasonality (Thorson 1950; Jablonski and Lutz 1983; Lapitkhovsky 2006). Whether these diversity-dependent factors are augmented by diversity-independent ones, such as the effects of higher temperature on ecological and evolutionary rates (e.g. Rohde 1992; Allen and Gillooly 2006; Allen *et al.* 2007; Gillman *et al.* 2009), is unclear, and mechanisms linking energy input to evolutionary dynamics remain poorly articulated and insufficiently tested (and see Roy *et al.* 2004 and Clark 2009 for mixed results in marine benthos).

Provincial patterns

It follows from the global LDG that provinces have higher diversities in the tropics, grading to lower diversities in polar provinces, with concomitant gradients in adaptive types and reproductive strategies. However, additional information on biodiversity regulation can be gleaned from the provincial level. In the ocean, the commonly cited positive correlation between area and biodiversity (e.g. Rosenzweig 1995) is absent; marine provincial area and biodiversity are not significantly correlated (Roy *et al.* 1998). The five tropical bivalve provinces have high diversities and are large and do show a significant relationship between diversity and area, but the 19 temperate provinces, which range over nearly an order of magnitude in area, show no such correlation (Text-fig. 2). Furthermore, the polar provinces are quite large (the Arctic shelf province has several times the area of the tropical Panamic shelf province) but have very low diversities.



TEXT-FIG. 2. Relationship between bivalve species richness and the geographical area encompassed by shallow marine provinces. Circles: tropical provinces; triangles: temperate provinces; diamonds: polar provinces. From Harnik *et al.* 2010.

A few temperate provinces have higher diversities than expected, given their latitudes, rivalling or even surpassing some tropical provinces. Two factors appear to be involved. First, some temperate provinces that flank tropical provinces are washed by strong, warm currents originating in tropical waters. Such currents provide routes for tropical species to invade, and conditions for their maintenance in, extratropical provinces. Examples include the Japonic provinces, washed by the Kuroshio and Tsushima Currents (Longhurst 1998), and the South Australian province, washed by the Leeuwin Current (Church and Craig 1998). Thus, higher diversity in these temperate provinces is related to tropical influences, not to area. And second, some temperate provinces have coastlines with important longitudinal components, such as the Oregonian provincial extension along the Aleutians, or are doubled around capes and thus have shorelines twice as long as their latitudinal extents, as the Magellanic province around Cape Horn. In these latter cases, higher provincial diversities may be supported by higher habitat heterogeneity along their extensive coastlines and bordering shelves than would otherwise be expected from latitudinal patterns alone (Valentine 2009). The most diverse tropical provinces, such as the Western Pacific, have greater longitudinal breadth than any temperate province, which may help to account for their high diversities. Nevertheless, the tropical condition appears to be the best correlate of high diversity, and it follows that tropical provinces are not diverse because they are large but because they are tropical.

Local patterns

The size of the species pools from which local faunas are drawn is known to affect local or regional diversities quite apart from such obvious effects as immigration along strong currents (MacArthur and Wilson 1967, and for marine examples see Witman *et al.* 2004 and Karlson *et al.* 2004). Most studies have focused on disjunct shelf-depth habitats, such as between oceanic islands, but conjunct intraprovincial regions with highly unstable trophic supplies (for example, in the upwelling compartment off Oman) appear to maintain high diversities because they are nested within diverse provinces. Within local biotopes, however, diversity is commonly affected by variations in habitat heterogeneity, which should affect the proportion of the ecologically appropriate fraction of the regional species pool that is present.

THE LATITUDINAL DIVERSITY GRADIENT DEEPER IN TIME

Evidently an LDG has been a pervasive feature of the global marine fauna, being reported from the Cambrian onward, though there have been few comprehensive studies of pre-Cenozoic faunas. The slope of the gradient has clearly varied and may have been weak or absent at times after extinctions that disproportionately affected low-latitude forms (Jablonski 2005). Here, we test the assumption that the present is a key to the past so far as the out-of-the-tropics scenario is concerned, by examining two previous studies of the LDG, one from the Mesozoic and one from the Late Palaeozoic.

A Mesozoic pattern

Crame (2002) documented and analysed the LDG shown by the bivalves of the Upper Jurassic Tithonian stage. The gradient, while much gentler than today's, was clearly present in both hemispheres, although there were no faunas appropriate for the study below 20 degrees paleolatitudes. Documentation is best in the north, then as now, and we discuss the findings there. Crame (2000) had previously studied the modern LDG in bivalves and determined that the steepest gradients occur among the younger bivalve clades, chiefly heteroconchs, concluding that heteroconch radiations probably occurred during late Mesozoic and Cenozoic times. From the shallow Tithonian gradient, it could be inferred that the increase in the slope of the LDG from the late Mesozoic until today was created in large part by heteroconch diversifications, which were greatest in low latitudes, raising the diversity peak there and increasing the slope. Subsequently, a study of the effects of the Cretaceous–Paleogene extinctions on evolutionary rates among bivalves supported Crame's thesis and showed that heteroconch diversification rates were strongly elevated following that extinction event and have remained high right through the Cenozoic (Krug *et al.* 2009*b*). However, the dynamic associated with the origin of the Tithonian gradient itself has not yet been documented. We therefore predict that (1) the Tithonian bivalve genera in lower latitudes will have a younger median age than in higher latitudes as a consequence of higher tropical origination rates, and (2) more genera will make their oldest appearances in the tropics as our knowledge of that record improves.

A Palaeozoic pattern

Molluscs were not a dominant clade in the Late Palaeozoic benthos, but brachiopods were widespread and relatively diverse, and show an LDG from their earliest radiation during Lower and Middle Cambrian (Ushatinskaya 1996) until at least the mid-Permian (Fitzgerald and Carlson 2006; Shen *et al.* 2009). The LDG of Carboniferous brachiopods has been the subject of a number of studies (e.g. Raymond *et al.* 1989; Leighton 2005; Powell 2005, 2007, 2009). Among these studies, Powell (2007) used the largest taxonomic database resolved to the narrowest time intervals to describe the LDG of brachiopod genera before, during and following the Carboniferous glaciations, dubbed the Late Palaeozoic ice age (LPIA, from about 327 to 290 Ma, Late Serpukhovian through Early Sakmarian). A strong latitudinal gradient was found before the LPIA, became much gentler during the glacial period, but then rebounded as the LPIA drew to a close. Narrowly distributed forms were youngest and hardest hit by extinction; wide-ranging genera were oldest and survived best. The rediversifications were clearly strongest in lowest latitudes (Powell 2007, fig. 1), grading to weakest poleward, just as appears to occur for bivalves after the end-Cretaceous extinction (Krug *et al.* 2009*b*). The post-LPIA brachiopod LDG owed its slope to the presence of the younger genera in the lower latitudes. Furthermore, the earliest Carboniferous faunas (Tournaisian) were of relatively low diversity and showed a gentle LDG, and the rise of a steep gradient prior to the LPIA was also because of the presence of a younger, rapidly diversifying fauna in low latitudes, where peak diversity increased markedly (Powell 2007, fig. 1). Fitzgerald and Carlson (2006), summing over the Palaeozoic, also found the shortest brachiopod genus durations in the tropics. We presume the progressive extinctions in a fauna adapted to tropical conditions were caused by climatic deterioration and associated environmental change during the ice age, as suggested by the equatorward contraction of generic ranges during the onset of the glacial period (Raymond *et al.* 1989; Leighton 2005). The rebound correlates with the waning of the ice age and was presumably permitted by climatic amelioration. Both pre- and post-LPIA diversifications required about 20 myr. The dynamics of both of these low-latitude radiations, with peak rates in the inner tropics and decreasing rates poleward, are consistent with our findings on the global dynamics of the Neogene gradient.

Nevertheless, LPIA brachiopod patterns diverge from Neogene mollusc patterns in the behaviour of diversity at the provincial level: during the LPIA diversity declined in the tropics and provinciality evidently weakened, whereas the Neogene refrigeration, including the Pleistocene glacial cycles, impinged less severely on the tropics, at the margins, and actually strengthened provinciality (Valentine *et al.* 1978; Crame and Rosen 2002). However, Palaeozoic foraminifera appear to show provincial diversity patterns more similar to those of Neogene molluscs than to Palaeozoic brachiopods (Groves and Yue 2009).

Perhaps clade-specific dynamics account for such differences, though sampling problems may also be involved.

Powell (2009) has suggested a different interpretation that brachiopod diversity has simply tracked continental shelf area over time, shifting from a high southern latitude maximum in the Cambrian, though the tropics during the Palaeozoic, to high northern latitudes in the Mesozoic and Cenozoic. This is an intriguing hypothesis, but comparisons of Powell's synthesis of brachiopod history to present-day invertebrate biogeography lead us to another view. As noted earlier, today's marine invertebrate diversity patterns are not correlated with area. Furthermore, modern LDGs are not centred on the geographical equator, but are skewed to the north at the present thermal equator, while the southern limits of tropical provinces may lie as far north as between 5 and 10 degrees south latitude. These offsets are effects of the present sizes and configurations of ocean basins and wind and ocean current patterns. From the Ordovician to the Permian, the densest brachiopod contours fall between 20 north and 20 degrees south palaeolatitude and would thus qualify as tropical by today's biogeographical standards (this effect is even stronger when North American and western European data are excluded to reduce sampling biases; Powell 2009, fig. 5). With today's refrigerated poles, the tropics are relatively narrow, but the distribution of reefs, larger foraminifera, and geochemical temperature proxies indicate broader tropical belts at different points in the Phanerozoic, further complicating use of equatorial proximity as a gauge of tropical/temperate patterning of past biodiversity (Jablonski 1993; Walker *et al.* 2002; Kiessling 2009).

Why are Palaeozoic and modern brachiopod LDGs different?

Living non-linguliform brachiopods are exclusively nonplanktotrophic and show an LDG that peaks in mid-temperate latitudes but has a reverse gradient to a lower tropical level (Cowen *in* Rudwick 1970; see also Zezina 2008, who however includes both deep-sea and shelf records), unlike their pattern in the Carboniferous. Poleward from its temperate high, this gradient follows the normal trend to a minimum in high latitudes. A similar pattern has been found in the bivalve order Anomalodesmata (Text-fig. 1C; Krug *et al.* 2007), which also has entirely nonplanktotrophic development and whose origination rates are greatest at their mid-latitude diversity peak and decline in either direction from there. Similar double gradients, or very low LDGs, some nearly flat, characterize some other nonplanktotrophic taxa as well (Valentine and Jablonski 1983; Krug *et al.* 2007), and several clades shift reproductive strategies with latitude via species replacements (Jablonski and Lutz 1983). These patterns suggest that nonplanktotrophy is disfavoured in the tropics but is advantageous in higher latitudes, in keeping with the seasonality hypothesis. As the late Palaeozoic non-linguliform brachiopods have a 'normal' LDG of the sort represented by planktotrophic forms today, we have suggested that the Palaeozoic brachiopod faunas included a high percentage of planktotrophs that produced the normal LDG (Valentine and Jablonski 1983). More recently, several studies (e.g. Freeman and Lundelius 2005, 2008; Popov *et al.* 2007) have suggested fairly widespread planktotrophy among Palaeozoic rhynchonelliform brachiopods.

Evidently the mass extinctions of the late Permian and late Triassic removed most or all of those lineages, and the survivors and their descendants were or eventually became entirely nonplanktotrophic. In any event, peak brachiopod diversity has been above 20 degrees north and south latitude since the Triassic (Powell 2009; see also Walsh 1996). Data are still ambiguous as to whether end-Permian and/or late Triassic extinctions were primary drivers of the biogeographical and macroecological shift, or if more attritional processes during the Triassic were involved (see also Zezina 2008, who argues that long-term changes in plankton composition put brachiopods at a disadvantage in shallow water).

Patterns of developmental modes and macroecology

A significant record of body fossils of eumetazoans began with the Cambrian explosion, at 530–520 Ma, with the appearance of about a dozen living phyla, and with the possibility that stem lineages of nearly or quite all of the living phyla had evolved but have not been found fossil. The early developmental modes of those explosion taxa are not known from direct evidence, though the small body sizes of most of their latest Neoproterozoic ancestors, indicated by trace fossils, suggests direct development for those earlier forms (see Chaffee and Lindberg 1986). During the Early Cambrian, most phyla are represented only by their stem groups (Budd and Jensen 2000); the last common ancestors of crown members of phyla chiefly appear after the explosion. Peterson (2005) developed molecular clock and fossil evidence to indicate that lecithotrophic larvae, perhaps planktonic but non-feeding, evolved multiple times during or shortly following the explosion, which would have been chiefly within the stem lineages of the phyla, while planktotrophic larvae appeared independently in several lineages, seemingly over a protracted interval through Cambrian and early Ordovician time, presumably originating in or being inherited by crown lineages of those phyla (see also Nützel *et al.* 2006; Runnegar 2007; Servais *et al.* 2008). Peterson attributed the rise of planktotrophy to pressure from predation on benthic larvae, following an earlier suggestion by Signor and Vermeij (1994), but there is no evidence of a latitudinal gradient in benthic larval predation, and planktotrophy may simply have arisen through selection involving the cost to benefit ratio between fecundity and mortality during a stabilizing trend in primary productivity.

We envision a causal chain of macroecological events that was initiated by phytoplankton diversification and stabilization of spatial gradients in the regime of primary productivity in the Cambrian. Diverse metazoan clades then evolved planktotrophic development, taking advantage of this change in the resource base that became available to developing embryos, particularly in tropical regions where productivity was most stable, and of the higher fecundities permitted by the relatively large body sizes attained by many metazoan clades. The consequences of this transition included the establishment or strengthening of the LDG and the initiation of an out-of-the tropics' dynamic and of a macroecological pattern that has persisted, though perhaps with interruptions, to this day. It is clear that global marine diversity during the Phanerozoic was closely associated with and partly reflected in the history of the LDG.

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