

Scales of climatic variability and time averaging in Pleistocene biotas: implications for ecology and evolution

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The Pleistocene (c. 1.6–0.01 million years BP) fossil record, having accumulated during a series of glacial and interglacial episodes, has contributed greatly to our understanding of the responses of species and communities to climatic changes over a spectrum of time-scales. For example, data from marine and terrestrial settings have shown that species tended to respond individually to the climate fluctuations, thereby giving rise to associations not represented in today's biota, and thus termed 'non-analogue' communities^{1–3}. However, while such re-shuffling of species' associations is well established, major problems remain, including the presence of anomalous fossil associations that include species of very different climatic provenance, and the surprising lack of accelerated extinctions or speciations associated with these extreme climatic cycles. Here, we review recent advances in climate studies and in paleontology that provide a new perspective on the nature of Pleistocene climatic fluctuations, and on the strengths and limitations of the fossil record in resolving the biotic responses to such changes. These advances shed new light on the Pleistocene biotic patterns and also have clear implications for ecological theory, providing the necessary framework within which the question of biotic response to global change should be addressed.

European lake sediments may also represent such climate flickers^{11,12}.

Flickering climates

Until recently, most analyses of the Pleistocene fossil record tacitly assumed that the major climate changes over the past 1.6 million years (My) could be explained by shifts between glacial and interglacial stages or substages (apparently modulated by the Earth's orbital parameters) on 10- to 100-thousand-year (ky) timescales⁴. However, the study of Pleistocene paleoclimates entered a new phase in 1992–1993 with the recovery of two long (>3000 m) ice-cores in central Greenland. Ice in these cores displays banding that accumulated in annual layers, and although the cores were drilled 30 km apart, generally the bands can be correlated. Climate proxies such as oxygen isotopes and atmospheric dust content provide striking evidence for extreme climatic fluctuations on a scale of about a 1000 years during the Late Pleistocene^{5,6} (~130 ky to 10 ky) (Fig. 1). These millennial-

Biotic responses to Pleistocene climatic fluctuations have traditionally been analyzed in the context of glacial–interglacial cycles on the scale of 10 000–100 000 years. However, emerging evidence indicates that short-term, high-amplitude, climatic 'flickers', close to the limits of the resolving power of the fossil record, occurred within the glacial and interglacial substages. Because species shift geographically in response to the climate flickers, community structures are fluid, with changes absorbed ecologically and not mediated macroevolutionarily. The rapidity of these shifts may also explain anomalous fossil assemblages.

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scale, high-amplitude 'flickers' are termed Dansgaard–Oeschger (D–O) cycles; they may have occurred in sudden steps, with the actual climate changes being completed on decades-to-century scales. D–O cycles are most prominent in the ice-core record from the last glacial period (23 cycles between 110 ky and 15 ky ago), and until recently were thought to have been absent from the Holocene interval (0–10 ky ago). However, new analyses of the ice cores⁸ and of ice-rafted debris (IRD) in the North Atlantic⁹ have revealed less-extreme millennial oscillations during the Holocene; the Little Ice Age of only 300 years ago may have been the most recent of these events. Ice-core evidence for high-amplitude fluctuations during the last (Eemian) interglacial is controversial¹⁰, but there are indications of circulation changes in the North Atlantic that are similar to those associated with D–O cycles¹¹. Eemian pollen fluctuations in

Evidence for D–O cycles can be traced widely, in part because of their relation to another set of Pleistocene climate signals, the Heinrich events. D–O cycles appear to come in packages that culminate in particularly intense cold phases, and high-resolution North Atlantic records of foraminiferal abundances and oxygen isotope data indicate that the climatic minima of D–O bundles coincide with layers of IRD, during what are now termed Heinrich events¹³. Heinrich layers have an unusual clay and detrital limestone composition, indicating a Canadian source. These layers document repeated floods of iceberg armadas shed into the ocean by sudden expansion and collapse of the North American ice sheets. Climate pulses that correlate with D–O cycles or Heinrich events have been identified on a global scale by a variety of climate-sensitive criteria. These data include: high-precipitation episodes recorded by pollen in sediments from Lake Tulane, FL, USA¹⁴; advances and retreats of mountain glaciers in the Rocky Mountains and Cascade Range in North America¹⁵, the Chilean Andes¹⁶ and the Southern Alps of New Zealand¹⁷; fluctuations in the accumulation of Chinese loess deposits¹⁷; the oxygen isotope record from the East Antarctic Vostok ice core¹⁸; and isotope variations, IRD events, and oxygenation cycles in North Pacific microfossils

and sediments^{19,20}. Even in cases where precise correlation of distant Pleistocene records with North Atlantic events is uncertain, the evidence of millennial-scale climate fluctuations is clear. The implications of these signals for understanding the modulation of the atmosphere-ocean climate system are an area of hot debate and active research^{16,21}, and the biological implications of this newly recognized scale of climatic variability are only now being explored.

Time-averaged assemblages

Our ability to track biological responses to D-O cycles depends on the resolving power of the fossil record. Post-mortem processes have the potential to bias the composition of fossil assemblages owing to (1) the selective destruction of species and age-classes, (2) removal from the life habitat, and (3) within-habitat mixing of successive generations. However, quantitative analyses of present-day shelled mollusks, mammals and plants indicate that the great majority of species with readily preservable remains are, in fact, represented in their local death assemblages, commonly with relative abundances statistically indistinguishable from a single live-community census (albeit data for mammals are limited to African savannahs)²². For these groups post-mortem transport into and out of a given habitat usually affects few individuals; exceptions (e.g. in some high-energy situations) are generally recognizable by independent sedimentary criteria²². Even wind-influenced pollen distributions, when collected from small lakes, tend to map closely on the geographic ranges of source species²³.

For fossil assemblages of these groups in low-energy settings, the most critical limitation on the resolving power of the fossil record is the timescale over which successive generations co-occur or are 'time-averaged' within single stratigraphic horizons. Sediment accumulation rates are generally low relative to population turnover times, and physical and biological agents (the latter ranging from trampling by wildebeests to repositioning by burrowing marine organ-

isms) further aggravate the mixing of organisms that lived many generations apart. Time resolution varies dramatically among localities and stratigraphic horizons, with some rare beds providing instantaneous Pompeii-like snapshots, and laminated deposits in lakes and some deep-sea basins permitting decadal resolution of pollen spectra, insects, microplankton and some fishes²². However, for marine invertebrates in shallow marine sediments, which provide the richest and most extensively studied fossil record, paleontological and radiocarbon data indicate that assemblages are

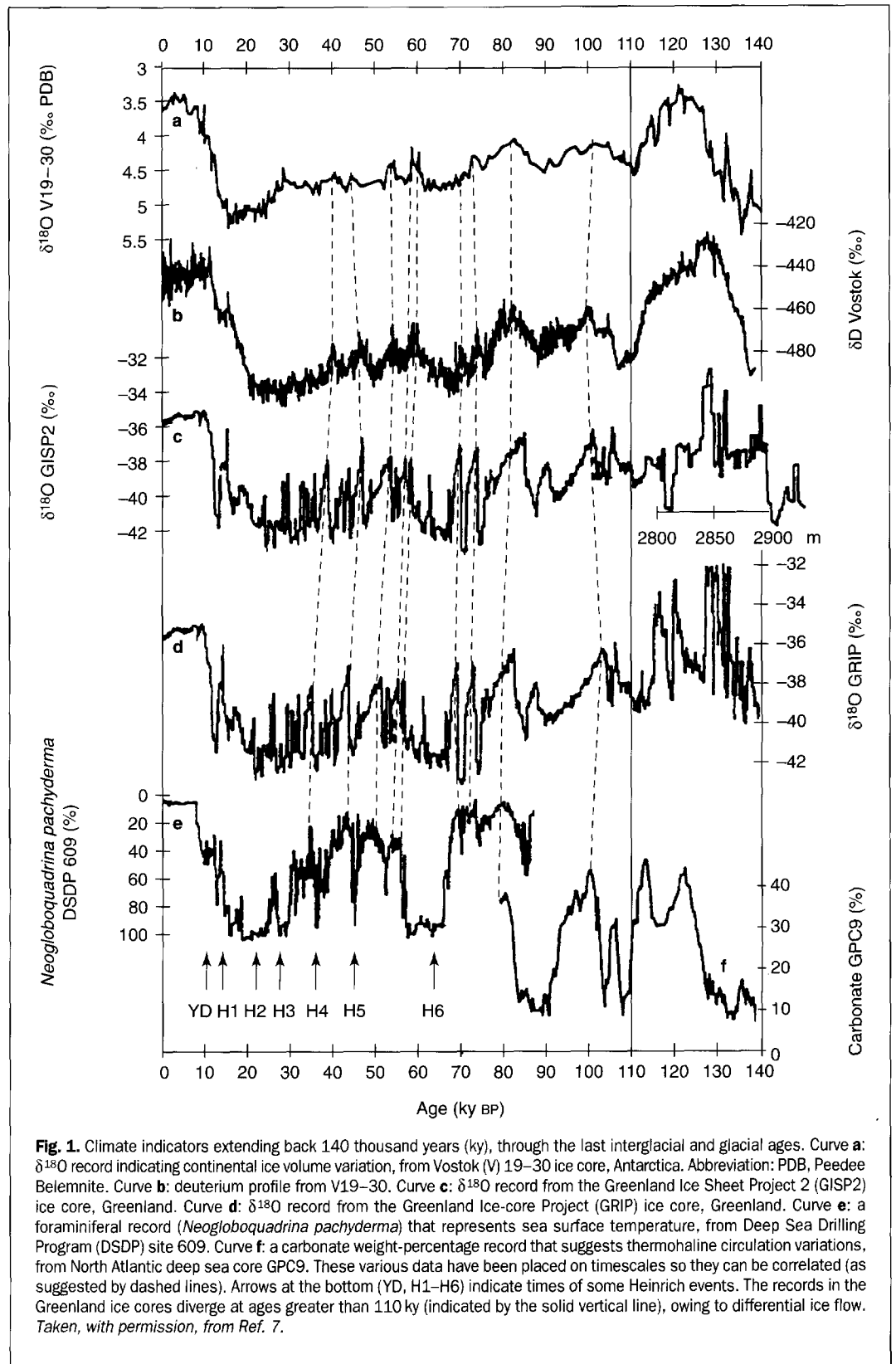


Fig. 1. Climate indicators extending back 140 thousand years (ky), through the last interglacial and glacial ages. Curve a: $\delta^{18}\text{O}$ record indicating continental ice volume variation, from Vostok (V) 19–30 ice core, Antarctica. Abbreviation: PDB, Peedee Belemnite. Curve b: deuterium profile from V19–30. Curve c: $\delta^{18}\text{O}$ record from the Greenland Ice Sheet Project 2 (GISP2) ice core, Greenland. Curve d: $\delta^{18}\text{O}$ record from the Greenland Ice-core Project (GRIP) ice core, Greenland. Curve e: a foraminiferal record (*Neogloboquadrina pachyderma*) that represents sea surface temperature, from Deep Sea Drilling Program (DSDP) site 609. Curve f: a carbonate weight-percentage record that suggests thermohaline circulation variations, from North Atlantic deep sea core GPC9. These various data have been placed on timescales so they can be correlated (as suggested by dashed lines). Arrows at the bottom (YD, H1–H6) indicate times of some Heinrich events. The records in the Greenland ice cores diverge at ages greater than 110 ky (indicated by the solid vertical line), owing to differential ice flow. Taken, with permission, from Ref. 7.

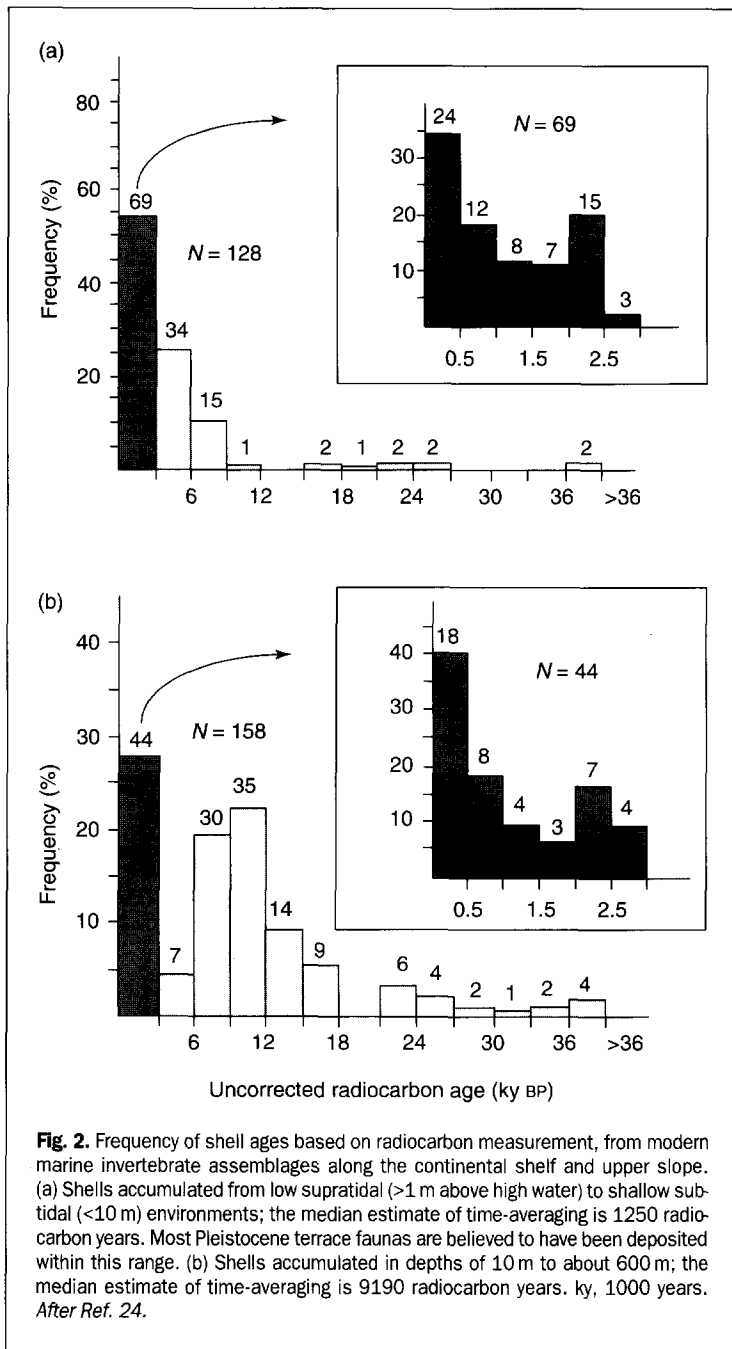


Fig. 2. Frequency of shell ages based on radiocarbon measurement, from modern marine invertebrate assemblages along the continental shelf and upper slope. (a) Shells accumulated from low supratidal (>1 m above high water) to shallow subtidal (<10 m) environments; the median estimate of time-averaging is 1250 radiocarbon years. Most Pleistocene terrace faunas are believed to have been deposited within this range. (b) Shells accumulated in depths of 10 m to about 600 m; the median estimate of time-averaging is 9190 radiocarbon years. ky, 1000 years. After Ref. 24.

typically time-averaged over hundreds to thousands of years in nearshore settings and thousands to tens of thousands of years offshore, on the continental shelf^{22,24} (Fig. 2).

On land, scales of time-averaging for vertebrate assemblages are less well-documented but appear to fall within the same range as marine invertebrates^{25,26}. By contrast, macrofloral assemblages, when they are preserved at all, tend to represent a much narrower time frame (single seasons to a few years), because they usually represent fossilized litter and their constituent leaves and flowers have brief residence times and short transport distances^{27,28}.

The time-averaging values cited here underscore a primary trade-off in the fossil record: a uniquely long temporal perspective but with resolution that is coarse compared with samples taken by ecologists from modern environments. Fortunately, typical scales of time-averaging are short relative to the average durations of species (10^6 – 10^7 years), thus the quantification of evolutionary patterns is unaffected. On the other hand, caution is clearly needed when attempting to interpret the fossil record of biotic responses to climate

flickers at the scales of D–O cycles (10^3 years). However, such cycles may indeed leave a detectable imprint on the fossil record, as we illustrate later in this paper, using biotic associations found in the marine Pleistocene record of California, USA.

Implications for ecology and evolution

That climate is an important determinant of species distributions has been demonstrated in a vast literature that covers a wide range of contexts from molecular physiology to biogeography. Recent ecological studies have demonstrated that population level dynamics of ecosystems are directly affected by decade- to century-scale climatic changes (e.g. Refs 29, 30). It is, therefore, expected that the millennial climate flickers discussed above would have major effects on the stability and composition of biotic communities. Since natural populations respond to climatic change by latitudinal shifts in abundances and/or geographic range boundaries^{1–3,30,31}, D–O cycles must repeatedly destabilize species interactions within communities. Depending on the magnitude and nature of the climatic shifts, species that had not previously lived together may come into contact; conversely, co-occurring species may become separated. In general, such individualistic adjustments of species distributions are common in the Pleistocene record, both in terrestrial and in marine environments. Many authors have also noted that these patterns undermine a notion of strong intracommunity cohesiveness, support a view of biotic communities as largely facultative associations, and constrain the timeframe available for obligate coevolutionary interactions^{1,2}.

The evidence for flickering climates cited above suggests that the biological patterns preserved in the Pleistocene record should now be interpreted within an even more dynamic environmental framework. D–O cycles may do more than simply accelerate the biogeographic shifts already observed over longer timescales, but little work has been done on the biotic consequences of oscillations at this temporal scale. We can conceive that millennial-scale fluctuations may have profound implications for terrestrial plant communities, where herbaceous species have potential migration speeds adequate to track D–O scale events, but trees will exhibit significant lags in biogeographic response³².

Another apparent paradox often noted for the Pleistocene is the failure of speciation or extinction rates to increase significantly in the face of extreme environmental instability^{2,33}. In marine mollusks, western Atlantic and Caribbean faunas seem to show increased turnover with the onset of Pleistocene glaciation³⁴, but eastern and western Pacific faunas do not^{35,36}. Among terrestrial mammals, it is not clear whether per-taxon extinction and origination rates show exceptional increases with the onset of the Pleistocene (end-Pleistocene megafaunal extinction aside)^{37,38}. The North American herpetofauna shows no unusual turnover³⁹, and it has been argued that some bird groups may actually show a drop in speciation rates (without increased extinction) during the Pleistocene⁴⁰; the bird fossil record, however, remains understudied. One interpretation is that the evolutionary stability of species is a direct consequence of environmental and ecological instability: as species track the shifting environments, populations break up and reform, thereby preventing long-term isolation and genetic differentiation^{33,41,42}. This hypothesis gains support from the geophysical evidence outlined here, which shows that the physical environmental and associated population parameters are even more dynamic than previously thought. Recent molecular analyses suggest that differences in the genetic population structures of a number of species may be attributable to

Pleistocene fluctuations (e.g. in the eastern Pacific^{43,44} and elsewhere⁴⁵). Indeed, the complexity of the spatial patterns in genetic structure uncovered by these studies undoubtedly reflects, at least in part, the multiplicity of scales over which environments fluctuate and biotas respond.

Biogeographic anomalies

The scale and pattern of the D–O cycles is of particular interest to paleontologists, because novel biological associations (created as species shift their ranges to exploit new geographies of climate) should last long enough for their representation in the fossil record to become likely. However, as discussed earlier, the cycles are sufficiently rapid that they may be incorporated into an average marine fossil deposit rather than as discrete assemblages, giving rise to a sort of climatic time-averaging.

Such an explanation may resolve a long-standing problem in Pleistocene paleoecology. Pleistocene shallow marine communities of the temperate regions commonly contain 'extralimital' molluscan species that today do not live in the region of their Pleistocene occurrences, but have cooler- or warmer-water distributions. In some Pleistocene associations, as in the Californian region, species that today live only in provinces to the north are commingled with those living only in provinces to the south, giving rise to 'thermally anomalous' associations³¹ (Fig. 3). Such associations, of species whose present ranges are disjunct by at least one entire province, are difficult to explain in terms of simple

glacial–interglacial climate cycles. The most spectacular of such associations are dated to oxygen-isotopic interglacial substage '5e' (at about 125 ky ago), when many tropical and subtropical species occurred together with cold-temperate species in warm-temperate Californian faunas. However, generalized marine climate-reconstructions have suggested that interglacial stage 5e had a similar climate to today⁴⁶, and some recent oxygen-isotope studies on fossils of temperate aspect even suggest slightly cooler sea-surface temperatures off California during substage 5e (Ref. 47).

Many hypotheses have been proposed to explain the anomalous associations⁴⁸, but none has been very satisfactory as a general explanation. The Pleistocene fossils generally occur in shell beds that mantle ancient surfaces of erosion or clastic sediment starvation. Close modern analogues of these shell beds generated by the Holocene (c. 10 ky BP to the present – post-glacial) sea-level rise display time-averaging of around 10⁴ years (Ref. 49). Such scales of accumulation suggest a different kind of explanation, as follows: the early 5e climates were warmer than today's, permitting the immigration of some tropical and subtropical species that give the essentially warm-temperate Californian faunas a warmer-water aspect; the immigrants were chiefly physiologically tolerant, shallow-water forms³¹. A millennial-scale climate flicker then interrupted this warm episode, bringing some cold-water immigrants from northern provinces into the warm-temperate fauna; the provincial barriers for such species are relatively easily penetrated, owing partly to cool-water upwellings³¹. The processes of time-averaging intermixed these disparate climatic elements within single shell beds to produce the anomalous assemblages.

There is some independent evidence to support the preceding scenario; early oxygen-isotopic paleotemperature studies of Pleistocene fossils suggested that southern extralimitals (i.e. species today restricted to regions to the south) grew in higher water temperatures, and northern extralimitals grew in lower temperatures, than those inferred for the bulk of the fauna⁵⁰. Further paleotemperature analyses of biogeographically distinctive faunal elements within single shell beds should provide a test of this hypothesis, and could account for the contradictory climatic interpretations sometimes found between biogeographical and isotopic data. We do not claim that time-averaging creates all or even most biogeographic anomalies, but rather that apparent conflicts between biogeography and independent climate proxies should be examined critically in this respect.

Conclusions

We have concentrated on climatic changes that reflect timescales from millennia to tens of millennia – from climate flickers to glacial–interglacial substages. Emerging evidence indicates that biotic responses to climate fluctuations also occur at all timescales, involving, for example, population-level changes that operate seasonally and on decadal and century scales^{29,30}, through the millennial and substage scales as hypothesized here, and upward across the geological timescale. However, the forcing factors at the millennial and finer scales are perilously close to the limits of resolution in the time-averaged fossil record, and significant environmental changes up to at least millennial scales may occur within the timespans represented by shell beds and many other fossil concentrations. Thus, special care is required to dissect the biological effects of this newly appreciated set of perturbations. In fact, climatic time-averaging of this sort may explain some of the more vexing problems of Pleistocene paleobiogeography in a wide variety of marine and terrestrial settings. On the other hand, many non-analogue

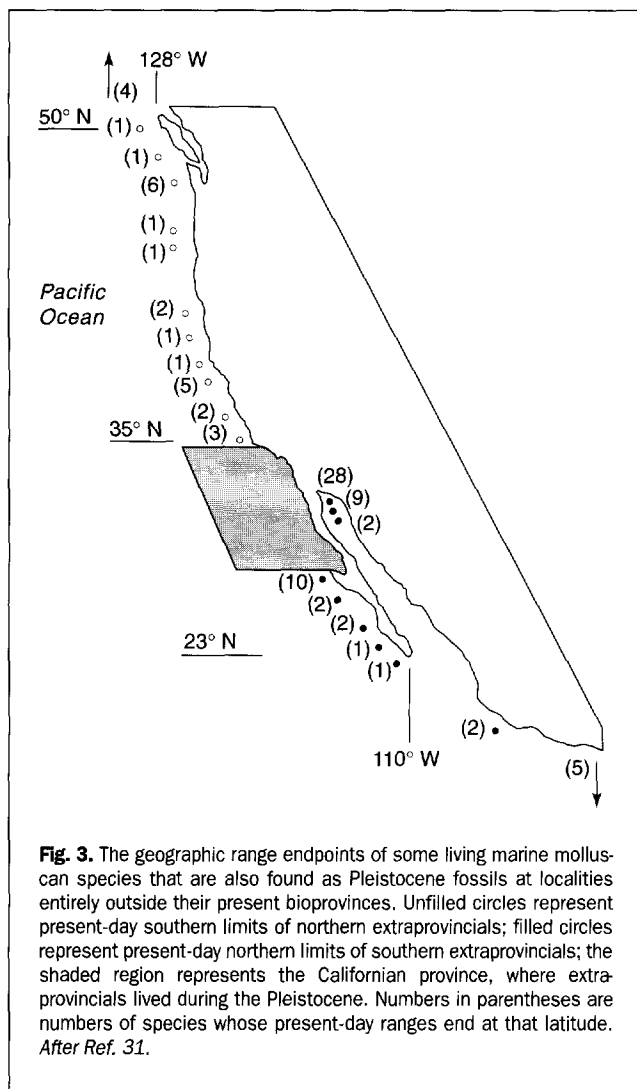


Fig. 3. The geographic range endpoints of some living marine molluscan species that are also found as Pleistocene fossils at localities entirely outside their present bioprovinces. Unfilled circles represent present-day southern limits of northern extraprovincials; filled circles represent present-day northern limits of southern extraprovincials; the shaded region represents the Californian province, where extraprovincials lived during the Pleistocene. Numbers in parentheses are numbers of species whose present-day ranges end at that latitude. After Ref. 31.

assemblages are undoubtedly real, and fit expectations from historical responses to decadal and century-scale climate changes.

Biotic responses to even the relatively short millennial events imply a flexibility of community structure that permits many species to respond rapidly to climatic challenges by migration rather than by extinction or speciation⁴². Bennett⁵¹ postulated that Milankovitch-scale events drive the reorganization of communities on the 20–100 ky timescale, and that this represents a special evolutionary tier. However, no single temporal scale within the Holocene–Pleistocene interval now stands out as a critical discontinuity. A more important message of these recent developments in geology, paleontology and climatology is the need for a renewed attempt to analyze the spatial and temporal scaling of different classes of environmental change relative to the potential response times of different populations, species and communities.

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The conodont controversies

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Some biologists may still not have heard of the conodonts. Although their apatitic skeletal elements (Fig. 1) were first found as microscopic fossils in the middle of the last century, for a long time their study was the domain of geologists, who found them useful for dating and correlating the strata in which they occurred. Biologically, conodonts provided some curiosity value, their affinities being an intriguing mystery; however, they were largely ignored in zoological texts. This was all changed by the discovery in 1982 of a fossil specimen of a nearly complete conodont animal, preserving much of the soft tissue as well as the skeletal elements¹. From this renaissance, new evidence on the nature of conodonts has accumulated dramatically, and has propelled the conodonts into the centre of the debate on the origin of the vertebrates.

Conodont anatomy

By 1995, the number of fossilized conodont animal specimens known had risen to 12. Ten of these came from the Carboniferous rocks of the Granton shore in Edinburgh, UK² (Fig. 2), augmented by a single, partially preserved fossil from Silurian deposits of Wisconsin, USA^{3,4}, and the well-preserved anterior portion of a giant specimen from Ordovician shales of South Africa⁵ (Fig. 3). The Carboniferous specimens clearly show that the conodonts were chordates. A series of chevrons preserved along the trunk of each specimen represents the muscle blocks, and there is a ray-supported caudal fin². Paired axial lines are interpreted as the remains of the notochord^{2,6}, a conclusion corroborated by decay experiments on the extant cephalochordate *Branchiostoma*⁷. The phosphatic skeletal elements form a bilaterally symmetrical feeding apparatus at the anterior end of the animal, set a little ventral to the trace of the trunk; there is no other biomineralized skeleton.

The discovery of fossilized conodont soft tissues has led to suggestions that these enigmatic animals were among the earliest vertebrates and that they were macrophagous, using their oropharyngeal skeletal apparatus to capture and process prey. These conclusions have proved controversial. There is now a consensus that conodonts belong within the chordates, but their position within the clade is hotly debated. Resolution of these questions has major implications for our understanding of the origin of the vertebrates and the selective pressures that led to the development of the vertebrate skeleton.

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Two of the Granton specimens preserve details of the head region, above and anterior to the feeding apparatus. Most prominent is a pair of lobes at the front of the animal, behind which two small discs may represent the otic capsules². Indistinct transverse traces behind the head may be the remains of branchial structures^{1,2}. The geometry of the anterior lobes has been confirmed by specimens from the Ordovician Soom Shale of South Africa, where completely preserved feeding apparatuses are relatively common, and more than 40 have been found with associated ring-like structures. These structures can be reconstructed as a pair of deep, hollow rings expanding outwards away from the axis of the animal and have been interpreted as sclerotic cartilages that surrounded the eyes⁸. Fibrous patches preserved in the same position on the more complete animal specimen from the Soom Shale (Fig. 3) appear to represent extrinsic eye musculature⁵. This specimen also displays exquisite preservation of the trunk muscle blocks, showing details of the rod-like muscle fibres, myofibrils, and even possibly the sarcomeres⁵.

Conodont hard tissues

The recognition that the conodonts were chordates has prompted a re-evaluation of the histology of the phosphatic elements of their feeding apparatuses. Most pre-Carboniferous conodont elements are constructed of two parts, the crown and the basal body. The crown commonly comprises two tissues: a hyaline portion comprising apatitic lamellae with incremental growth lines, and an opaque tissue, traditionally known as 'white matter', which is present in the centres or cores of cusps and denticles. The basal body is more variable and may be lamellar or spherulitic, and may or may not contain tubules. Examination of sectioned and etched specimens using light and scanning