

Orbital Climate Cycles in the Fossil Record: From Semidiurnal to Million-Year Biotic Responses

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Abstract

Understanding climate change, its effect on terrestrial and marine ecosystems, and possible ways to prevent future climate disasters is a major challenge for society, involving specialists in climate science, terrestrial and marine ecology, paleontology, and sedimentary geology. One approach is to study the deep-time record, especially when the time involved in a particular climatic change can be calibrated. Cyclostratigraphy is a useful tool for this. Throughout Earth's history, different scales of orbital cycles have had significant impacts on atmosphere–ocean dynamics; these impacts are preserved in the ecological and sedimentary record. Most characterizations of these cycles are based on the sedimentary record. But fossil records of past biota, corresponding to individual organisms and communities, have proven very useful in cyclostratigraphic research: From semidiurnal cycles mainly recorded in fossil skeletons to million-year-scale cycles involving mass extinctions, various cases illustrate their worth. This article reviews the use of the fossil record to recognize several cycles, from ecological timescales (≤ 1.0 yr to 10 kyr cycles; calendar and solar bands) to geological timescales (> 10 kyr cycles; Milankovitch and galactic bands).

1. INTRODUCTION

Climate change continues to be a subject of intense debate involving climate scientists, economists, engineers, politicians, and the general public. Even though extensive studies have been conducted, significant uncertainties remain about the magnitude of expected changes and the timescales over which various components of the Earth system will respond.

The effects of climate change on terrestrial and marine ecosystems and the organisms inhabiting them, including humans, are evident (see Natl. Res. Council. 2010). Biota are highly sensitive to both major and minor shifts in climate, which determine responses such as migration, speciation, and even global extinctions. Several strategies are used to understand the climate system; the analysis of Earth's past climate dynamics is one of the most direct approaches. This prompted the National Science Foundation, the US Geological Survey, and Chevron Corporation to commission the National Research Council to develop a better understanding of the past climate as a tool to characterize the response of Earth systems to future climate change. The National Research Council report (Natl. Res. Council. 2011) *Understanding Earth's Deep Past: Lessons for Our Climate Future* provides an overview of research initiatives to understand the deep-time record, the ecological and environmental impacts of past climate on terrestrial and marine environments, and the proposed strategies to prevent or mitigate future climate change, as well as extensive observational and paleoclimate modeling studies. The fossil record provides well-documented examples of (a) the impacts of different scales of cyclic climatic changes on the terrestrial and marine environments, (b) the feedback between past climate change and terrestrial and marine environments, and (c) the impacts of past climate change on terrestrial and marine biota. The study of past organisms' responses to previous climate change is thus a potentially fruitful strategy for understanding the impact of climate change on biota and for predicting responses to future change. As addressed in the more recent National Research Council report (Natl. Res. Council. 2011), a better understanding of past climate for future predictions requires improved dynamic models, more spatially and temporally resolved paleoclimate and paleontological data sets with high precision and chronological constraint, and data-model comparisons.

One of the most important challenges when using the geological record for understanding past climatic change is calibrating the timescale of these changes and of the biota's recovery. On this matter, cyclostratigraphy has demonstrated great potential to reveal millions of seasonal cyclic climatic signals from the past (see Hinnov 2000 for new advances and perspectives and Erwin 2006 for the importance of high-resolution absolute dating methods in cyclostratigraphy) and to predict climate changes from a half day to a million years in the future. However, as revealed in recent reviews of cyclostratigraphy (D'Argenio et al. 2004, Hilgen et al. 2004, Strasser et al. 2006), cyclostratigraphic research concerns primarily the stratigraphic record, the sedimentary record, or lithofacies. Those cycles recognized through changes in the biotic component were relatively underappreciated; allusions to paleontological data were scarce (e.g., Imbrie 1985, Fischer 1986, Fischer & Herbert 1986, Fischer & Bottjer 1991, House 1995, Weedon 2003). Thus, what about the paleontological record? Should it be included in the stratigraphic or the sedimentary record, or does the paleontological record have its own identity to be considered as an independent reference in the context of cyclostratigraphy?

The goals of this contribution are to highlight the role of the biotic component, and therefore the paleontological record, in cyclostratigraphic research and to provide an updated review on the applications of fossil data in the characterization of different climate cycles, with a focus on the responses of past organisms to orbital variations. This article reviews the use of the biotic component, and hence the paleontological record, in cyclostratigraphic research from ecological timescales (≤ 1.0 yr to 10 kyr cycles; calendar and solar bands) to geological timescales (10 kyr

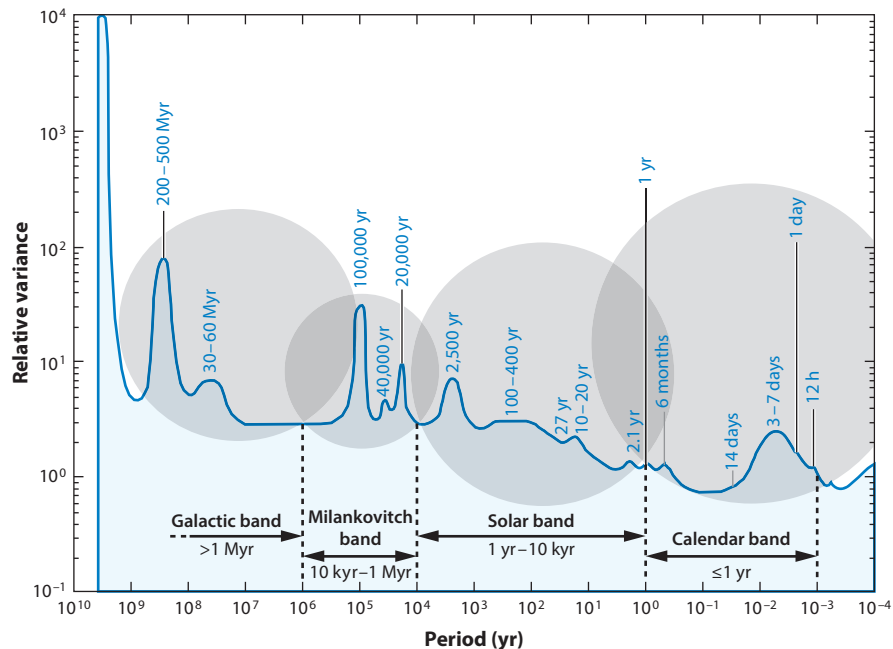


Figure 1

Idealized sketch of the planetary climate variability spectrum (modified from Mitchell 1976) with details of the calendar, solar, Milankovitch, and galactic band periods.

to >1.0 Myr cycles; Milankovitch and galactic bands) (**Figure 1**). Moreover, future directions for cyclostratigraphic research are proposed. For a comprehensive list of relevant references, see the **Supplemental Material** (follow the **Supplemental Material** link from the Annual Reviews home page at <http://www.annualreviews.org>).

Supplemental Material

2. CALENDAR BAND: SCLEROCHRONOLOGY AND DENDROCHRONOLOGY AS FUNDAMENTAL TOOLS

The calendar band includes cycles with frequencies of ≤ 1.0 yr, related to tides (gravitational changes in the Earth-Moon system) and solar cycles (variations in energy received from the Sun at semidiurnal to annual scales) (House 1995) (**Figure 1**). This band embraces cycles of different temporal scales found in sedimentary records due to the presence of rhythmites and of growth bands of plants and animals. Since the earliest studies in the 1960s, analysis of the paleontological record has identified daily, monthly, and annual growth bands in Paleozoic and Mesozoic invertebrate fossils (corals and bivalves) by geochronometry (e.g., Wells 1963, Scrutton 1964). These pioneering studies gave rise to the widely developed disciplines of sclerochronology and dendrochronology.

2.1. Tidal Cycles: The Imprint in Paleomarine Intertidal and Subtidal Communities

Tidal height amplitudes are modulated at a range of temporal scales, exhibiting twice-daily (semidiurnal), daily (diurnal), lunar, luni-solar, half-synodic-monthly (14.76 solar days), and

synodic-monthly (29.53 solar days) periodicities (see Mazumder & Arima 2005 and Coughenour et al. 2009 for detailed reviews of tides, tidalites, and tidal rhythmites). Variations in tidal amplitudes, usually of smaller magnitude, also reflect longer-term periods: the 8.85-yr period (the lunar apsides cycle, caused by the changing orientation of the lunar orbital ellipse); the 18.61-yr period (the lunar nodal cycle, which marks one revolution of the precessing lunar nodes, where the lunar orbit intersects the ecliptic, or apparent, path of the Sun); and the 20,940-yr period (the perihelion cycle, which represents the combined effects of the precession of Earth's rotational axis and its eccentric orbit) (Coughenour et al. 2009).

Tidal cycles have a well-recognized stratigraphic/sedimentary signal preserved in tidal rhythmites (Mazumder & Arima 2005). However, ancient tidal rhythmites can give rise to certain misinterpretations as a consequence of the number of factors and paleorotational parameters affecting paleotidal periods (e.g., meteorological storms, atmospheric pressure). Tidal cycles bear a special influence on intertidal and subtidal areas, in particular bivalve communities.

Modern and fossil bivalves have been the major focus of attention in sclerochronological analyses because of their well-defined record of cyclical growth. Growth patterns could have a partially endogenous origin, but there is a general consensus that environmental fluctuations—such as changing light, nutrient availability, dissolved oxygen concentration, temperature, and salinity—dominate. The main mechanism that determines calcium deposition and growth patterns in bivalves living in intertidal and subtidal environments is the tide (House & Farrow 1968; Pannella & MacClintock 1968; Pannella 1972, 1976). After these earlier studies, Pannella (1976) reported growth patterns from modern bivalve shells that were differentiated by time (**Figure 2**):

1. semidiurnal (one-half of a lunar day), reflected as one depositional event (one organic and one inorganic layer) every 12.42 h;
2. diurnal (one lunar day), reflected as one depositional event every 24.84 h;
3. weekly (one-half of the semimonthly inequality, or 6–8 days), recorded, as occurs with the fortnightly periodicities, as blended patterns of intermediate periodicity (13–15 diurnal increments);
4. fortnightly (one-half of a synodic month, or 14.77 days), reflected in the thickness of inorganic layers (spring tide increments are generally thicker than neap tide ones);
5. monthly (one anomalistic month, or 27.55 days), reflected in animals living where parallax inequality is large; and
6. semiannual (one-half of a tropical year), recorded in spring and fall growth bands (periodicity of 160–170 diurnal increments).

Recognition of different tidal cycles in the growth patterns of fossil specimens has increased in recent years. Variations over time have been documented—from the Paleozoic to the Recent in the number of days per lunar month and per year (from Pannella & MacClintock 1968 and Pannella 1972 to Ohno 1989 and Zhao et al. 2007, who applied new methodologies and techniques). Hence, the traditional sclerochronological studies involving geochemical and isotopic analysis of a particular taxon were overtaken by those using novel methods, such as the multitaxa and multiproxy approaches (Schöne et al. 2006), chemical marking and cathodoluminescence (Lartaud et al. 2010 and references therein), and fluorescence spectrometry (Wanamaker et al. 2009). Primarily through the analysis of cyclic annual increments preserved in the outer and middle shells, sclerochronology has been used for environmental interpretations, determinations of individual ages, and chronological approaches (Witbaard et al. 1997, Marchito et al. 2000, Richardson 2001, Strom et al. 2004, Helama et al. 2006, Schöne et al. 2011).

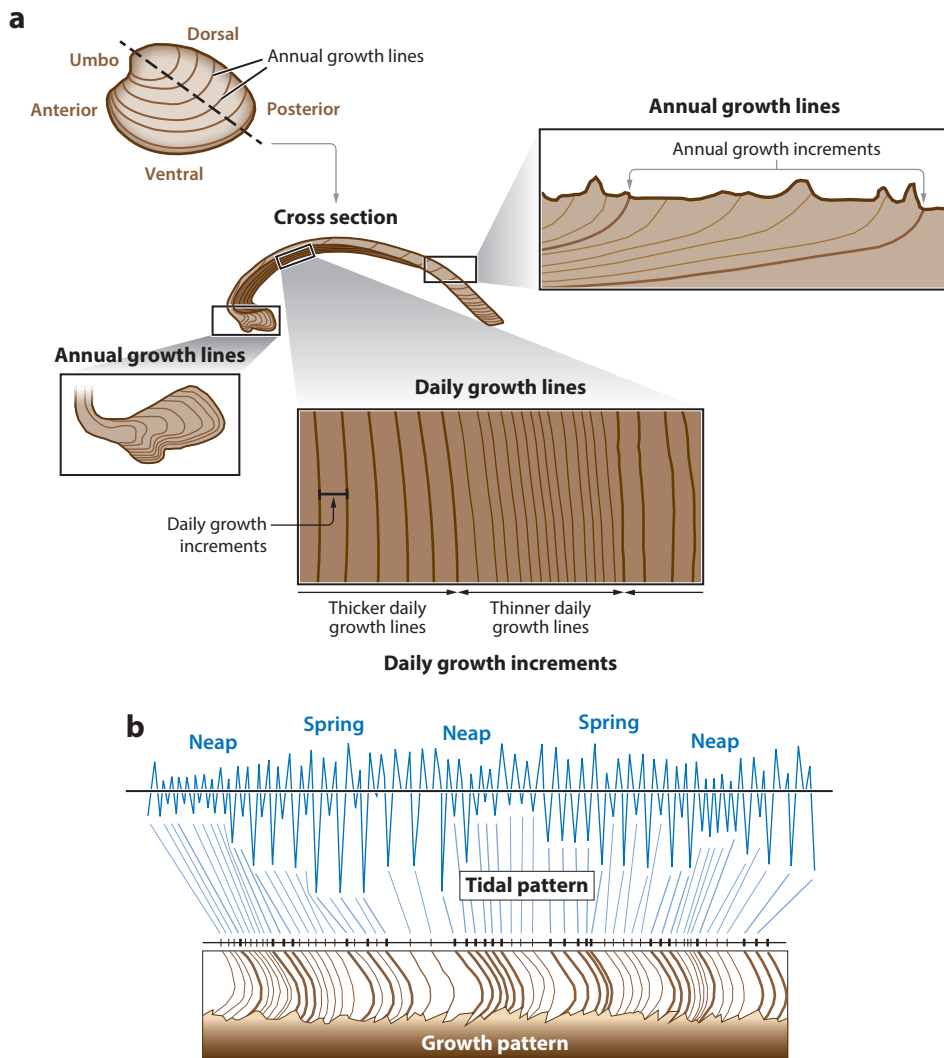


Figure 2

Schematic illustration showing (a) daily and annual growth lines in different parts of a bivalve shell and (b) a typical growth sequence with the proposed tidal pattern, showing the differences between neap and spring intervals.

2.2. Solar Cycles: Influence on Terrestrial and Marine Paleobiota

The rotation of Earth about its axis generates a circadian rhythmicity that induces significant environmental changes; some of these changes determine the behavior of organisms. The annual cycle caused by Earth's changing orbital position over the course of the year induces variations in incoming solar radiation, thereby producing the seasonal climate system, which markedly affects the development, reproduction, and distribution of organisms. Some cyclic changes in circadian and annual periodicity can be detected in modern and past organisms from terrestrial and marine environments through the analysis of variations in their accretionary hard tissues. Trees and

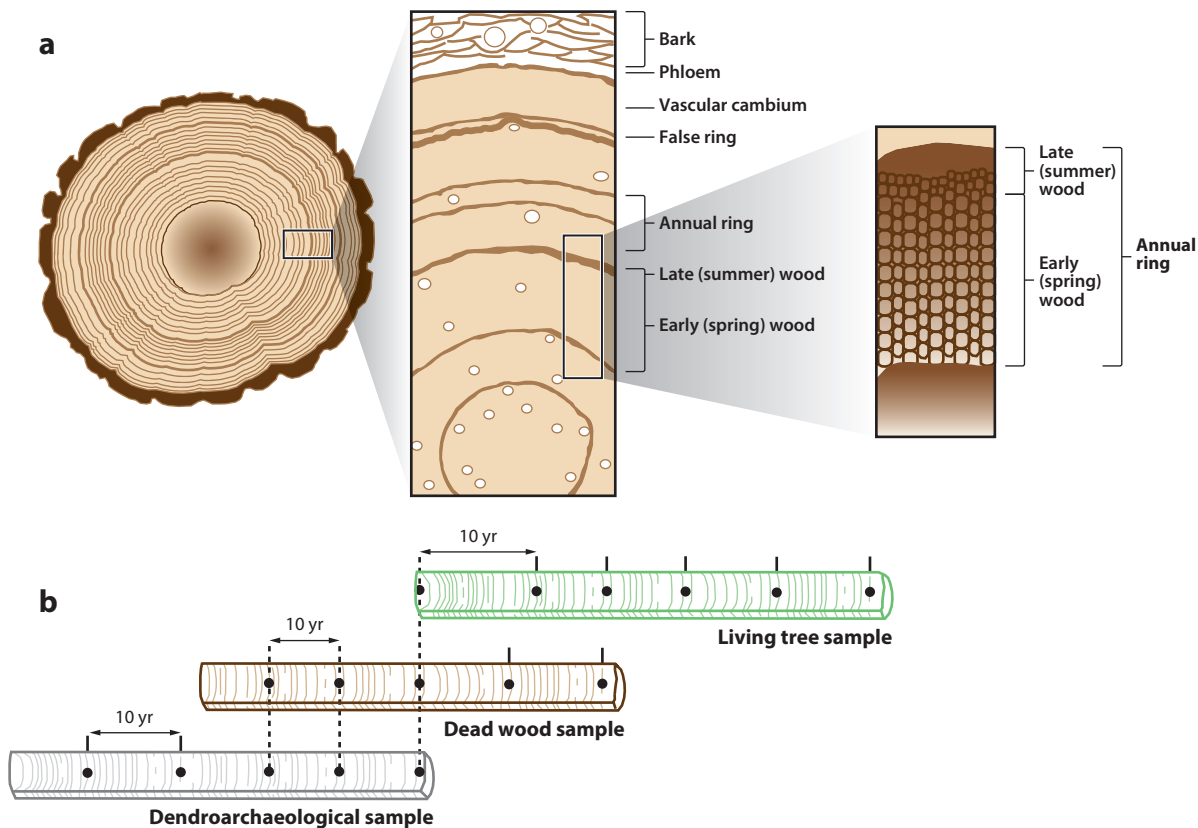


Figure 3

(a) General sketches of a cross section of tree-ring sequences, showing the differentiation of late (summer) and early (spring) wood that forms the annual ring, and detail of the cells. (b) A typical cross-dating example, showing annual rings and 10-yr periods (*points*).

corals are especially useful in this type of analysis, which is less often applied to organisms such as brachiopods, gastropods, nautiloids, otoliths, and stromatolites.

2.2.1. Trees. Tree-ring growth patterns are useful for cyclostratigraphic analysis in the ranges of the calendar and solar bands (**Figure 3**) (see Creber & Francis 1999 for methods applied to fossil trees and Woodhouse & Bauer 2009 for detailed information on the methodological approach). The analysis of cyclic growth rings makes it possible to absolutely date tree-ring chronology back to 10,461 BC, and tree-ring-based ^{14}C calibration can reach back into the Central Younger Dryas (Friedrich et al. 2004). Except for some scarce examples (Jefferson 1982 and Ammons et al. 1987, for Cretaceous and Eocene trees, respectively), the rings of fossil trees cannot be used for dating, but it is generally accepted that they support very detailed information about environmental features of the past (Creber & Francis 1999), from the Permian to the Eocene (Francis et al. 1994, Francis & Poole 2002, Jahren & Sternberg 2008).

2.2.2. Corals. The annual growth of skeletons in present-day corals provides significant information on coral biology, environmental conditions, and the chronological changes to their framework (Nova Southeast. Univ. Oceanogr. Cent. 2011). Fossil corals, one of the first paleontological

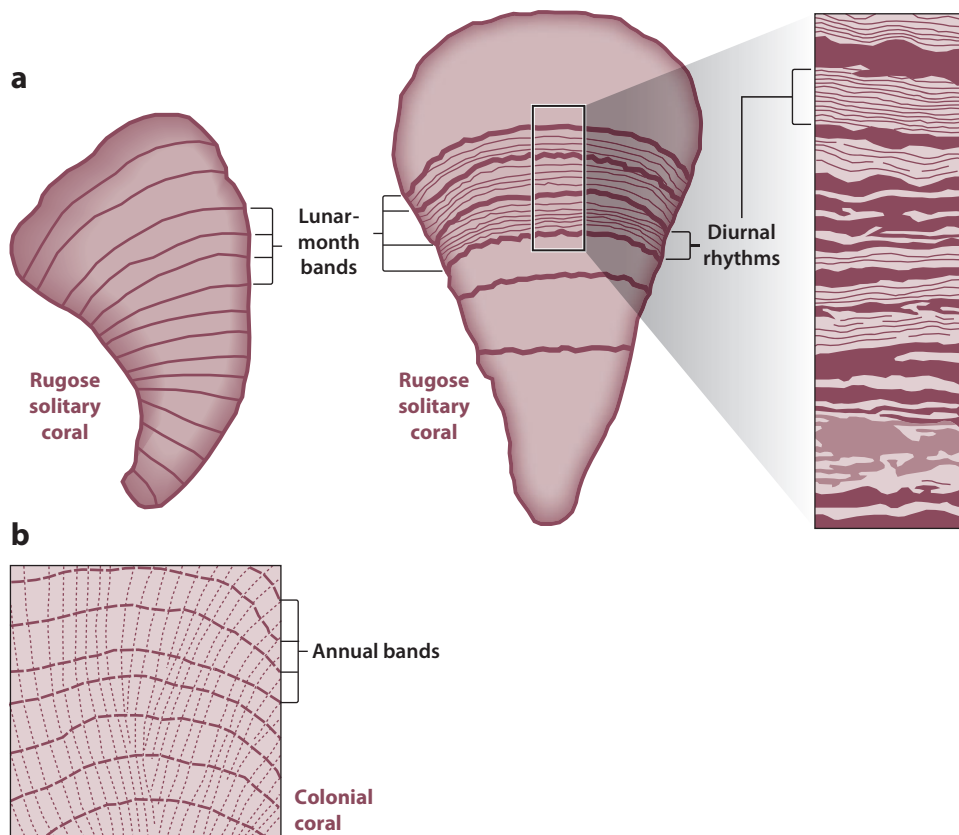


Figure 4

Sketch of (a) diurnal rhythms and lunar-month bands on the epitheca of rugose solitary corals and (b) annual bands in colonial forms.

records identified as evidence of high-frequency rhythms over time, gave rise to several papers during the 1960s (e.g., Wells 1963, Scrutton 1964) that described different cyclic patterns at frequencies of ≤ 1.0 yr in Devonian solitary coral growth, stimulating their use as paleontological clocks (**Figure 4**). Fine ridges (striate growth lines) on the surface of the coral epitheca were interpreted as circadian increments of growth (Wells 1963). Groups of these fine growth ridges forming regular bands between constrictions were associated with a lunar-monthly breeding periodicity (Scrutton 1964). Major annulations were related to yearly fluctuations in growth produced by annual changes in environmental conditions (Wells 1963). Sclerochronology on present-day *Porites* has demonstrated that tidal water-level changes induce high-frequency variations, opening the possibility of a subannual, lunar cyclicity record (Cohen & Sohn 2004). Moreover, analysis has also been conducted on fossil reef-building corals from the Miocene, Jurassic, and Triassic (Ali 1984, Insalaco 1996, Reuter et al. 2005). Modern methodologies have been applied to growth patterns in fossil corals from the Cambrian to the Pleistocene (Reuter et al. 2005; see Lough 2010 for a recent review).

2.2.3. Brachiopods. Mazzullo (1971) interpreted daily growth increments and monthly markings (i.e., bands) on Silurian and Devonian brachiopods. Growth increments in fossil terebratulid and

strophomenid brachiopods were associated with daily periodicity (MacKinnon & Williams 1974, Pope 1976), although the interpretation of daily cyclicity was later questioned because the growth rhythms registered in fossil brachiopods are related to tidal cyclicity (Rosenberg 1982).

2.2.4. Gastropods. Growth pattern analyses in gastropods are comparatively scarce because their coiling complicates such research efforts (Tojo & Ohno 1999). Initial approaches based on measurement of the distance between microgrowth lines and bands of recent intertidal gastropods led to the interpretation of tidal and solar cycles; of twice-daily, fortnightly, and annual cycles (Antoine & Quemerais-Pencreach 1980, Ekarante & Crisp 1982); and of the interference of semidiurnal tidal and solar-daily periodicity (Ohno & Takenouchi 1984). Tojo & Ohno (1999) revealed a semidiurnal tidal growth pattern with a period of 12.4 h and a neap-spring arrangement. The few studies on fossil gastropods mainly focus on annual/seasonal isotopic oscillations and on relatively recent specimens, usually Eocene (Andreasson & Schmitz 1996, Haveles & Ivany 2010) and occasionally Miocene (Andreasson & Schmitz 2000).

2.2.5. Nautiloids and ammonoids. Kahn & Pompea (1978) studied the growth records preserved in *Nautilus* shells and in fossil nautiloid shells beginning in the Ordovician. As a working hypothesis, they accepted that the rate of secretion of growth lines was circadian (one growth line deposited each day) and that chambers were created about once a month (one septum each lunar synodic month), findings supported by the daily rhythm of activity and depth migration in *Nautilus*. This paper was very controversial (see Pompea & Kahn 1979), and its conclusions were deemed unfounded (e.g., Hughes et al. 1980). Doguzhaeva (1982), working on “growth rings” from two ammonoid shells, concluded that a fortnightly or lunar-monthly periodicity for chamber formation and a daily periodicity for growth line secretion exist. The arguments formulated against Kahn & Pompea’s (1978) hypothesis were applied by Landman (1983) to Doguzhaeva’s (1982) study.

2.2.6. Otoliths. The accretionary growth of otoliths, calcareous concretions located in the inner cast of fish, was traditionally associated with a circadian rhythm that was physiologically controlled and influenced by environmental conditions (Pannella 1971) (**Figure 5**). Other recurrent patterns show fortnightly and monthly periodicity (Pannella 1971). More recently, the premises that incremental growth is constant and that the width of increments is proportional to fish growth were questioned (Campana & Neilson 1985). However, more recent analyses confirm the daily deposition rate of otolith microincrements from present-day fish (e.g., Panfili et al. 2002). Contributing to this controversy are the comparatively poor geological record [except in Tertiary sediments (Woydack & Morales-Nin 2001)] and frequent alteration of the otolith microstructure.

2.2.7. Stromatolites. Subsequent work by Pannella (1976) supports his original interpretation (Pannella 1972) of the tidal and annual bands in Precambrian stromatolites, but he emphasizes that not all laminae have the same chronological meaning: Laminae may be generated daily or semidaily, or even randomly, according to a particular environment (from subtidal to supratidal). Since then, numerous authors have studied cycles in fossil stromatolites (e.g., Jones 1981, Cao 1991).

3. SOLAR BAND: ATMOSPHERIC/OCEANOGRAPHIC CYCLIC PHENOMENA DETERMINING VARIABLE BIOTIC RESPONSES

Orbital cycles between the annual and Milankovitch bands, in what is referred to as the solar frequency band (1.0 yr to 10.0 kyr), are mainly dominated by solar phenomena and atmospheric

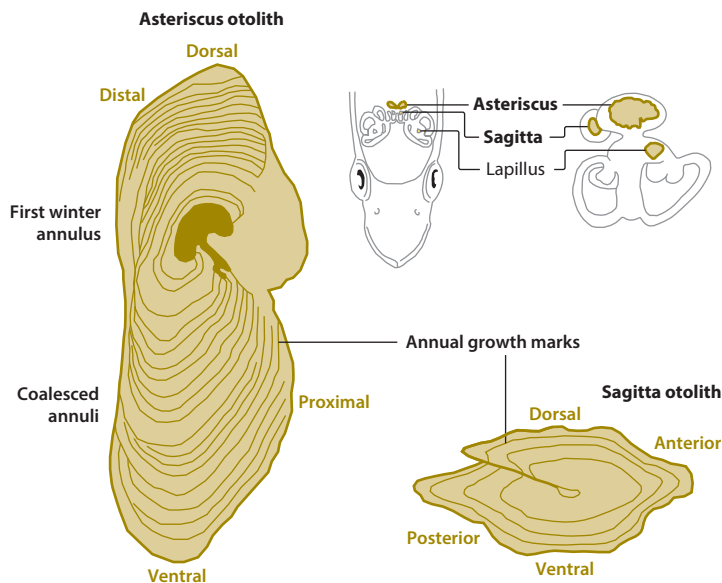


Figure 5

Position of the effects of otoliths of the inner ear of teleost fish and an illustration of sagitta and asteriscus showing annual growth marks.

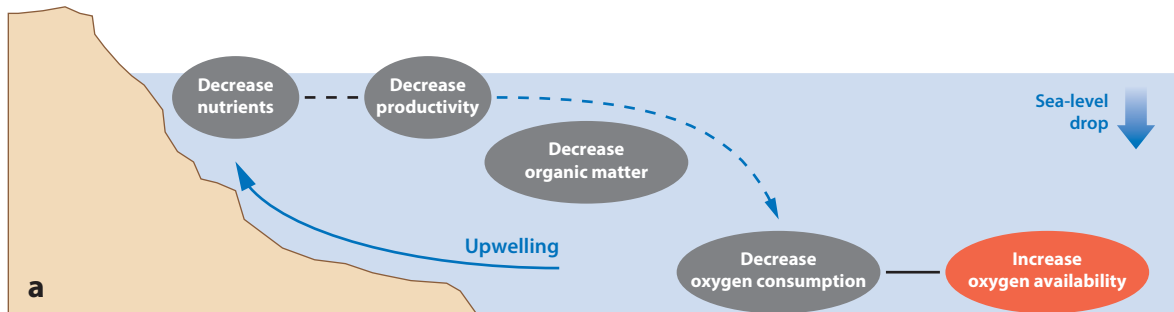
and magnetospheric interactions (Fischer & Bottjer 1991) (**Figure 1**). Some of the frequently differentiated phenomena within the solar band are solar activity and climatic cycles, such as D-O cycles, H events, and El Niño–Southern Oscillation (ENSO) cycles; however, these phenomena are not well understood in the context of cyclostratigraphy and have relatively unstable frequencies (Hilgen et al. 2004).

Solar activity cycles, associated with variations in solar radiation and the energy received from the Sun, include the Schwabe cycle or solar year (~11 yr), the Hale cycle (~22 yr), the Gleissberg cycle (~87 yr), and the Suess cycle (~210 yr). The first two in particular are frequently registered in the sedimentary record by annual lacustrine rhythmites (Kemp 1996a,b). Likewise, lunar cycles such as the lunar perigee (8.85 yr) and the nodal period (18.6 yr), mainly related to tides, can be recognized in sedimentary rhythmites (see, e.g., Coughenour et al. 2009 for discussion and an updated review). However, paleontological records of solar activity cycles are very scarce: One example of a probable solar year (~11 yr) cycle in diatomaceous lamina within the past 160 kyr has been found (Bull et al. 2000) (see below). However, the other solar band quasiperiodic phenomena—ENSO cycles, D-O cycles, and H events—are widely registered in the cyclic fossil record (see below).

3.1. The Significant Influence of the El Niño–Southern Oscillation on Modern and Past Biota

The ENSO cycle is a phenomenon of ocean–atmosphere interaction occurring in the tropical Pacific, characterized by fluctuation between exceptionally warm conditions (the so-called El Niño) and cold ones (La Niña) (Tudhope et al. 2001). This cycle is considered to be the single most important source of year-to-year climatic variability. Alternation between El Niño and La Niña typically recurs every 2–7 yr (Allen 2000). Decadal and glacial–interglacial ranges [10⁵-yr timescales (Tudhope et al. 2001 and references therein)] are also registered. ENSO phenomena

El Niño conditions



La Niña conditions

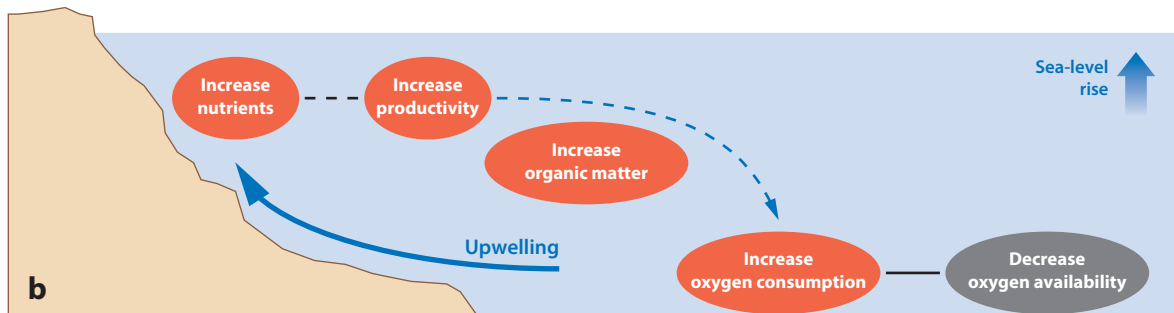


Figure 6

General sketches of the effects of (a) El Niño and (b) La Niña conditions on the relationship between upwelling conditions, nutrients, productivity, organic matter, and oxygen consumption and availability affecting planktonic and benthic habitats during El Niño–Southern Oscillation phenomena.

have influenced Earth’s climate for at least the past 130 kyr (Tudhope et al. 2001), although the intensity of the ENSO cycle has not been stable over time (Donders et al. 2008 and references therein). Continual/permanent El Niño-like conditions have been established for the early Pliocene (Fedorov et al. 2006) and an ENSO-timescale variability for the Eocene (Huber & Caballero 2003). Atmospheric teleconnections show the ENSO phenomenon to have a global impact on patterns of weather variability—including changes in precipitation, tropical storms, ocean dynamics, and primary production—affecting marine and terrestrial communities (**Figure 6**). Cycles linked to the ENSO phenomena are mainly recorded in recent fossil records from marine communities, but examples from the terrestrial paleoenvironment are also reported.

3.1.1. El Niño–Southern Oscillation phenomena in the marine fossil record. Subdecadal to interannual variations in the ENSO induce significant alteration in the marine environment, primarily affecting the planktonic community. Changes in the limiting marine environmental factors that control communities, such as temperature, sea level, currents, thermocline, upwelling, and nutrients, can be directly associated with ENSO phenomena.

3.1.1.1. The fossil record of El Niño–Southern Oscillation cycles in the planktonic community. Isotopic and geochemical analyses on planktonic microfossils, together with variations in the abundance, distribution, and diversity of fossil assemblages of phytoplankton and zooplankton, have

been used to reveal paleo-ENSO cyclicity. The isotopic composition of planktonic foraminifera has been used to quantify ENSO phenomena affecting sea-surface conditions during the Holocene (Koutavas et al. 2006) as well as thermocline and upwelling during the Pliocene (Scroxton et al. 2011). Subdecadal and decadal climatic signals related to ENSO are widely recognized in modern sediments based on the analysis of the diatom component and its relationship to changes in marine production (e.g., Dean & Kemp 2004). Cyclic changes in phytoplankton composition related to ENSO activity have also been recorded in the fossil record, as these changes cause variations in marine productivity (e.g., Bull et al. 2000). Analysis of coccolithophore assemblages from several records over the past 250 kyr shows different cycles related to climatically induced changes associated with ENSO conditions or ENSO-like events, and these changes determine cyclic variations in sea-surface productivity (Grelaud et al. 2009).

3.1.1.2. Cyclic changes in the benthic community and environmental factors influenced by the El Niño–Southern Oscillation. Some of the limiting factors affecting benthic habitats are sensitive to ENSO fluctuations. The growth pattern in a single coral head allows for records of a few hundred years (for a recent review, see Jones et al. 2009), making coral highly useful for reconstructing modern seasonal to interannual variations in ocean features associated with ENSO climate variability (Kilbourne et al. 2007; see Gagan et al. 2000 for a summary of the use of coral research for the reconstruction of multidecadal climate variability and ENSO). Isotopic and geochemical analyses of the extensively studied *Porites* reveal interannual variations in precipitation, sea-surface temperature, and sea-surface salinity owing to paleo-ENSO phenomena in some intervals over the past ~350 kyr (Corrège et al. 2000, Tudhope et al. 2001). Interruptions in seasonal and annual deposition by trace fossils provide indirect evidence of changes in the concentration of dissolved oxygen at the sediment–water interface. Such interruptions range from a slight disturbance of a few millimeters per lamina to burrows reaching several decimeters deep; these fix alternations of varved and bioturbated sediments related to the ENSO system at different scales ranging from a few years to decades to millennia during the Upper Pleistocene (Anderson et al. 1992) and the Miocene (Ozalas et al. 1994) (**Figure 7**). The concentration of benthic foraminifera, as a proxy for the flux of organic matter to the seafloor, sheds light on the relationship between the ENSO, nutricline, and productivity (Ortiz et al. 2004).

3.1.2. El Niño–Southern Oscillation phenomena in the terrestrial fossil record. Two major proxies from the terrestrial fossil record are commonly applied to recognize ENSO cycles: tree rings and pollen assemblages. Trees several thousand years old facilitate the recognition of “recent” cyclic paleoenvironmental climatic changes related to ENSO phenomena (e.g., Christie et al. 2009). Fossil examples and conclusive interpretations are relatively scarce, and only short-term cycles of 2–7 yr have been tentatively interpreted as having been produced by ENSO forcing phenomena (see Boninsegna et al. 2009 for a review of dendroclimatology in South America). Variations in the abundances of particular pollen taxa have been considered evidence of cyclic climatic changes related to submillennial-scale ENSO forcing from the Eocene (Heusser & Sirocko 1997, Lenz et al. 2010).

3.2. Influence of Dansgaard-Oeschger Cycles and Heinrich Events on Past Biota

Oxygen isotope measurements in Greenland ice cores demonstrate that a series of rapid millennial-scale climatic changes (see Bard 2002 for a review), characterized by warm and cold oscillations and referred to as D-O cycles, punctuated the last glaciation (Dansgaard et al. 1982, Oeschger

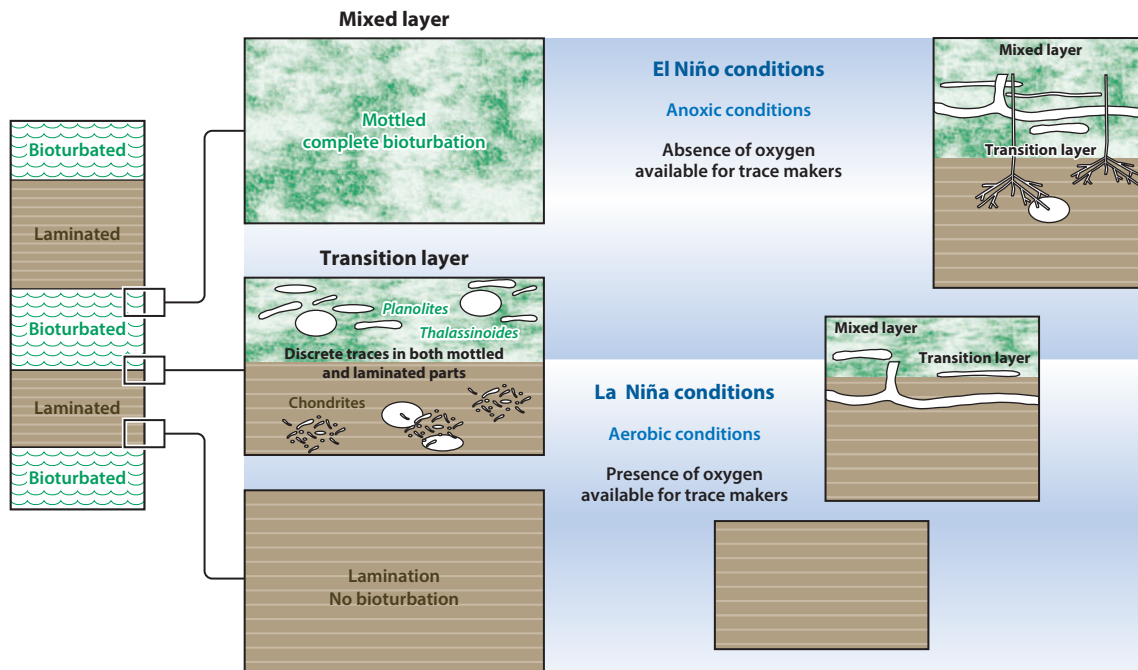


Figure 7

Alternations of laminated and bioturbated intervals corresponding to La Niña and El Niño conditions, with recorded ichnofabrics and tiered evolution.

et al. 1985). These climatic shifts have a periodicity close to $1,479 \pm 500$ yr (Bond et al. 1997), although a range between 2,000 and 3,000 yr has also been surmised (Bond & Lotti 1995). Marine sediments from the North Atlantic contain conspicuous layers of detrital rocks related to discharges of icebergs (ice-rafted debris) from the Laurentide and European ice sheets; these were named H events (Heinrich 1988, Bond et al. 1993; see Hemming 2004 for a review). H events are associated with the coldest phase in a series of D-O cycles, occurring with a periodicity of 7,000–10,000 yr (Bond & Lotti 1995). The D-O cycles and the H events are arranged in a so-called Bond cycle (Bond et al. 1993), consisting of several D-O cycles ending in an H event. These climatic variations are correlated with changes in paleoecological oceanic features; the succession of stadials (cold) and interstadials (warm) associated with these cycles has been documented in other regions of the world, affecting both hemispheres (see Leuschner & Sirocko 2000 for a compilation of numerous records worldwide, Broecker 2006 and references therein, and Paillard 2001 for a critical review).

3.2.1. Dansgaard-Oeschger cycles and Heinrich events in the marine paleontological record. Paleontological records, and most notably microfossil assemblages or isotopic signals from microfossil shells, were used in pioneering papers to provide evidence of millennial-scale cyclic climatic changes during the last glacial period and to define the phenomena of D-O cycles, H events, and Bond cycles, mentioned above. Since then, a variety of paleontological proxies have been applied to identify these cycles and events. However, in this review, I do not look to isotopic procedures or molecular proxies used as geochemical tools but focus instead on the composition of assemblages.

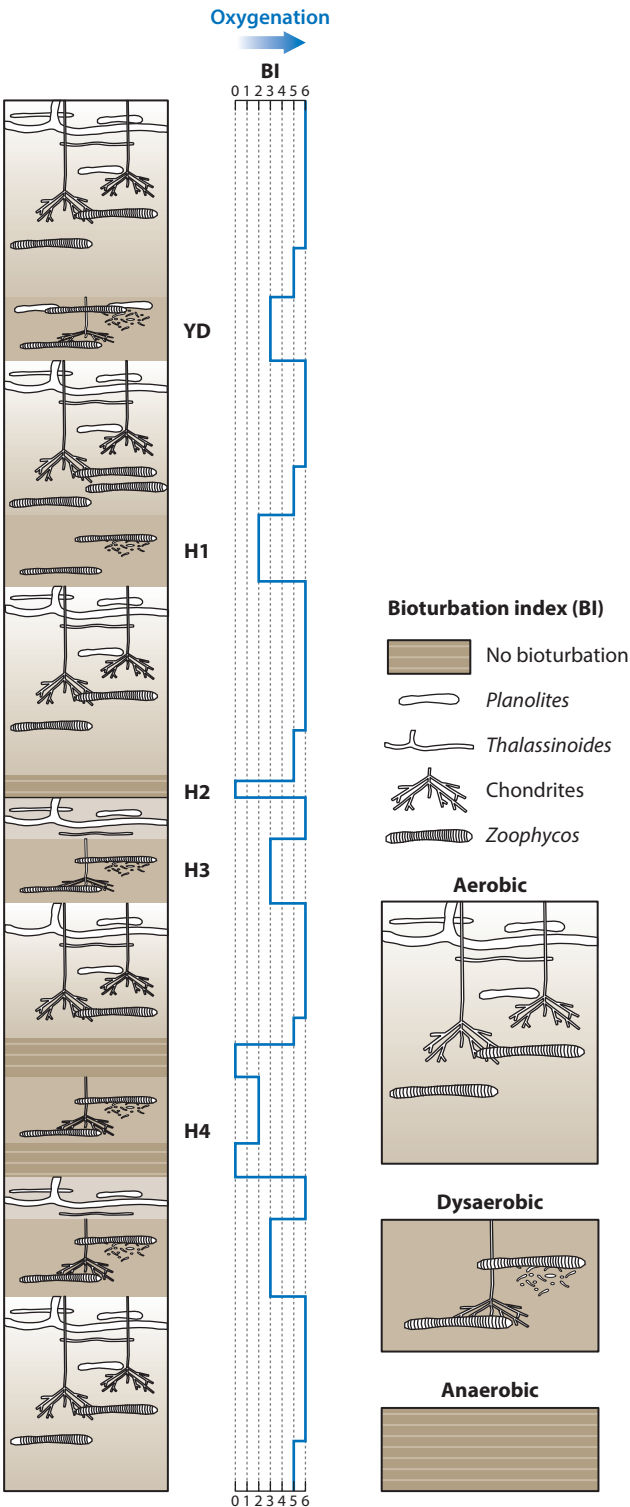
3.2.1.1. Impact of Dansgaard-Oeschger cycles and Heinrich events on planktonic habitat.

Millennial-scale climatic changes associated with D-O cycles and H events bear a significant impact on plankton communities (Pielou 2008). Short-term environmental changes correlated with H events and compared to multicentennial-scale patterns related to D-O cycles have been characterized using the abundance and diversity of Holocene and Pleistocene coccolithophore assemblages belonging to the Atlantic and Pacific Oceans and the Mediterranean and Red Seas (Colmenero-Hidalgo et al. 2004, Legge et al. 2008, Grelaud et al. 2009). The distribution of dinoflagellate cysts, changes in transfer functions based on dinocyst assemblages, and variations in the diversity of taxa and species have been broadly used as proxies to identify past D-O cycles and H events, as reflected in physicochemical properties of the overlying water masses (de Vernal et al. 2000, Rochon et al. 2008, Penaud et al. 2011, and references therein). In several intervals from the past ~70 kyr, millennial-scale cycles in dinoflagellate assemblages were related to D-O variability associated with warmer interstadials and colder stadials, whereas pronounced fluctuations indicated drastic climatic and oceanographic changes concomitant with H events (Sánchez Goñi et al. 2000, Mertens et al. 2009). Occasionally, the response of radiolarian assemblages, especially fluctuations in cold-water species, reveals high-frequency variability corresponding to D-O cycles and H events from the past 150–160 kyr (Pisias et al. 2001, Cortese & Abelmann 2002, Gorbarenko et al. 2010). As a general rule, planktonic foraminifera show a significantly low abundance in H event layers (Stein et al. 2009 and references therein). Planktonic foraminiferal abundances, and changes between and into particular species, have been interpreted as the consequence of sea-surface temperature and salinity in millennial-scale cyclic fluctuations in conjunction with D-O climatic cycles and H events for the past 80 kyr in the Northern and Southern Hemispheres (Pérez-Folgado et al. 2003, Chang et al. 2008, Stein et al. 2009).

3.2.1.2. Response of fossil benthic biota to Dansgaard-Oeschger and Heinrich phenomena. The relationship between sea-surface features (temperature, salinity, productivity, surface-ocean circulation) and those of deep-sea benthic environments (deep-ocean circulation, bottom temperature) validates the usefulness of paleobenthic biota when interpreting cyclic paleoceanographic changes in light of D-O cycles and H events. Cyclic fluctuations in faunal composition, species richness, and accumulation rates of benthic foraminifera have been associated with millennial-scale H events and D-O cycles from the past 160 kyr in the Pacific and Atlantic Oceans and the Norwegian Sea (Thomas et al. 1995, Cannariato et al. 1999, Rasmussen et al. 2003). In some cases, changes in species diversity in deep-sea benthic Ostracoda in the Late Pleistocene have been linked to climatic changes associated with H events (Yasuhara & Cronin 2008). In the mid-1990s, several papers highlighted the usefulness of bioturbation to record millennial-scale cycles, mainly with regard to variations in bottom-water oxygenation. A bioturbation index based on lamination styles and degrees of bioturbation, mainly revealing bottom-water oxygenation, has been widely applied to identify D-O events over the past 60 kyr (Behl 1995, Behl & Kennett 1996, Leuschner & Sirocko 2000). Cyclic alternations of dark-colored, organic-carbon-rich, laminated intervals (related to anoxic to suboxic conditions) with light-colored, carbonate-rich, bioturbated sedimentary sequences (corresponding to oxic bottom-water conditions) were associated with rapid D-O and H-style events and were used to determine millennial to centennial fluctuations in the intensity of southwest monsoonal circulation (Schulz et al. 1996, von Rad et al. 1999). Condensed trace-fossil tiered structures and high proportions of low-oxygen-tolerant benthic foraminifera were found to reflect a major drawdown of bottom-water oxygenation during H events (Baas et al. 1998) (**Figure 8**).

Figure 8

Idealized ichnofossil assemblage distribution, tiered pattern, bioturbation index (BI) 0 to 6, and oxygenation through a section involving the last Heinrich events (H1 to H4) and the Younger Dryas (YD). Adapted from Baas et al. 1998.



3.2.2. Fossil vegetation indicating Dansgaard-Oeschger cycles and Heinrich events affecting the terrestrial paleoenvironment. Molecular biomarkers (e.g., *n*-nonacosane and *n*-hexacosanol) of higher plants have been used to interpret rapid cycles of hydrographic changes in response to D-O and H event variability (Cacho et al. 2000); however, this particular line of research lies beyond this review's focus on variations in terrestrial assemblages. Changes in diatom productivity, individual species, and assemblages registered throughout the past 60 kyr in Lake Baikal (Russia) and the lake Les Échets (France) have been linked to the lacustrine responses to variations in temperature related to cyclic millennial-scale climate shifts in view of H events and D-O cycles (Mackay 2007, Ampel et al. 2008). Changes in pollen communities from the past 60–65 kyr have been recorded worldwide, revealing centennial- and millennial-scale cyclical changes associated with D-O cycles and H events but with regional differences (Sánchez Goñi et al. 2000). A recent special issue of *Quaternary Science Reviews*, “Vegetation Response to Millennial-Scale Variability During the Last Glacial” (Sánchez Goñi & Harrison 2010), provides a global synthesis of the high-resolution paleovegetation records from the last glacial, demonstrating the relationship between millennial-scale cyclic variability of D-O and H events and changes in pollen composition in records from North America, South America, Asia, and Europe. Vegetation changes in Central American lowlands associated with H events have recently been reported (Correa-Metrio et al. 2011). Variations in plant macrofossils during the Quaternary have occasionally been used to identify cyclic changes in precipitation and the thermal regime related to rapid climatic changes induced by D-O and H phenomena (Postigo-Mijarra et al. 2010, van Geel et al. 2010).

4. MILANKOVITCH BAND: ORBIT-INDUCED CYCLIC CHANGES DETERMINING VARIABLE PALEOCOMMUNITY RESPONSES

4.1. Evolutionary Patterns, from Stasis to Extinction, at the Milankovitch Timescale

The primary quasiperiodic orbital variations within the Milankovitch frequency band of 19–406 kyr correspond to the cycles of precession (at about 19 and 23 kyr, with extremes at 14 and 28 kyr), obliquity (with the most power at 41 kyr and minor components at about 28 and 54 kyr), and eccentricity (the short term at about 100 kyr, with major components around 97 and 127 kyr, and the long term at about 400 kyr); eccentricity forcing includes longer-period components, in the range of 2–2.8 Myr, that emerge from the interactions of different cycles (Hinnov 2000, Fischer et al. 2004) (**Figure 1**). The paleontological record is acknowledged as a highly valuable tool for recognizing the different scales of Milankovitch cyclic variations in the terrestrial and marine environment. At present, however, there is no general consensus regarding the response of paleocommunities to orbit-induced paleoenvironmental changes. In the wake of the three-tier hierarchy proposed by Gould (1985) to describe evolutionary changes, Bennett (1990) included a new second tier for evolutionary process at the Milankovitch timescales of 10–100 kyr, characterized by the disruption of communities and the loss of small adaptive changes. Speciation is accordingly concentrated in the third tier within geographically isolated populations, because of perpetual environmental changes on Milankovitch timescales (Bennett 1990). Later, Bennett (2004) concluded that although speciation and extinction occur within the Quaternary in response to orbit-forced climatic changes, responses are uncommon because stasis is the typical evolutionary response of species to Milankovitch oscillations. The debate persists, especially surrounding Bennett's second and third tiers and the incidence of orbital forcing determining diverse and complex evolutionary responses, including stasis, speciation, and extinction phenomena in Quaternary plant communities (Willis & Niklas 2004) and origination, extinction, and turnover

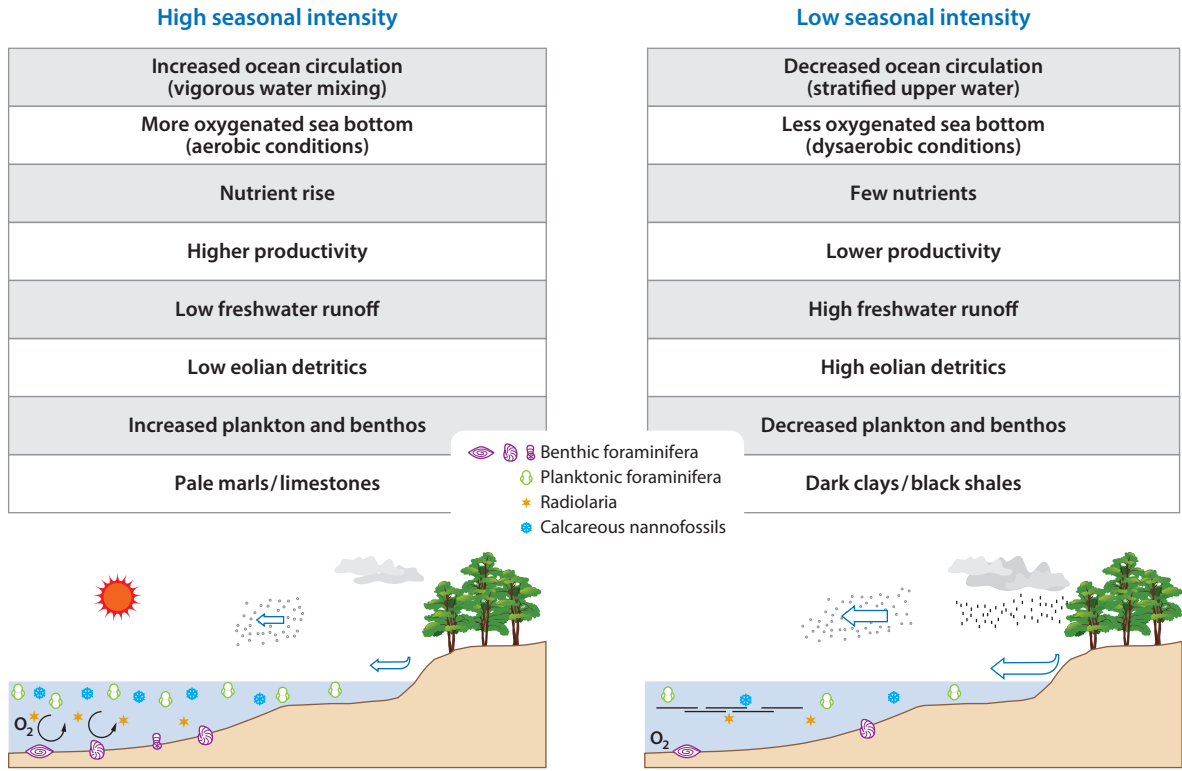


Figure 9

Changes in environmental features related to climatic changes induced by Milankovitch cycles affecting seasonality, oceanic circulation, oxygenation, nutrient availability, productivity, runoff, eolian impacts, lithofacies, and microscopic communities (plankton and benthos). Also shown are the habitats of the microfossil groups in the water column and on the seafloor, from endobenthic to planktonic. Adapted from Mutterlose & Ruffell (1999), MacLeod et al. (2001), Poletti et al. (2004), and Sluijs et al. (2005).

in mammalian species (van Dam et al. 2006). At the root of the debate lie two key issues: the resolution of the fossil record and the absence of absolute timescales.

4.2. Cyclic Changes in Paleocommunities: The Record of Milankovitch Forcing

Marine and terrestrial environments, and their inhabiting communities, are influenced by orbit-induced climatic changes (Figure 9). In a complex way, these changes determine variations in atmosphere-ocean dynamics, ice mass, sea level, nutrient availability, oxygen distribution, temperature, and other conditions. Yet their impact is dissimilar for different communities, and there is no single generalized response; the best fossil record is that of marine microorganism communities.

4.2.1. Marine environment: the incidence of Milankovitch insolation on microfossil communities. Marine communities of microorganisms have been extensively studied to advance our knowledge of orbital-scale cycles using the relationship between (a) the limiting ecological and sedimentary parameters that configure their ecological niche and (b) changes in insolation owing to Milankovitch-scale forcing. However, whereas extensive information from upper-water

environments and the corresponding planktonic communities has been published, data from seafloor environments (bottom waters and within-sediment habitats) and the corresponding benthic communities are very scarce.

4.2.1.1. Planktonic communities and Milankovitch effects. Planktonic foraminifera have traditionally been used to detect cyclic Milankovitch forcing, especially using oxygen isotope ratios in calcitic shells (from Hays et al. 1976; see Fischer et al. 2004 for a historical review) as well as changes in communities (abundance, composition, diversity, and others). The Mediterranean region is considered crucial in cyclostratigraphy (see Fischer et al. 2009 for a recent review); Albian sediments (coccolith-globigerinacean marls) from the Umbria-Marche Basin in Italy are particularly important references (Grippo et al. 2004) that reveal the influence of precession, obliquity, and eccentricity cycles on planktonic foraminifera (Fischer et al. 1991, Erba & Premoli Silva 1994, Galeotti 1998). Other geological intervals and/or areas confirm the usefulness of planktonic foraminifera assemblages for the recognition of Milankovitch cycles: Examples include Maastrichtian hemipelagic strata of the Black Nose (MacLeod et al. 2001) and Paleocene pelagic sequences of the southern Alps in northern Italy (Poletti et al. 2004). Radiolarian assemblages were among the first paleobiotic proxies used to determine Milankovitch-scale climatic effects (Hays et al. 1976). The application of spectral techniques revealed, for the first time, the coincidence of global paleoclimatic changes with the components of precession, obliquity, and eccentricity during Quaternary ice ages. Quantitative data from radiolarian microfossil assemblages, including radiolarian transfer functions (e.g., Cortese & Abelmann 2002), allow interpretation of Milankovitch-scale cycles associated with climatic changes that determine variations in paleo-sea-surface temperatures, productivity, monsoon dynamics, and upwelling (Chen et al. 2003, Gupta 2003). Nannofossils were a pioneer group in the application of spectral methodologies to cyclostratigraphic research. Milankovitch cycles were recognized principally because of the composition and relative abundance of key taxa (the diversity index) as they relate to changes in fertility and sea-surface temperature in response to insolation-driven climatic changes from the Pleistocene (Marino et al. 2009), Pliocene (e.g., Gibbs et al. 2004), Miocene (Beaufort & Aubry 1990), Cretaceous (e.g., Erba et al. 1992, Mutterlose & Ruffell 1999), and Jurassic (Claps et al. 1995).

4.2.1.2. Benthic communities: from epibenthic to endobenthic environment. Marine benthos occupy different seafloor habitats, from the sediment surface (occupied by epifauna) to the sediment (inhabited by shallow and deep infauna). Although benthic foraminifera mostly represent epifauna or shallow infauna from the uppermost centimeters of the sediment, other benthos—especially macrobenthos—can reside at different depths within the sediment, producing biogenic structures of varying depth. Oxygenation, temperature, nutrient type, and availability are major control factors in the benthic environment. Variations in benthic foraminifera assemblages may display Milankovitch-scale cyclic fluctuations associated with changes in specific environmental features. Extensively studied are the European Cretaceous rhythmic successions, showing changes in benthic assemblages related to orbit-induced cyclical fluctuations for the Hauterivian and Barremian (Mutterlose & Ruffell 1999), Aptian-Albian (Galeotti 1998), and Cenomanian (Leary & Hart 1992). Younger and older examples, including those from the Quaternary (Badawi et al. 2005), Pliocene (Becker et al. 2005), or Upper Jurassic (Rodríguez-Tovar et al. 2010), are comparatively scarce. Macrobenthic communities, as revealed by their trace-fossil record, have occasionally been studied to characterize Milankovitch-scale cycles. In the earliest papers, Early Cretaceous alternations between bioturbated limestone and laminated marls or calcareous claystone were related to Milankovitch cycles (Molinie & Ogg 1992 and references therein). Semiquantitative studies and spectral analyses of paleoichnological data from Cretaceous, Paleocene, and Eocene

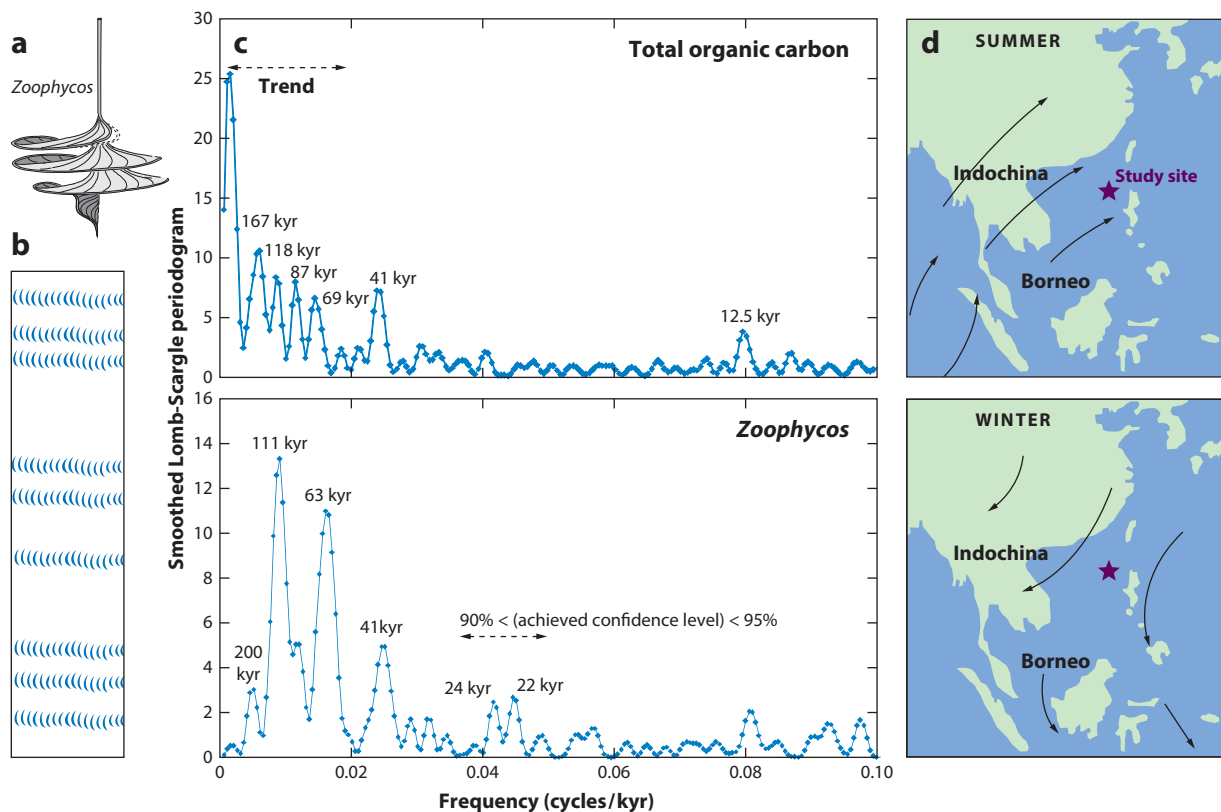


Figure 10

(a) Model of *Zoophycos*; (b) theoretical record of *Zoophycos* in cores; (c) spectral analyses of total organic carbon and *Zoophycos* distribution in the deep-sea piston core covering the past 425 kyr obtained in the northeastern South China Sea, showing conspicuous peaks correlated with short-term eccentricity, obliquity, and precession cycles (Rodríguez-Tovar et al. 2011); and (d) Asian summer (top) and winter (bottom) monsoons in the studied area (the star shows the location of the studied core) (Rodríguez-Tovar et al. 2011).

sediments showed periodicities correlated with precession, obliquity, and eccentricity cycles (Erba & Premoli Silva 1994, Poletti et al. 2004, Heard et al. 2008).

Recently, cyclostratigraphic analysis of several sediment parameters and *Zoophycos* distribution in a deep-sea piston core covering the past 425 kyr from the northeastern South China Sea revealed well-developed cyclical patterns (Rodríguez-Tovar et al. 2011) (Figure 10). Conspicuous cycles registered in the spectral analyses were correlated with Milankovitch orbital-scale cycles of short-term eccentricity, obliquity, and precession. East Asian monsoon dynamics in the Milankovitch orbital-scale cycles could induce environmental changes, including variations in the organic material reaching the seafloor, and influence the behavior of the *Zoophycos* trace maker and thus its cyclical occurrence (Rodríguez-Tovar et al. 2011) (Figure 10).

Cyclic variations in other benthic communities are comparatively poorly studied, and in some cases, the proposed relationship with climatic changes at the Milankovitch scale is inferred without any spectral treatment. Cyclic changes in marine benthic molluscan species from the Pleistocene (Kitamura 2004) and the Miocene (Aswan & Ozawa 2006) were related to sea-level fluctuations linked with climate changes and Milankovitch-scale obliquity cycles, and marked differences in the community structure and diversity of benthic macrofauna (primarily bivalves, brachiopods, and

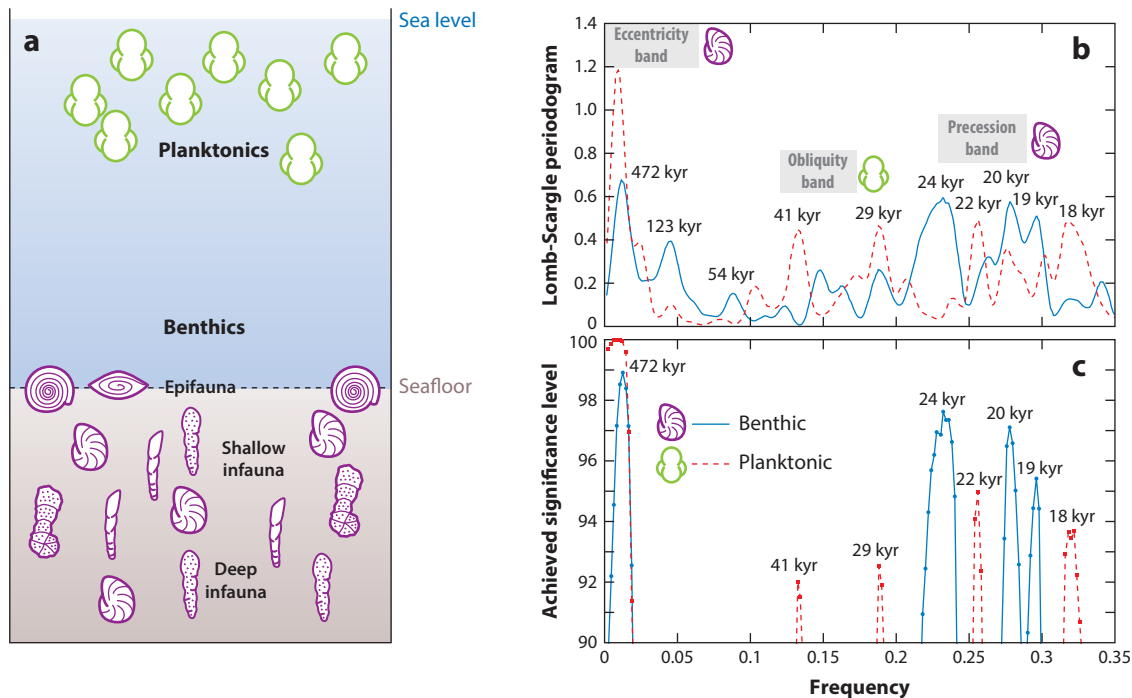


Figure 11

(a) Theoretical distribution of Late Jurassic planktonic and benthic foraminifera from the western Tethys (south Iberia). (b) Lomb-Scargle periodogram of the planktonic and benthic abundance time series bands showing the peaks for different bands in response to Milankovitch cycles and (c) the achieved significance level, given by the permutation test for evaluating the statistical significance of the spectral peaks. Panels b and c adapted from Rodríguez-Tovar et al. (2010).

echinoderms, but also bryozoans, serpulids, corals, sponges, and cirripedes) from the Cenomanian were interpreted as representing Milankovitch precession forcing (Lauridsen et al. 2009).

Cyclostratigraphic analysis of planktonic and benthic foraminiferal assemblages in Upper Jurassic sediments from the Tethys revealed different cyclic patterns as variable responses to the differing habitats (Rodríguez-Tovar et al. 2010) (**Figure 11**). Planktonic foraminifera were especially sensitive to obliquity-scale fluctuations related to changes affecting upper waters, usually caused by varying water temperature. In contrast, the benthic component was affected more by cyclic changes on precession timescales and, to a lesser extent, by short eccentricity variations associated with the influence of Milankovitch climatic variations on bottom-level conditions such as nutrient availability and substrate oxygenation (Rodríguez-Tovar et al. 2010) (**Figure 11**).

4.2.2. Terrestrial environment: the incidence of Milankovitch insolation on flora and fauna communities. Studies of Milankovitch effects on terrestrial ecosystems that are based on the paleontological record are comparatively scarce. Nonetheless, flora and fauna communities demonstrate clear responses in terms of geographic distributions resulting from climatic variations, especially when tied to Milankovitch-scale fluctuations in the growth of large terrestrial ice sheets.

Cyclic changes in terrestrial vegetation associated with Milankovitch-induced climatic fluctuations have been characterized using spectral techniques on pollen records from the Pleistocene (e.g., Molfino et al. 1984, Hooghiemstra & Melice 1994) and pre-Pleistocene, especially in

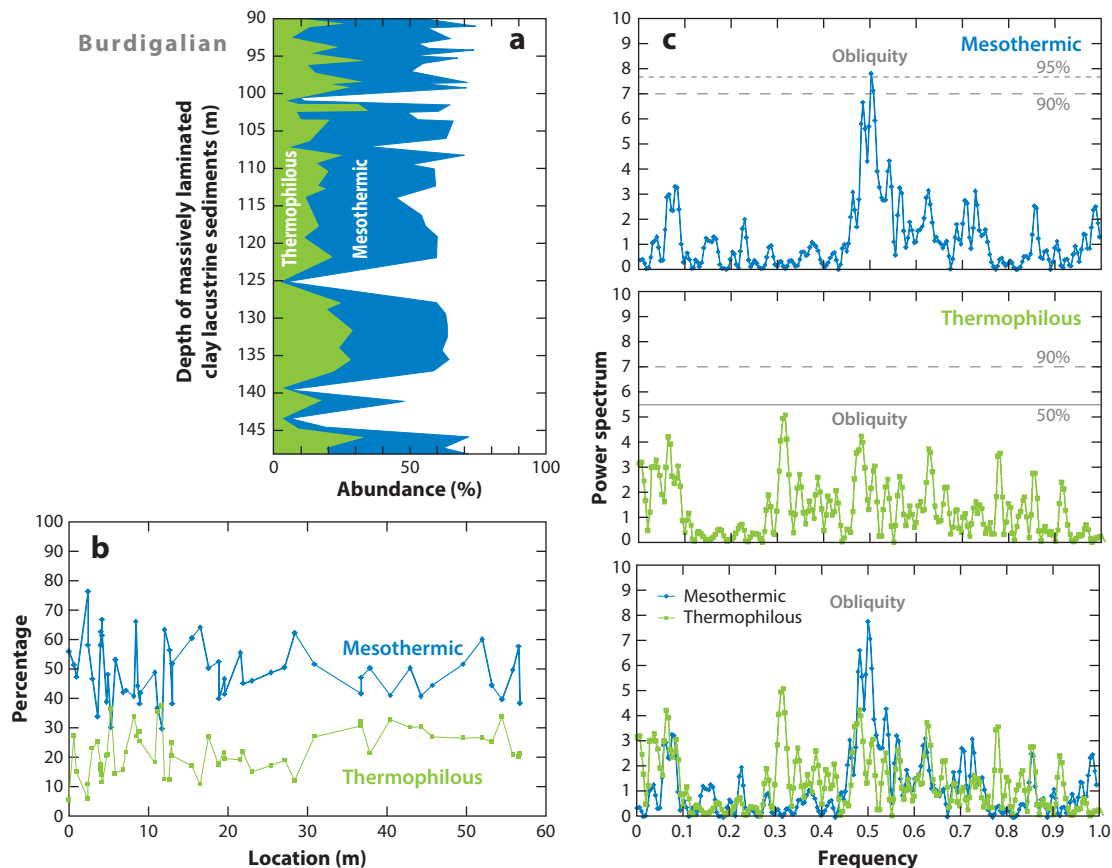


Figure 12

(a) Pollen diagram of thermophilous and mesothermic groups and comparative abundance along the studied core. (b) Sequential variations of the relative abundance of thermophilous and mesothermic groups along the studied interval. (c) Spectral analyses of the relative abundance of the two selected groups, each showing a significant peak at the obliquity range. Adapted from Jiménez-Moreno et al. (2007).

Pliocene and Miocene times (e.g., Versteegh 1994, Santarelli et al. 1998, Popescu et al. 2006), but also in Cretaceous (Tribovillard & Gorin 1991) and Jurassic times (Waterhouse 1999). Alternation of pollen taxa recorded in Miocene lacustrine deposits, belonging to thermophilous (tropical and subtropical) and mesothermic (warm-temperate) groups, shows cyclic patterns associated with changes in temperature and precipitation controlled by astronomically forced obliquity cycles (Jiménez-Moreno et al. 2005, 2007) (**Figure 12**).

The relationship between terrestrial animal community evolution (changes in diversity, origination, and extinction) and climatically induced paleoenvironmental changes has been addressed by many studies (e.g., Fortelius et al. 2006, Badgley et al. 2008), but explicit allusions to Milankovitch-scale forcing are rare. However, Oligocene biota recorded in paleosols revealed paleoclimatic and ecosystem oscillations that correspond with the 41–100-kyr Milankovitch timescale (Retallack et al. 2004); Neogene species variations in small mammals at cycles with periods of 2.4–2.5 and 1.0 Myr were associated with long-period eccentricity modulation and nodes of the 1.2-Myr obliquity cycle (van Dam et al. 2006); and orbital-scale paleoseasonality revealed important effects on early hominid evolution (Kingston 2005). African climate change between

markedly wetter and drier conditions, associated with Earth's orbital variations of precession, obliquity, and eccentricity during the Plio-Pleistocene, was related to the proposed diversification in the hominid lineage (deMenocal 2004, Campisano 2012, Natl. Res. Counc. 2010).

5. LONG-TERM CYCLES: PERIODICITIES IN ORIGINATION, BIODIVERSITY, AND EXTINCTION DERIVED FROM THE FOSSIL RECORD

Long-term cycles with periods of tens to hundreds of millions of years are not included among the sedimentary cycles considered in cyclostratigraphy owing to the weak evidence of their presence in the geological record and the absence of a convincingly demonstrated origin (Hilgen et al. 2004). The longer-term cycles are therefore discussed in this review with caution. Few references to frequency bands corresponding to the longest cycles are found in the cyclostratigraphic literature (**Figure 1**): the tectonic band (>400 kyr) in Imbrie (1985); the “remaining frequency bands” (Fischer & Bottjer 1991, p. 1065); and the galactic band of House (1995), consisting of long orbital cycles (>1.0 Myr). One recent review shows that the periodicities of approximately 26–50, 69, 140, 180, and 550–730 Myr are associated with recurring periods of especially high extinctions and geological activity, suggesting a common underlying galactic cause of mass extinctions mediated through galactic effects on geological, solar, and extrasolar processes (Gillman & Erenler 2008).

5.1. The 26-Myr Cycle and Mass-Extinction Events

An extensive and interesting debate surrounds possible periodicities in origination, biodiversity, and/or global mass-extinction events. Although Fischer & Arthur (1977) were the first to relate the major extinction events registered since 250 Ma to periodic intervals of ~32 Myr, the publications of Raup and Sepkoski popularized this hypothesis (Raup & Sepkoski 1982, 1986; Sepkoski & Raup 1986). Raup and Sepkoski described a periodic pattern in the mass-extinction record [12 extinction events since 250 Ma in the first paper (Raup & Sepkoski 1982)], with a 26-Myr interval between events (**Figure 13**). They favored an extraterrestrial origin, such as the passage of the Solar System through the spiral arms of the Milky Way galaxy (Raup & Sepkoski 1982). Several contemporaneous studies established a similar periodicity in the mass extinctions during the entire Phanerozoic Eon (see Lewis & Dorne 2006 for a detailed review) and proposed speculative causes, principally involving comet impacts on Earth: (a) the vertical oscillation of the Solar System around the plane of the galaxy, causing an increased flux of comets and comet-derived bodies near Earth and then leading to large-body impacts (Rampino & Stothers 1984, Schwartz & James 1984); (b) an unseen companion of the Sun that could periodically perturb the Oort cloud of comets that surrounds the Sun, producing variations in comet impacts on Earth (Davis et al. 1984, Whitmire & Jackson 1984); or (c) the existence of a planet X and a comet disk determining periodic comet showers (Whitmire & Matese 1985). On the basis of the chronology of the onset of major continental flood basalt volcanism, Rampino & Stothers (1988) later concluded that volcanic episodes since 250 Ma were quasiperiodic, with a mean cycle duration of 32 ± 1 Myr (close to the estimated dates of mass extinctions of marine organisms), and invoked showers of impacting comets combined with the intense volcanism as the cause for the global catastrophes.

From the very beginning, however, Raup and Sepkoski's proposal of a periodicity underlying mass extinctions was met with criticism on different fronts (Hoffman 1985, Quinn 1987, Patterson & Smith 1989). More recently, on the basis of the extinction of genera presented in two compendiums—the data set of Sepkoski (2002) and the Paleobiology Database of Alroy et al.

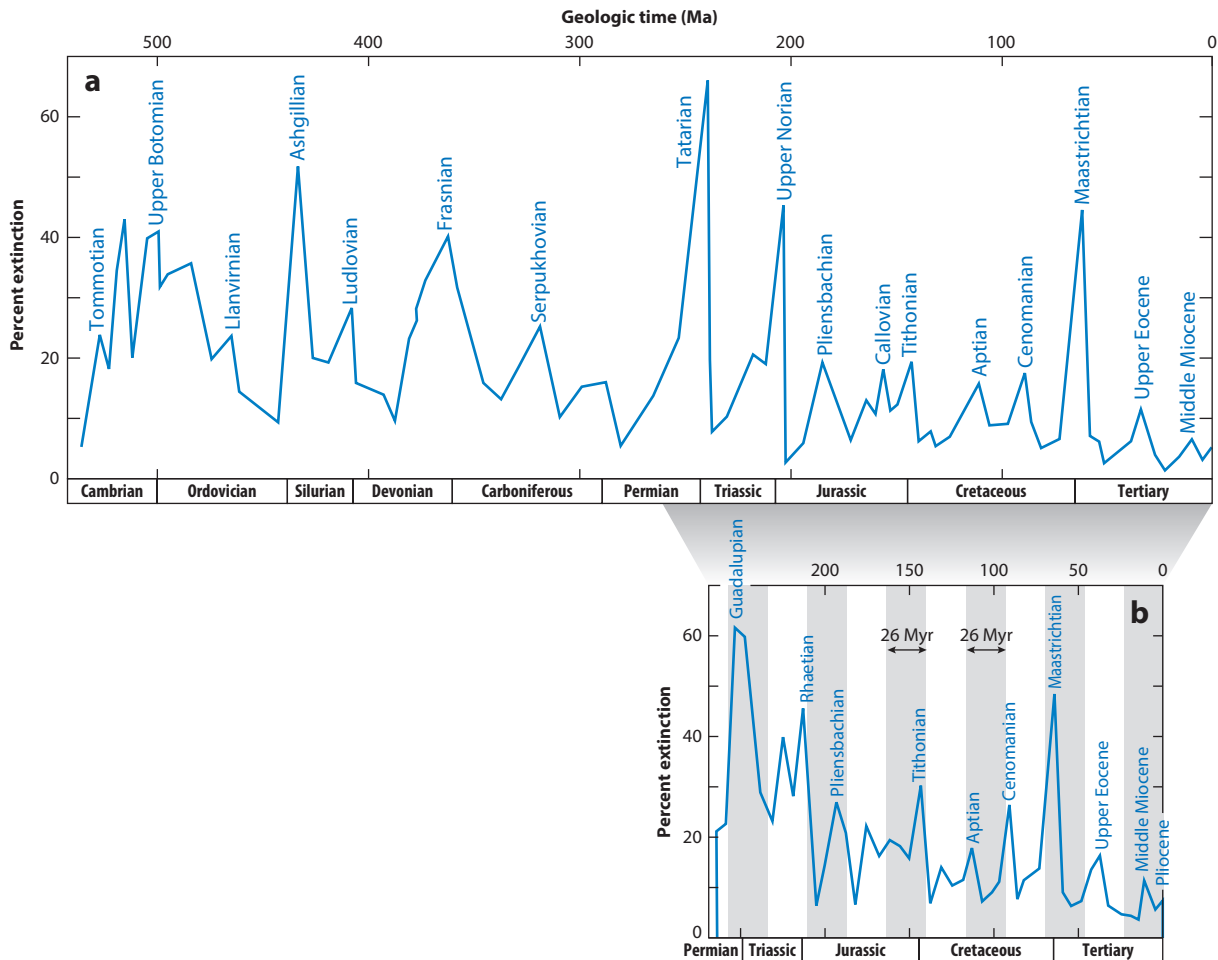


Figure 13

(a) The most important extinctions of “multiple-interval” genera through the Phanerozoic. (b) Enlargement of the 10 major extinctions of marine genera since 250 Ma, evidencing the 26-Myr periodicity according to Raup & Sepkoski (1986). Each shaded region marks off a 26-Myr interval.

(2008)—over a period of ~500 Myr, a significant period of 27 Myr was detected using either of the two data sets, all extinction local maxima, or just those previously classified as mass extinctions (Melott & Bambach 2010). This latter research also shows the fossil record to be inconsistent with perturbations expected in the orbit of a dark solar companion with the requisite orbital period (Melott & Bambach 2010), undermining the Nemesis hypothesis (Davis et al. 1984, Whitmire & Jackson 1984) as the causal factor behind the extinctions.

5.2. Biodiversity Fluctuations During 62-Myr Periods

In the past decade, largely as a consequence of Sepkoski’s publication *A Compendium of Fossil Marine Animal Genera* (Sepkoski 2002), several analyses of the collected taxa were conducted; most of these focused on extinctions, but some examined originations. It was concluded that the number of mass-extinction events and their timing did not fit Raup and Sepkoski’s hypothesis

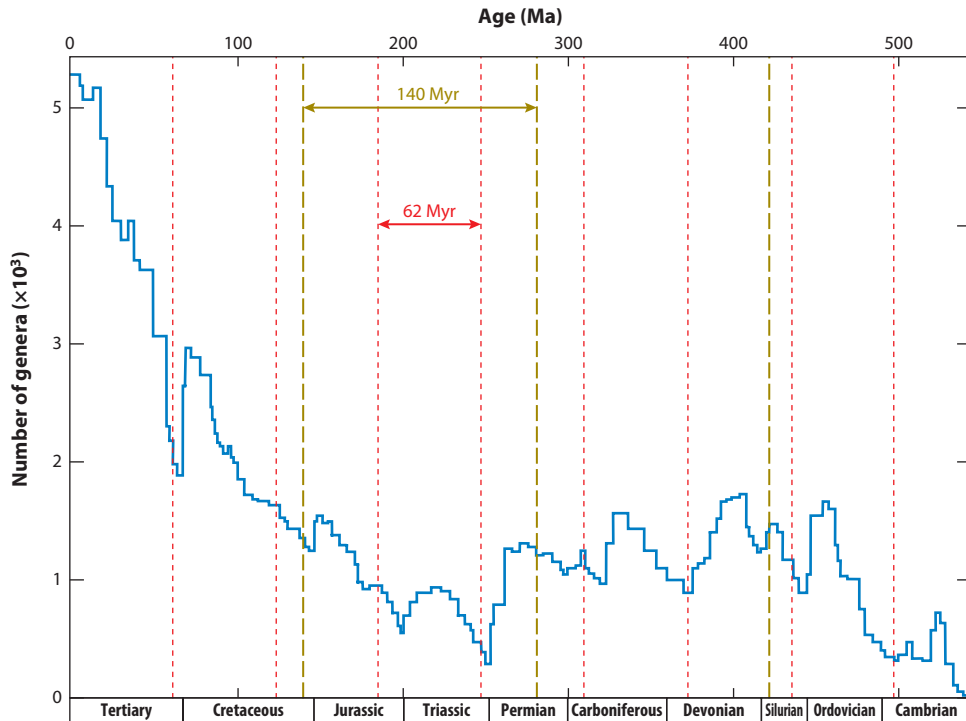


Figure 14

Diversity of known marine animal genera versus time from Sepkoski's compendium (Sepkoski 2002), converted to the *Geologic Time Scale* of Gradstein et al. (2005) (simplified from Rohde & Muller 2005); 140-Myr and 62-Myr intervals are indicated, respectively, by brown dashed and red dotted lines.

(Peters & Foote 2002; see Bambach 2006 for a detailed review). However, Rohde & Muller (2005), by shifting their focus from extinctions to diversity, derived a strong cycle of 62 ± 3 Myr in genus diversity during the Phanerozoic; a weaker cycle, with the same period, was also detected in the patterns of first and last appearances (originations and extinctions/pseudoextinctions) (**Figure 14**). The authors linked the origin of this periodicity to an increase in the rate of comet impacts on Earth (caused by phenomena similar to those outlined in Section 5.1), to periodic volcanism (caused by the regularity of mantle plumes reaching Earth's surface), and to climatic changes (affected by solar cycles or by Earth's orbital oscillations) (Rohde & Muller 2005). Rohde & Muller's proposal was rapidly revised, and a number of subsequent papers supported their findings; however, some authors discarded the idea that the 62-Myr cyclicity represents a biological signal, arguing that it can be explained by a rock outcrop (Smith & McGowan 2005). Later, additional mechanisms were proposed to support the 62-Myr periodicity of fossil biodiversity, including the enhancement of cosmic rays when the Solar System moves to the northern side of the galactic plane (Medvedev & Melott 2007, Melott et al. 2008). This periodicity was registered not only in the Sepkoski compendium (Rohde & Muller 2005, Cornette 2007, Lieberman & Melott 2007) but also in the Paleobiology Database (Melott 2008). More recently, it has been interpreted as real in the fossil record of marine animal biodiversity using an expanded analysis of the three different data sources for global marine diversity [i.e., the Sepkoski data set (Sepkoski 2002), the Paleobiology Database (Alroy et al. 2008), and *The Fossil Record 2* (Benton 1993, 1995; described in Melott & Bambach 2011)].

5.3. Possible Paleoenvironmental Changes at Cycles of 140 and 250 Myr

Together with the significant 62-Myr cycle, Rohde & Muller (2005) also recognized a 140-Myr diversity cycle that could be linked to a climate/glacial/cosmic cycle (**Figure 14**), although the authors warn that less-ambiguous data are needed to verify this interpretation. Rampino & Stothers (1984) affirmed that during the Phanerozoic Eon, apart from the long-term periodicity at 33 ± 3 Myr, there was another dominant cycle of 260 ± 25 Myr, suggesting a possible interaction of the Solar System with interstellar clouds when it moves cyclically through the galaxy. This cycle nearly coincides with the cosmic or galactic year—with a duration between 220 and 250 Myr (a period of about 201.5 Myr is now proposed based on current astronomical data) (Lewis & Dorne 2006)—as the period required for the Solar System to move around the Milky Way galaxy, a time span associated with major glaciation periods. However, the suggested relationship between the cosmic year and the major glaciations is considered highly speculative by some (House 1995).

SUMMARY POINTS

1. Sclerochronological and dendrochronological analyses of fossil skeletons are essential for the recognition of ≤ 1.0 -yr cycles and also hold great potential for the study of longer (decadal to centennial) cycles when working with fossils of long-lived organisms.
2. Fossils reveal cycles belonging to the calendar bands (from semidiurnal to annual periodicities) as demonstrated for samples from the Paleozoic, especially bivalves for tidal cycles and corals and trees for solar cycles.
3. In the solar band (1.0 yr to 10.0 kyr), the most widely recognized cycles in the fossil and subfossil records correspond to the quasiperiodic phenomena of the El Niño–Southern Oscillation (ENSO), the Dansgaard-Oeschger (D-O) cycles, and the Heinrich (H) events.
4. ENSO cycles are mainly characterized by variations in the abundance, distribution, and diversity of marine planktonic fossil communities but are also characterized by the growth patterns of single individuals (e.g., corals and trees).
5. Regional/local ecological factors can induce a localized response of the communities involved, thereby distorting the terrestrial paleontological record of global solar band cycles.
6. Milankovitch band cycles have been broadly recognized in the fossil record, confirming paleoenvironmental changes that are orbit induced on marine and terrestrial communities.
7. Marine paleobiota reveal a well-developed Milankovitch record, mainly for Cretaceous successions, with a significant response involving variations at the community level (abundance, composition, diversity) or in specific environmental conditions (e.g., temperature, salinity). To date, planktonic assemblages have been studied more than benthic ones.
8. Cyclic changes in the range of millions of years, therefore included in the so-called galactic band (> 1.0 Myr), are based primarily on analyses of paleontological data. Apparently cyclic mass extinctions recorded in the fossil record, together with cyclic changes in origination and biodiversity, reveal periodicities at approximately 26, 62, 140, and 250 Myr. These are usually associated with geological, solar, and extrasolar processes induced by galactic phenomena.

FUTURE ISSUES

1. Paleontological analysis of the highest-frequency cycles corresponding to the calendar band ought to integrate comparatively little-studied fossils belonging to poorly studied areas and/or from rarely analyzed habitats.
2. A comprehensive approach should be developed for solar and Milankovitch bands, integrating terrestrial and marine proxies and data from paleocommunities belonging to different habitats in a single environment.
3. Cyclostratigraphic analysis must be based on a detailed sampling procedure—especially for microfossils, in view of their possible redistribution through bioturbation—with an emphasis on the recommended specific counting techniques. Statistically significant cycles need to be differentiated from spurious ones by means of spectral techniques.
4. Cyclostratigraphic analysis of the solar band should focus on the comparatively poorly characterized cycles—that is, the Schwabe cycle or solar year (~11 yr), the Hale cycle (~22 yr), the Gleissberg cycle (~87 yr), and the Suess cycle (~210 yr).
5. For the Milankovitch band, the variable response of paleocommunities to Milankovitch-scale environmental changes must be addressed, evaluating the influence of orbital effects on the speciation and extinction of taxa.
6. The study of Milankovitch band cycles should be approached in those pre-Quaternary intervals that have been comparatively disregarded to date.
7. At the scale of the million-year cycles (the galactic band), advances must focus on the analysis of a new paleontological database to confirm the proposed cycles and explore the speculative origin invoked for the cyclic phenomena behind quasiperiodic mass extinctions, originations, and biodiversifications registered in the fossil record.

DISCLOSURE STATEMENT

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