

Paleoecology

Ecology of prehistoric times, extending from about 10,000 to about 3.5×10^9 years ago. Although the principles of paleoecology are the same as those underlying modern ecology, the two fields actually differ greatly. Paleoecology is a historical science that must rely on empirical data from fossils and their enclosing sedimentary rocks to make inferences about past conditions. Experimental approaches and direct measurement of environmental parameters, which are critical components of modern ecology, are generally impossible in paleoecology. Furthermore, distortion and loss of information during fossilization means that fossil assemblages and distributions are rarely congruent with living communities. Hence, the resolution of ancient ecosystems must remain relatively imprecise. The lack of precision is compensated for by the fact that paleoecology deals with processes occurring over vast spans of time that are unavailable to modern ecology. Long-term changes in communities (replacement) may be discerned and related to patterns of environmental change. More significantly, overall patterns of ecological change in the global biosphere may be documented; evolutionary paleoecology focuses on recognition and interpretation of long-term ecological trends that have been critical in shaping evolution.

Among the goals of paleoecology are the reconstruction of ancient environments (primarily depositional environments), the inference of modes of life for ancient organisms from fossils, the recognition of recurring groupings of ancient organisms that define relicts of communities (paleocommunities), the reconstruction of the interactions of organisms with their environments and with each other, and the documentation of large-scale and long-term patterns of stasis or change in ecosystems. See also: Ecosystem

Paleoenvironmental Interpretations

To reconstruct ancient marine environments, many different parameters must be inferred, such as temperature, water salinity, oxygen levels, nutrient concentrations, and water movements and depth (Fig. 1). In this regard, paleoecology interfaces directly with the fields of sedimentology and stratigraphy, including study of modern depositional environments. See also: Depositional systems and environments; Stratigraphy

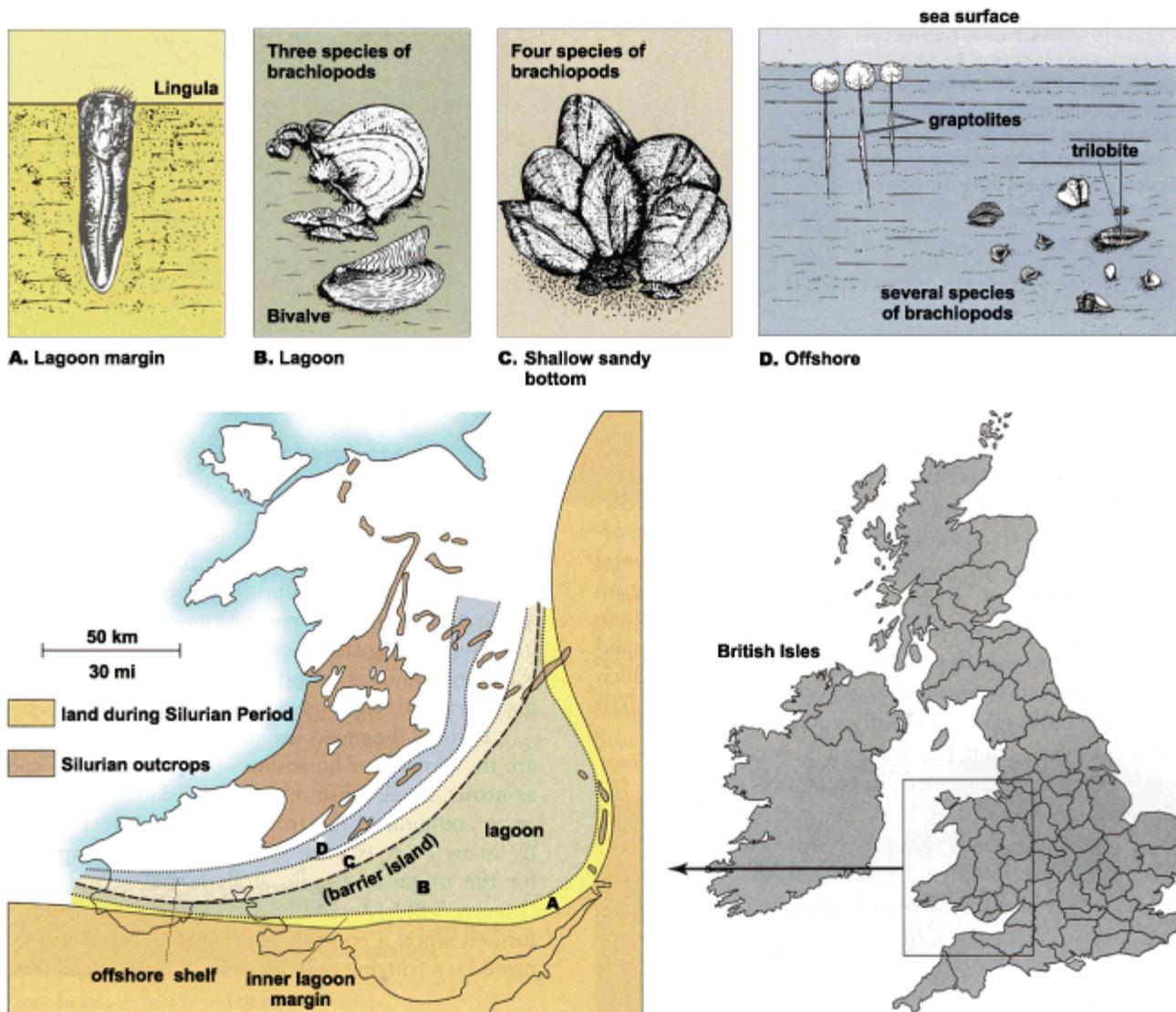


Fig. 1 Zonation of Silurian (425 million year old) marine communities in the Welsh Basin, United Kingdom. Marine animal communities were typically arranged in belts parallel to shoreline and related to water depth. A classic study using fossil communities in basin analysis (Ziegler, 1965) mapped out the distribution of different communities of marine fossils, primarily brachiopods, to show the contouring of belts of ancient environments from the shoreline in the southeast to deep basinal environments. (Reprinted with permission from S. Stanley, *System History*, 2d ed., Freeman Co., 2005)

Taxonomic uniformitarianism

One of the most useful, but also potentially misused, aspects of paleoecological application is known as taxonomic uniformitarianism. This concept relies on studies of modern organisms to determine limiting environmental factors, such as salinity tolerance, temperature preference, or depth ranges. Fossils of the same or closely related species are then inferred to have had similar environmental preferences, and their occurrence is judged to indicate that particular strata were deposited under a comparable range of environmental conditions. Such an approach is valid for very closely related organisms in relatively recent geologic time. Species and even genera may have relatively uniform environmental ranges through time, but the same cannot always be said of higher taxa such as families. At the level of order or class, only the broadest uniformitarian generalizations apply. For example, it is probably valid to consider fossil nautiloids or echinoderms as indicators of normal marine salinities, as all living representatives of these taxa have very limited abilities for osmotic regulation and therefore are restricted to near-normal salinity. Similarly, the restriction of photosynthetic

organisms (such as algae) to the euphotic zone may be useful in determining relative depth. However, the precision and reliability of taxonomic uniformitarianism breaks down in increasingly ancient samples.

Morphologic features

Certain features of the morphology of fossils may be useful in making environmental inferences without reliance on evolutionary relationships. For example, the presence of entire margins and drip tips on leaves of plants is indirectly related to humid, warm climates, and so the proportions of leaf floras with entire margins and drip tips have been used as an index of paleolatitudinal zonation. Growth forms of colonial organisms relate to environmental factors such as turbulence and sedimentation rates. Flexible or articulated skeletons or flat encrusting form in colonial marine animals are associated with highly turbulent shallow-water environments where streamlining becomes important. Delicately branched, inflexible colonies typify quiet areas and, commonly, areas of high turbidity where a branching skeleton may shed sediment more readily than a flat or globose form. Such ecologically related morphology may transcend taxonomic boundaries.

Skeletal mineralogy and geochemistry

The microstructure and geochemistry of organism skeletons may provide clues about ancient environments. For example, the presence of growth banding in skeletons provides evidence for seasonal variability in climates. The skeletons of fossil organisms, if they are well preserved, also encode valuable environmental information in the form of trace elements and isotopic signatures. For example, the calcium carbonate skeletons of marine invertebrates incorporate trace elements whose proportion is related both to physiology and environmental factors such as temperature and salinity. The isotopic composition of oxygen or carbon within carbonate skeletons is a function of isotopic composition of the seawater in which the skeleton was secreted as well as of water temperature. If temperature can be determined independently, the ratio of ^{18}O to ^{16}O (often expressed as a deviation from a standard and referred to as $\delta^{18}\text{O}$) can be used to determine whether a shell was secreted in water of normal (35‰) or abnormal salinity. Conversely, if a given shell can be assumed, on independent evidence, to have come from a normal marine environment and is unaltered, then $\delta^{18}\text{O}$ may be used to determine paleotemperature. In general, carbonate secreted at lower temperatures is preferentially enriched with respect to ^{18}O , and so, $\delta^{18}\text{O}$ is useful for temperature determination. See also: Geologic thermometry

Comparative taphonomy

Taphonomy, which deals with processes and patterns of fossil preservation, has a critical dual role with respect to paleoecology. On the one hand, preservational processes impose distinct biases on the fossil record that must be considered carefully in any attempt at paleoecological reconstruction. On the other hand, the bodies and skeletons of dead organisms constitute biologically standardized sedimentary particles whose orientations, sorting, and general preservational condition bear the imprint of environmental processes active in the depositional environment. Comparative taphonomy uses the differential preservation of fossils as a source of paleoenvironmental information. The degree of preservation of fossils reflects biostratinomic processes, such as current-wave transport, decay, disarticulation, fragmentation and corrosion of skeletons, and fossil diagenetic factors acting after final entombment of the remains in sediment.

Evidence of mode of death of organisms may also provide critical details. For example, layers of beautifully preserved fish or reptile carcasses signify mass mortalities that involved changes in the water column itself. But such mass mortalities can be recorded only if they were also timed with burial events.

Soft tissues can be preserved only by exceptionally rapid burial in anoxic sediments followed by very early coating or impregnation by minerals. Such deposits not only yield important data on the paleobiology of organisms but also provide detailed insights into depositional environments.

Usually, however, only skeletal remains are preserved. Skeletons composed of bivalved shells (for example, brachiopods and pelecypods) or, particularly, of multiple articulated elements (for example, echinoderms, arthropods, and vertebrates)

are sensitive indicators of episodic burial rates. Experimental studies have demonstrated the rapidity of disarticulation under normal marine conditions; most starfish, for example, disintegrate into ossicles in a few days. Hence, intact preservation of these organisms signals episodic burial events. See also: Fossil

Individual skeletons, or parts of skeletons, may become physically fragmented, chipped, or abraded. Such evidence reflects the general degree of turbulence of a particular depositional environment. Similarly, the degree to which skeletal remains are size-or shape-sorted may signify the extent of current and wave processing. Skeletal destruction by bioerosion, physical abrasion, or chemical solution is generally a good indicator of residence time of skeletons on the sea floor prior to burial. The orientation of fossils may yield specific clues as to the extent and types of environmental energy. Pavements of convex-upward valves typically are associated with persistent current reworking, whereas abundant concave-upward shells may signify an episode of stirring of the shells from the sea bottom and resettlement during storms. Furthermore, alignment of elongated shells may provide data on the orientation of unidirectional currents or the propagation direction of oscillatory waves. Vertically embedded specimens of ammonoids are typical of water areas with depths less than 30 ft (10 m). Finally, the early diagenetic features of fossils reflected in solution, compaction, and mineralization may yield information about sediments and bottom water geochemistry, water pH and oxygen content.

Various aspects of biostratigraphic and diagenetic fossil preservation can be combined to form predictive models of taphonomic facies or taphofacies. Certain suites of quantifiable preservational conditions, for example, characterize particular environments, and so their recognition by paleoecologists may help to “fingerprint” those environments. See also: Sedimentology; Taphonomy; Trace fossils

Paleoautecology

Paleoautecology, the interpretation of modes of life (broadly, niches) of ancient organisms, involves a multidisciplinary approach. Although ancient modes of life cannot be determined completely, paleoecologists can often assign fossils to generalized guilds in terms of types of feeding, substrate preference, and degree of activity.

A thorough understanding of the biology of closest modern analogs is particularly important in any attempt to reconstruct paleoautecology. If the species or a closely related species is extant, then its mode of life, general physiology, and even behavior can be inferred with some confidence through the use of taxonomic uniformitarianism, provided that the biology of living relatives is well understood. “Living fossils,” or relict extant taxa, such as Nautilus, sclerosponges, horseshoe crabs, and modern stalked crinoids provide valuable clues for interpreting the paleobiology of extinct organisms. See also: Living fossils

Functional morphology

For extinct organisms that have no adequate modern analogs, alternative approaches, particularly functional morphology, provide some hints as to life modes. Comparative morphology seeks analogies between the anatomical features of fossil skeletons and those in living forms for which the function can be determined. In some cases, structures in unrelated organisms have evolved convergently, and their function may be interpreted by analogy. When no biological analog exists, a physical or mechanical model, or paradigm, may provide clues to interpreting structures in extinct organisms.

An experimental approach to functional morphology may also provide useful insights. Models of ammonite shells, for example, have been tested in flumes in which artificial currents are produced to determine frictional drag effects of shell shape and sculpture. Certain shell shapes were found to be more hydrodynamically streamlined and probably correspond to more rapidly swimming modes of life. Testing the resistance of different brachiopod shell architectures to crushing, as by predators, has shown that certain features of shell architecture, such as ribbing and deflections of shell margins, can increase shell rigidity.

Fossil data

Certain natural experiments also shed light on the paleobiology of extinct organisms. The fact that oysters encrusted the shells of living ammonites has enabled paleontologists to calculate the buoyancy compensation capabilities of those ammonoids. Encrustation and boring of cephalopod shells by bryozoans and barnacles that grew preferentially aligned toward currents has demonstrated a predominance of forward swimming motion in these extinct hosts.

Remnants of soft parts, muscle scars, gut contents, and associated trace fossils all provide information useful in the reconstruction of ancient ecological niches. Rare occurrences of rapidly buried fossils in unusual positions can be interpreted as original life positions. Unusual associations with substrates or other organisms also provide insights. Finally, the consistent association of poorly understood fossil species with other fossils whose modes of life are well known or with sediments that indicate particular environments may help to establish the habits and environmental ranges of extinct forms.

Population studies

Certain properties of species, such as mortality patterns, birth rates, and numbers of individuals per age class, can be studied only at the level of populations. Despite the difficulties of studying fossil populations, it is still possible to make some inferences about population parameters. For example, the distribution of individuals of a particular species into different age or size classes may yield some indirect data on the age-frequency distribution of a population that can be used to construct crude mortality curves showing age-at-death relationships. Some species may display a high juvenile mortality, a feature typically associated with stressed environments and rather opportunistic species; others, in stable environments, may display delayed mortality.

Of particular ecological importance is the population strategy of a given species of organisms. Two end-member conditions have been recognized: opportunistic species, sometimes termed r-selected forms, and equilibrium, or k-selected, species. Opportunistic organisms are typically rather generalized in habit and habitat preferences, are commonly stress-adapted, and display exceedingly high rates of reproductive maturation and fecundity. Extremely opportunistic, or “weedy,” species of this sort are recognizable in the fossil record by their widespread distribution and occasional presence in extremely dense, monospecific populations on single beds of rock that are otherwise barren of fossils. Equilibrium species, on the other hand, tend to occur in moderate or small numbers in a narrow range of environments commonly associated with diverse assemblages of other species, such as in reef environments. The distinction between equilibrium and opportunistic mode of life may have important implications for understanding the distribution and evolutionary patterns of fossil taxa as well as for interpreting the stability of particular ancient environments. See also: Population ecology

Paleosynecology

The study of interrelationships within organism communities that coexist in time and space is known as synecology. At the most basic level of synecology are the interacting pairs of organisms that coexist in a particular environment. Paleosynecology also involves study of ancient community structure and dynamics.

Organism interactions

Interactions range from tolerance to symbiosis, which involves highly dependent and coevolved species pairs. Although interactions are very difficult to determine with fossils, there are cases where strong clues are observed. In some instances, organism interaction may be very indirect. For example, the accumulation of shells on a sea floor may lead to colonization by other organisms that require hard substrates to encrust onto or bore into, a process referred to as positive taphonomic feedback. Conversely, armoring of muddy sea bottoms with shell debris will inhibit burrowing organisms (negative taphonomic feedback).

Shallow-burrowing nuculid bivalves convert muddy sea bottoms into a water-rich pelleted floc. The high turbidity and instability of this fluid substrate may inhibit the settlement of many epifaunal suspension-feeding organisms. Such negative feedback is referred to as trophic group amensalism.

Mutualism, involving symbiotic algae called zooxanthellae, is inferred for many fossil reef-dwelling organisms, including various corals, sponges, and even some bivalves, based on taxonomic uniformitarianism as well as morphology and evidence for prolific skeletal growth. Such mutualism is difficult to substantiate for extinct groups, although distinctive patterns of carbon isotopes within skeletal carbonates may prove a useful fingerprint of secretion aided by zooxanthellae.

Many marine organisms use the skeletons of other living organisms as substrate or to obtain an elevated feeding position without having any effect on the hosts. Evidence of this type of commensal interaction is abundant in the fossil record.

Parasitic interactions are very difficult to observe in fossils because they normally involved the soft tissues of the host. However, rare evidence for paleopathology (fossil diseases) can be documented from Paleozoic times onward in certain organisms such as echinoderms or vertebrates that have an internal skeleton, or endoskeleton. For example, malformations in fossil crinoids may record parasitism.

Fossil evidence for competition is best seen in cases of spatial competition. For example, certain types of bryozoans appear to overgrow other species preferentially. Many aspects of fossil distribution have been attributed to the effects of competition or the evolutionary response for reducing competition by niche partitioning. Examples include the subdivision of many marine communities into distinct feeding groups based on vertical height (tiering) above and below the sediment-water interface. Some researchers have claimed that competition is a primary motor of evolutionary change, often alluding to Darwin's analogy of the wedge, in which more and more species are packed into a particular ecospace by increasingly finely divided specialized niches.

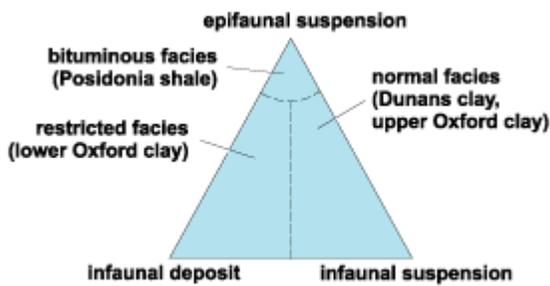


Fig. 2 Classification of shales in terms of percentages of three benthic habitat groups: epifaunal suspension-feeding bivalves (those living at the sediment-water interface and filtering seawater), infaunal (living within and feeding on the sediment), and suspension-feeding groups. (After K. A. Morris, Comparison of major sequences of organic-rich mud deposition in the British Jurassic, J. Geol. Soc. London, 137:157–170, 1980)

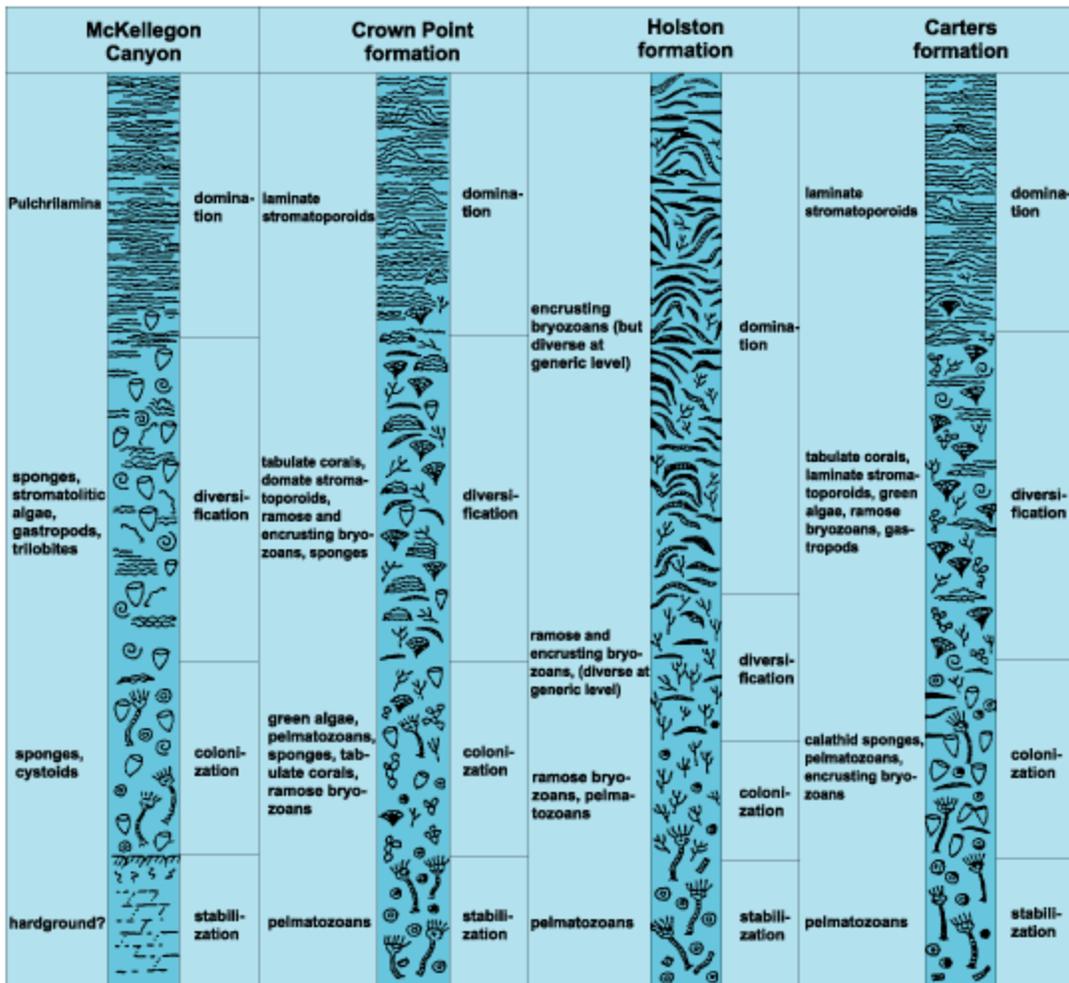


Fig. 3 Comparison of four developmental stages in four ancient reef masses. (After K. R. Walker and L. P. Alberstadt, Ecological succession as an aspect of structure in fossil communities, *Paleobiology*, 3:238–257, 1975)

Predation or carnivory is probably one of the most significant ecological interactions in any environment. Direct predator-prey links are difficult to establish in the fossil record, but there are several lines of evidence that may be used. Bite marks of particular types, such as tooth marks of mosasaurs on ammonoids, provide one line of evidence, so do boreholes of predatory snails on particular prey species and remnants of prey shells preserved in the stomach contents or coprolites (fossilized feces). In turn, numerous morphological trends may signify antipredatory adaptations. The fossil record of predation extends back to the Early Cambrian, as evidenced by bite marks in trilobites, which commonly show a preference for the right side of the prey. The frequency of healed and unhealed predatory fractures in some shells increases significantly in the Paleozoic in concert with the rise of fossil evidence for shell-crushing predators. The earliest shell-drilling snails appear to have been Ordovician in age, but the habit of drilling shells for predation probably evolved independently at least four times in different groups of gastropods.

Paleocommunities

The fossil record contains highly biased remnants of past communities or paleocommunities. Paleocommunities are generally recognized as recurring associations of fossil species. Multivariate statistical techniques such as cluster analysis and ordination analysis are commonly employed to aid in discerning the recurrent groupings of fossil species, or persistent gradients of species composition. Such analyses are based upon field studies in which data on the presence, absence, or relative abundance of fossil taxa have been recorded in a large number of samples, typically from many stratigraphic levels.

Taphonomic biases

Statistically defined groupings may or may not represent real ecological entities. For example, in most offshore marine environments, the transport of skeletons between environments is minimal. However, because of differential preservation, the proportions of organisms in the living assemblages (biocoenoses) are not always faithfully reproduced in the death assemblages of skeletal remains (taphocoenoses). Nearly all soft-bodied organisms are lacking in the death assemblage, and those with fragile skeletons tend to be underrepresented. Moreover, because of the accumulation of skeletons over extended periods of time, death assemblages commonly display mixtures of organisms that inhabited slightly differing environments at different times, a phenomenon referred to as time averaging. Fossil assemblages actually may be more diverse than living assemblages of skeletonized organisms at any one time. They record a very biased and averaged-out view of communities that existed over a long period of time.

Relationship to environments

In most studies of paleocommunities, recurrent groups can be related to environments, as inferred from independent evidence such as rock type, sedimentary structures, taphonomy, trace elements, and isotopic studies. Classic studies modeled paleocommunity distribution patterns on relative bathymetry or distance from shoreline, but many later studies emphasized the control of paleocommunity distribution by multiple factors. Depth-related factors such as turbulence, light penetration, and oxygen level are clearly important controls in many cases. However, sedimentation-related factors such as rates of deposition, turbidity, and substrate consistency may be equally important, giving rise to a much more complex array of paleocommunities (Fig. 1).

After recurring associations of fossils are recognized, they are generally analyzed in terms of organism interactions and trophic (feeding) relationships. Primary producers of ancient ecosystems, such as algae, are likely to be poorly preserved or absent from the fossil record, but some links in ancient food chains may be recognizable. One aspect of paleocommunity structure that is commonly analyzed is the proportion of different feeding (trophic) and life-habit guilds. Certain marine paleocommunities are dominated by skeletons of infaunal deposit feeders, others by epifaunal suspension feeders. Unfortunately, live-dead comparisons in modern communities suggest that the original proportions of various life habitat groups are not preserved in the fossil record. But the biased trophic proportions of the taphocoenoses may still relate in a meaningful way to the original environment. Consistent differences in the proportions of infaunal suspension-feeding, infaunal deposit-feeding, and epifaunal suspension-feeding bivalves have been detected in differing ancient oxygen-restricted facies (Fig. 2). See also: Food web

Temporal changes

Communities and paleocommunities are not static entities in time, but undergo important structural changes on at least three different time scales: succession, replacement, and evolution. Because it operates on a very short time scale, from decades to centuries, ecological succession can be resolved only in a few fossil samples (Fig. 3). Some instances of supposed ecological succession, such as encrusting communities upon shells, may in fact reflect taphonomic feedback. Allogenic succession represents changes in communities induced by physical environmental change. Good examples are seen in many hardgrounds, areas of early lithified sea floors (Fig. 4). See also: Ecological succession

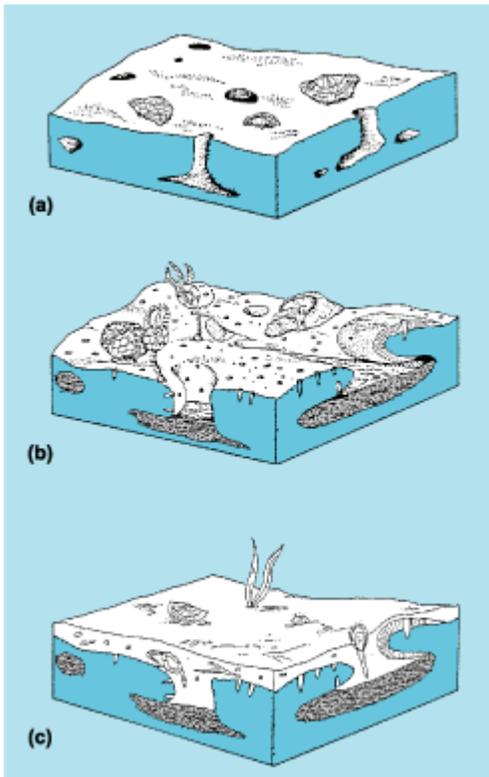


Fig. 4 Formation and burial sequence of Bobcaygeon hardground. (a) Soft-bottom community of strophomenid brachiopods and infaunal burrowers inhabiting carbonate mud. (b) Hardground community consisting of boring and encrusting organisms. (c) Post-hardground community inhabiting muds that blanketed the hardground. (After C. E. Brett and W. D. Liddell, *Preservation and paleoecology of a Middle Ordovician hardground community*, *Paleobiology*, 4:329–348, 1978)

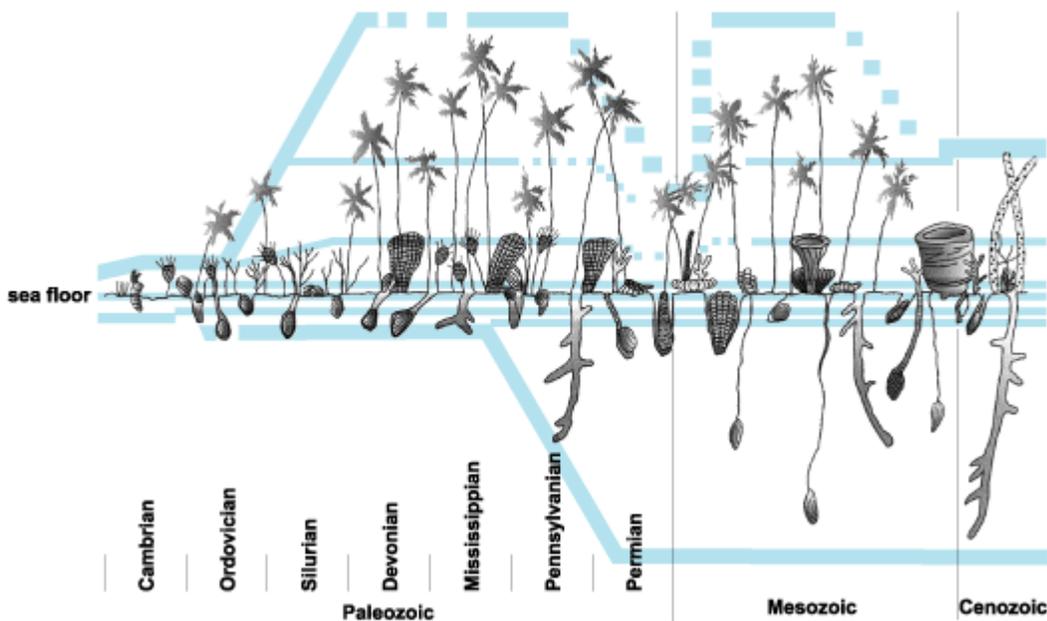


Fig. 5 Tiering or vertical depth stratification in marine communities through time. Note the rapid rise of the highest-tier (level) organisms (crinoids or sea lilies, bryozoans) from a few centimeters to over a meter above the sea floor during the Ordovician Period. Branching bryozoans and shorter-stemmed crinoids took advantage of an intermediate tier 10–20 cm above the sea bottom, while burrowing clams and worms dug down to a tier about the same distance into the sediment. In

the middle Paleozoic, still much deeper burrowing forms evolved the ability to mine sediments down to nearly a meter. Note minor readjustment of the tiers associated with mass extinctions at the Paleozoic-Mesozoic and Mesozoic-Cenozoic era boundaries. (Modified from W. I. Ausich and D. J. Bottjer, J. Geol. Educ., 1991)

Longer-term changes in community composition, encompassing thousands of years, are not truly succession, but instead record allogenic effects such as sea level or climate variations. These changes are properly termed community replacement, and involve wholesale migration or restructuring of communities at particular locations due to changing environments. In many instances, particular fossil assemblages appear to track shifts in preferred environments and facies within sedimentary cycles. Habitat tracking may provide important clues to deciphering patterns of environmental fluctuations such as transgressive-regressive cycles. On a scale of millions of years, communities show evolutionary changes because their component species have evolved. See also: Ecological communities

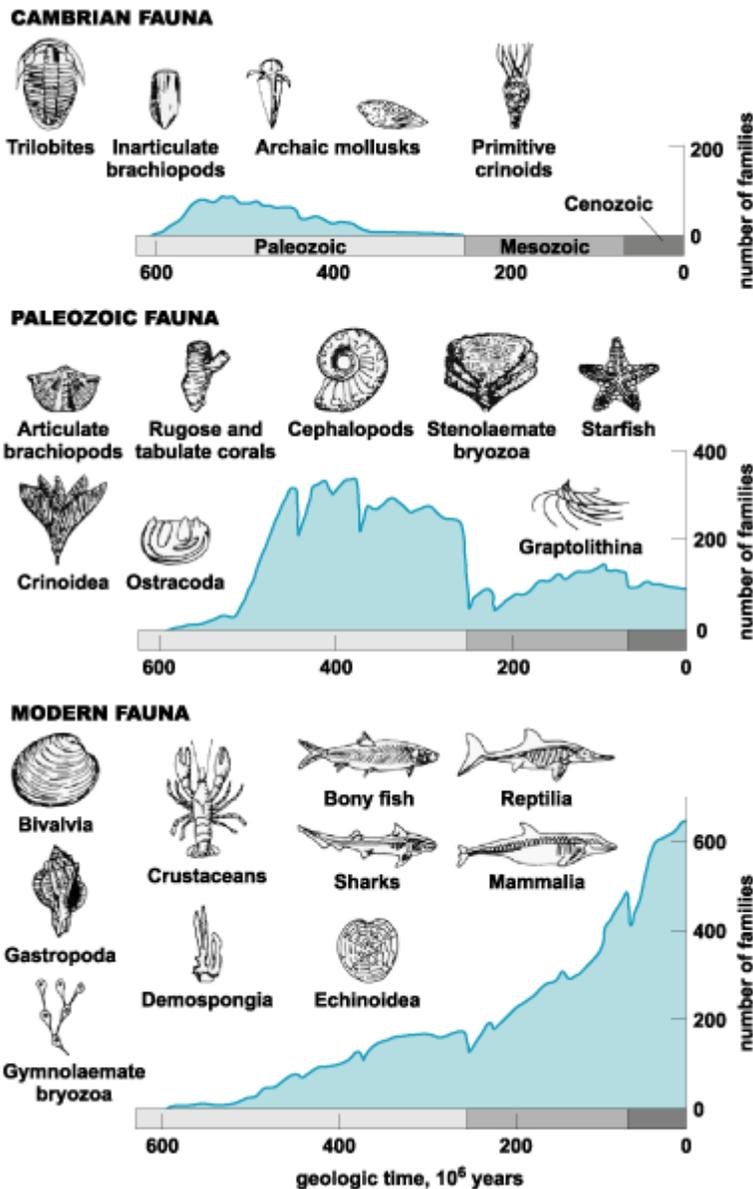


Fig. 6 The three great marine evolutionary faunas of the Phanerozoic. The Cambrian fauna, composed of trilobites, primitive groups of brachiopods, and mollusks arose early during that period to a diversity of about 50 families, then dwindled during the later Paleozoic as more archaic groups migrated offshore and were replaced by the “Paleozoic fauna,” typified by rugose and tabulate corals, brachiopods, bryozoans, crinoids, and graptolites. The latter diversified rapidly in the Ordovician Period to over 300 families and then fluctuated around this level until the end of the Paleozoic Era. The great Permian-Triassic extinction reduced the “Paleozoic fauna” and may have favored the rise of the “Modern fauna” during the Mesozoic and Cenozoic eras with diversities as high as 620 families, including especially mollusks, crustaceans, and both sharks and bony fishes. (Modified from J. J. Sepkoski, Jr., *Paleobiology*, 1981)

Larval ecology and evolution

Ecological patterns such as larval type affect overall patterns in life history. Larval ecology of marine animals controls their geographic distribution. Species with long-lived larvae may be dispersed much more widely than forms with short-lived planktonic phases or direct development from eggs. In turn, geographic distribution, whether localized or cosmopolitan (global), undoubtedly plays an important role in their tendency toward speciation as well as extinction. Thus, it may be possible to develop models to better explain evolutionary patterns in different groups in relation to paleoecology.

Evolutionary Paleocology

Organisms evolve within the context of other organisms, not in a vacuum. There is substantial fossil evidence to indicate increasing complexity of organism interactions through time. This escalation in the intensity of predatory interactions, for example, may have important implications for evolutionary change. For example, trends of increased spinosity, greater shell thickness, increasingly restricted apertures, and other antipredation adaptations may reflect the intensification of predatory behavior by shell-boring and crushing predators.

Increased vertical stratification or tiering in marine-level bottom communities through time has been recognized (Fig. 5). Cambrian communities possessed mainly low-lying suspension-feeding and scavenging organisms that lived mostly just above or below the sediment-water interface. By mid-Paleozoic time, crinoids extended up to heights of several feet or more off the sea floor, and various burrowers extended downward a couple of feet or more into the sediment. The Mesozoic rise of deep-burrowing clams and other infauna increased the infaunal tier to over 3 ft (1 m). The increased vertical structuring of these communities may represent a response to increasing crowding. By feeding at different levels in the water and substrate, organisms were able to further subdivide the resources of a given environment.

Marine animals form a hierarchy of ecological units through the Phanerozoic time interval. These range from blocks of relative stability at time scales of a few million years, to broader intervals of general stability of faunas, to three great evolutionary faunas.

First, at a scale of a few million years, groups of species may show considerable ecological stability punctuated by episodes of abrupt change. Brett and Baird (1995) introduced the concept of “coordinated stasis” to describe a pattern of approximately concurrent long-term stability and abrupt change in many taxa. During a large proportion of geologic time a majority of genera and, in some cases, species show little or no change in morphology. Moreover, general groups of communities or “biofacies” also may be similar throughout blocks of stability referred to as “ecological-evolutionary units and subunits.” These relatively stable intervals, spanning up to several million years, are punctuated by much shorter intervals, perhaps a few tens of thousands of years, of abrupt change across many biofacies, local extinction of many long-standing lineages, immigration and emigration from the local basin, and general faunal turnover. The original example of the Silurian–Devonian (380 to 440 million year old) fossil assemblages of eastern North America—in particular, the Middle Devonian Hamilton Group—features examples of assemblages, separated by up to 5 million years, with nearly identical composition and similar guild structure and even relative abundance. Consideration of a larger number of case studies ranging in age from Cambrian to modern suggests that this original example represents one end member in an

array of conditions ranging from similar cases but some with somewhat more species level variability, to examples of nearly continual change in species composition, and biofacies ecological structure. This variability probably depends on local environmental variability. The observed pattern of similarities between samples from cases of coordinated stasis could imply a form of stable, lock-step tracking of certain well-organized “communities.” However, this pattern could also be the result of recurrence of a similar assemblage due to persistence of environmental gradients and because species do not drastically change their habitat preferences through time. The retention of habitat preferences by species is perhaps the most important aspect of ecological stasis. It would appear that under appropriate conditions species can simply track shifting preferred environments for millions of years rather than adapt to local change.

At the next larger level, marine communities appear to show strong similarities of family- and genus-level composition, as well as general ecological structure (guilds, trophic structure, diversity, and so on) for tens of millions of years. These blocks of relative stability, termed ecological-evolutionary units (EEUs) by Boucot (1990), were terminated by major extinctions. Raup and Sepkoski also recognized five major mass extinctions—the “Big Five” (Late Ordovician, Late Devonian, Permian-Triassic, Late Triassic, and Cretaceous-Tertiary) that stand out from background rates of extinction. These and lesser mass extinctions played critical roles in restructuring the ecology of the biosphere, including changes in guild structure and tiering patterns. Ecological-evolutionary units are bounded by major biotic turnover events, involving widespread extinctions including the “Big Five” mass extinctions. Again, the EEU concept implies that the ecological history of life was not one of continuous, gradual change. Rather, it was characterized by extended periods of near equilibrium that were interrupted by much shorter periods of crisis and major ecological restructuring.

The largest scale of faunal pattern consists of “evolutionary faunas.” By analyzing patterns of marine family and genus level diversity using a large database, Sepkoski (1981) recognized three such units through the past 540 million years of the Phanerozoic Eon, each characterized by a different pattern or trajectory of diversification (Fig. 6). The “Cambrian fauna”—typified by trilobites, lingulid brachiopods, and certain primitive groups of mollusks and echinoderms—appeared during the earliest Paleozoic, diversified in the Cambrian, and then began to decline as the second or “Paleozoic fauna” diversified. The latter was characterized by rugose and tabulate corals, articulate brachiopods, bryozoans, and crinoids which formed the major faunas of shallow seas from the Ordovician to the Permian Period and displayed a relatively stable “platform” of family diversity. Finally, the “Modern fauna,” characterized by mollusks and crustaceans, arose in nearshore environments during the early Paleozoic, but expanded greatly following the end Permian mass extinctions. Sepkoski and Sheehan (1983) recognized that evolutionary innovations tended to arise first in shallow, nearshore environments. Through time the newly arising groups typical of the “Paleozoic” and then the “Modern” faunas tended to spread offshore, while more archaic forms were displaced to deep ocean “refugia.” This is one of the most profound of all paleoecological patterns, and the explanation of this pattern remains imperfectly understood. It may imply that stressed nearshore settings favor evolution of new life strategies and/or that there has been a general intensification of energy utilization through time such that more archaic “Cambrian” or “Paleozoic” faunas were relatively “low energy” and had less competitive ability than physiologically more sophisticated, “high-energy” Modern faunas. See also: Ecology; Paleoclimatology; Paleogeography; Paleontology

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Bibliography

- * A. J. Boucot, *Principles of Benthic Marine Paleocology*, 1981
- * R. J. Dodd and R. J. Stanton, Jr., *Paleoecology, Concepts and Applications*, 2d ed., 1990
- * J. J. Sepkoski, Jr., A factor analytic description of the Phanerozoic marine fossil record, *Paleobiology*, 7:36–53, 1981
- * M. J. P. Tevesz and P. L. McCall (eds.), *Biotic Interactions in Recent and Fossil Benthic Communities*, 1983

* G. J. Vermeij, *Evolution and Escalation: An Ecological History of Life*, 1987

Additional Readings

* D. W. J. Bosence and P. A. Allison (eds.), *Marine Palaeoenvironmental Analysis*, Geol. Soc. Spec. Publ., 83, 1996

* A. J. Boucot, *Evolutionary Paleocology of Behavior and Co-evolution*, Elsevier, Amsterdam, 1990

* P. J. Brenchley and D. A. T. Harper, *Palaeocology: Ecosystems, Environments and Evolution*, Chapman & Hall, London, 1998

* C. E. Brett and G. C. Baird, Coordinated stasis and evolutionary ecology of Silurian to Middle Devonian marine biotas of the Appalachian Basin in D. Erwin and R. Anstey (eds.), *New Approaches to Speciation in the Fossil Record*, pp. 285–315, Columbia University Press, New York, 1995

* P. H. Kelley, M. Kowalewski, and T. A. Hansen, *Predator-Prey Interactions in the Fossil Record*, Kluwer/Plenum Press, New York, 2003

* R. E. Martin, *Taphonomy: A Process Approach*, Cambridge Paleobiol. Ser. 4, Cambridge University Press, 1999

* J. J. Sepkoski Jr., A factor analytic description of the Phanerozoic marine fossil record, *Paleobiology*, 7:36–53, 1981

* J. J. Sepkoski, Jr., and P. M. Sheehan, Diversification, faunal changes, and community replacement during the Ordovician, in M. J. S. Tevesz and P. McCall (eds.), *Biotic Interactions in Recent and Fossil Benthic Communities*, pp. 673–717, Plenum Press, New York, 1983

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