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Review

Paleophysiology: From Fossils to the Future

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Future environments may resemble conditions that have not existed for millions of years. To assess the adaptive options available to organisms evolving under such circumstances, it is instructive to probe paleophysiology, the ways in which ancient life coped with its physical and chemical surroundings. To do this, we need reliable proxies that are based on fundamental principles, quantitatively verified in living species, and observable in fossil remains. Insights have already come from vertebrates and plants, and others will likely emerge for marine animals if promising proxies are validated. Many questions remain about the circumstances for the evolution of environmental tolerances, metabolic rates, biomineralization, and physiological responses to interacting species, and about how living organisms will perform under exceptional conditions.

Predictions, Proxies, and the Past

Understanding how organisms will respond to future conditions is a key challenge because ecosystems are being disrupted by rising temperatures, increasing levels of carbon dioxide (CO₂), and changing ocean chemistry. Although much is known about how individuals react physiologically to change on short timescales, long-term responses involving genetic adaptation have received less scrutiny. To assess the adaptive possibilities for response to conditions that have not existed for millions of years, it is instructive to probe paleophysiology (the ways in which ancient life coped with its physical and chemical surroundings) and to ask how species succeeded or failed in the face of both gradual and catastrophic environmental change.

The geological record shows that some of the conditions projected for the future will come to resemble the circumstances that were common in the prehuman past. We also know that extinctions of the past were selective with respect to traits such as metabolic rate, thermal tolerance, photosynthetic capacity, and internal homeostasis. However, much remains to be learned about the physiology of ancient organisms, especially marine ones.

To reconstruct paleophysiology, we need indirect proxies, founded on basic principles and quantitatively verified in living organisms, which are observable on fossil remains. The aim is not to infer ancient environments, although that is also important; rather, the goal is to understand the physiological performance and limitations of fossil species.

Here, I outline some potential strategies and pitfalls in this endeavor. I highlight some approaches that have already yielded deep insights, and discuss others that are promising but untested. Throughout, I emphasize outstanding questions and point to ways in which paleophysiological data can inform predictions about adaptations in the future.

The Role of 'Living Fossils'

Intuitively, the most appealing approach for inferring paleophysiology is to study 'living fossils'; that is, species that have changed little morphologically (and presumably physiologically) over

Trends

Conditions of the past can provide a key to those of the future.

The physiology of fossil life shows how organisms can adapt to future change.

Reliable proxies are needed to infer paleophysiology.

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long periods of time. To validate this approach, it is essential to identify taxon-independent traits that reliably indicate performance characteristics, such as growth rate, activity level, and environmental tolerances. The following examples from brachiopods and cephalopods illustrate the promise and limitations of this approach.

Brachiopods

Brachiopods are marine lophotrochozoans whose bivalved shells superficially resemble those of the molluscan class Bivalvia. Following their Cambrian origin, they became morphologically and ecologically diverse during the Paleozoic and Early Mesozoic. From the Early Cretaceous period onward, the group became restricted to deep, cold, dark or oxygen-poor waters. Living species are morphologically conservative and have low levels of metabolism, growth, feeding, and reproduction [1–3], with a small body relative to their shell [4,5].

The generally smaller sizes of brachiopods compared with bivalves suggests that brachiopods have always been less energetic than bivalves [6]. Data on body sizes also imply that the metabolic energy use of brachiopods has declined by half since the Paleozoic, whereas that of bivalves has risen by two orders of magnitude [6]. To test these hypotheses, we need a metabolic proxy applicable to animals with shells that, as in brachiopods and bivalves, add skeletal material along the growing margin in a spiral direction. For bivalved animals, a potential proxy is shell convexity. Species with highly convex valves grow slowly and have a low rate of expansion of the growing margin away from the axis of coiling [7,8], whereas flat or weakly inflated valves grow fast and have high rates of spiral expansion. Living brachiopods have strongly convex valves, reflecting the observed slow growth, whereas Paleozoic forms and living bivalves vary from inflated to almost flat. Together with the presence of spines and other structures indicating an active shell-secreting mantle margin, the convexity criterion suggests a wider range of metabolic rates for Paleozoic brachiopods and post-Paleozoic bivalves than for living brachiopods. Both the convexity proxy and the distribution of valve inflation in these bivalved groups over time require quantitative verification.

Shell geometry likely also indicates metabolic performance in univalved gastropods and cephalopods [8]. Slowing growth with increasing ontogenetic age is reflected in a gradual or sudden departure from logarithmic-spiral growth in gastropods, whereas complex apertural margins, shell resorption, and prominent internal and external shell sculptures imply high activity by the shell-secreting mantle and of the animal as a whole. These possibilities can be explored with cephalopods, a group in which metabolic activity appears to have increased over time [9].

Cephalopods

Most Paleozoic and Mesozoic cephalopods had an external shell in which the liquid- and gas-filled chambers, separated from each other by perforated septa, enabled the animal to control its vertical position in the water. Except for six species of *Nautilus* and *Allonautilus*, cephalopods with such shells have all but disappeared in favor of coleoids (squids and their relatives). *Nautilus* has been used as a 'living fossil' model for shell-bearing cephalopods. Its bulky shell, simple septa, jet-propulsion involving periodic contractions of the body into the shell, slow swimming, and tolerance of low-oxygen conditions are all consistent with low metabolic rates [9,10], which likely also characterized fossil straight-shelled and coiled nautiloids.

However, shell-bearing ammonoids were probably less physiologically constrained [11]. Similar to squids, they used contractions of their muscularized mantle to power jet propulsion. Many Mesozoic species had complexly fluted septa and other indications of higher activity [12].

The same proxy can also be used in bivalves and brachiopods, in which the relative contributions of muscles can be estimated by measuring the area of adductor muscle scars on the inner

surface of the valves. As in the case with the convexity criterion discussed above, the muscle proxy requires quantitative evaluation in living species whose metabolic activity is either known or measurable under controlled conditions.

Ammonoids nearly became extinct several times during their Devonian to Cretaceous history before finally disappearing at or shortly after the end-Cretaceous crisis. It will be important to infer the physiological tolerances and activity levels of survivors during various crises and to ascertain whether the physiological traits of these survivors were sufficient for any ammonoid during the final catastrophe.

Tolerance of Extremes

Many physiological characteristics were likely shaped by extreme conditions, such as those during a biotic crisis [13]. For example, the end-Permian mass extinction was apparently less severe for animals tolerant of hypercapnia (a high concentration of CO₂ in the blood) [14]. Cessation of activity during one or more life stages probably also enabled lineages to persist through times of prolonged stress [13]. This capacity might have helped small mammals to weather the end-Cretaceous extinction, as exemplified by tenrecs (mammals endemic to Madagascar), which estivate for periods of up to 9 months [15]. Proxies observable in fossils will be needed for inferring metabolic cessation and ascertaining how this capacity evolved.

An important open question is whether species with low-energy modes of life, such as brachiopods and stalked crinoids, can achieve the near-inanimate state, or whether this capacity exists only in animals and plants with high metabolic performance during favorable periods. The answer might be group specific. Brachiopods and crinoids took great losses during the end-Permian crisis, and their living representatives do not seem capable of persisting in a prolonged inanimate state. By contrast, mosses are low-energy plants that can survive for long periods in a completely dried-out condition [16], and were apparently little affected during the mass extinctions. More energy-intensive plants with resistant spores and seeds can shut down metabolism for extended periods and were also unlikely to be as adversely affected as species without such inanimate life stages. Finding proxies for metabolic cessation and mapping that capacity on phylogenies will help to infer tolerances of fossil species and changes in tolerance over time.

Extreme warmth will confront many species in the future. Sea surface temperatures (SSTs) above 31°C, which under open-sea conditions are today confined to restricted areas such as the Persian Gulf, will become widespread. In fact, tropical seas might reach temperatures not seen since the mid-Cretaceous [120–90 million years ago (Ma)] when SSTs reached 36°C in the tropics and 31–35°C even at mid latitudes [17]. Evaluating which taxa were able to tolerate or thrive during the hot Cretaceous could offer insights into the kinds of organism that could do so in the future.

Given that oxygen concentrations in water fall as temperatures rise, aerial respiration is likely essential for high-functioning aquatic animals at elevated temperatures. This hypothesis can be tested first by establishing proxies for high-temperature tolerance that can be observed in fossils, and second by examining patterns of differential survival of taxa during the mid-Cretaceous and also during the Early Triassic, when conditions might have been even hotter [18,19].

Terrestrial endotherms and all tropical organisms function close to their upper thermal limits [20,21]. For subtropical and temperate land plants, a mean temperature of 21.4 + 2.2°C appears to yield the maximum average photosynthetic rate [22]. As temperatures rise, these tolerances and maxima will be severely tested. Internal homeostatic thermoregulation and behavioral choice of thermal environments are options available to mobile animals but not to plants or

attached marine animals. Fossil discoveries can complement work on living species to determine how thermal tolerances and other environmental limits work and how they can expand.

Biom mineralization

The increased acidification of the ocean as CO₂ levels continue to rise interferes with the precipitation of calcium carbonate (CaCO₃) in many species. However, the fossil record indicates that calcifying organisms built robust skeletons during times when long-term CO₂ levels were high, as during the Devonian, Jurassic, and Cretaceous [23,24]. How they did this remains largely unknown, and reliable proxies for resistance to acidification have not yet been identified. One possibility is that, because sources and sinks of CO₂ were balanced, waters were not highly acidic [25,26]. Another is that, as in most species today, mineralization occurs beneath a dissolution-resistant organic layer [27]. Still another possibility is that organisms whose skeletons comprise calcite are more resistant to acidification than those precipitating the less-stable mineral aragonite.

Among photosymbiotic foraminifers, the ability to calcify at low pH depends on which source of carbon the symbionts use. Diatoms, whose principal source is dissolved CO₂, make their foraminiferan hosts resistant to low pH, whereas dinoflagellates, which use bicarbonate HCO³⁻, increase the vulnerability of their hosts [28]. It remains unclear how calcification by free-living or symbiotic bacteria [29] is affected by acidification. Calcification crises occurred during several sudden brief spikes in CO₂, often coinciding with mass extinctions [30–32], but even then many biom mineralizing lineages survived [33–36]. Calcifying lineages that disappeared did so in response to factors other than ocean chemistry [34].

The larval stage is the most vulnerable period of calcification and other metabolic processes under stress, as established for bivalves [37] and sea urchins [38], and as suggested for the last-surviving ammonoids [39]. Future calcification crises may be worst for species with small planktonic stages, manifested in excessive costs involving allocation of ATP [38].

Corals

With some exceptions, reef-building corals and their symbionts (the dinoflagellate *Symbiodinium*) thrive in warm, nutrient-poor, well-oxygenated marine waters. Uniformitarian logic implies that ancient reefs built by photosymbioses arose under similar circumstances, but is undermined by two facts. First, many reef-builders thought to have housed photosymbionts lived in turbid, more nutrient-rich waters [40]. Second, molecular data show that *Symbiodinium* has an Early Eocene origin [41], implying that earlier symbioses relied on other light-demanding mutualists with potentially higher tolerances for low light, turbidity, and the thermal conditions [40]. In future work, proxies are needed that reflect physiological tolerances, activity, and limitations in symbioses not based on *Symbiodinium*. At least for photosymbiotic bivalves, diagnostic isotopic signatures are of limited value in fossils because they are expressed mainly in lipids and bulk organic matter, which decay soon after the bivalve dies [42]. Skeletal isotopes may still be useful [43] in combination with morphology for identifying and characterizing fossil photosymbioses [44]. Such work may show how healthy photosynthetic reefs can exist in a future of higher temperatures and acidity, as they did in the past.

Vertebrates

Progress in paleophysiology based on reliable proxies has been especially dramatic in the study of vertebrates and plants. Extensive bone remodeling, for example, implies rapid growth in vertebrates, and temperature-dependent isotopic signatures in bone tissue permit inferences about body temperatures in fossils. It has become clear from these lines of evidence and from metabolic models that Mesozoic reptiles were able to maintain high growth rates and a high

body temperature [45–50], but debate still rages about whether these animals were true endotherms. Recent work indicates that a high diversity of melanosomes, associated with melanin-based coloration, is a good proxy for high metabolic rate in vertebrates, and that pterosaurs and dinosaurs excluding maniraptorans (the group including birds) had a low diversity of melanosomes, implying slower metabolism [51]. The barb structure of feathers, together with changes in the functional relation between the tail region and the anterior appendages (wings) during the transition from theropod ancestors to true birds, indicates that endothermy in birds evolved during the Cretaceous, well after the Late Jurassic origin of gliding flight in the bird clade [52,53].

It remains unclear when mammalian endothermy arose. Most mammals, similar to dinosaurs and birds, move with the limbs held directly beneath the body, a posture enabling rapid and sustained locomotion associated with a high metabolic rate. The synapsid ancestors of mammals tended to have a more sprawling posture, as in ectothermic lizards, with the limbs held to the side of the body, although transitions to a more erect posture of the hind limbs characterizes some Permian and Triassic forms [54]. The presence of turbinates (structures in the nasal cavity that conserve moisture during breathing) has been taken as a proxy for endothermy [55,56]. The rapid growth of Permo-Triassic therapsids [57–59] likely indicates high activity levels, but the transition to endothermy, marked by the appearance of turbinates, appears to be a Late Triassic event coinciding with the origin of small mammaliaforms.

Plants

Land plants face a functional trade-off between carbon acquisition and water loss [60]. Gas exchange with the atmosphere takes place via pores (stomata) on leaves and stems. A low stomatal density, measured by the stomatal:nonstomatal cell ratio, limits water loss but also means a low uptake of CO₂, a low photosynthetic capacity and, in large sun-exposed leaves, the potential for overheating. The low stomatal density of Devonian and most Mesozoic plants indicates high CO₂ levels and high water-use efficiency [61–64]. During the Late Paleozoic (Late Carboniferous and Permian), when atmospheric oxygen levels were at least 20% higher than current levels and the CO₂ partial pressure was perhaps as low as that during the Pleistocene, the high cost of photorespiration would have limited plant productivity [63] in the absence of specialized carbon-concentrating mechanisms. Among flowering plants adapted to freshwater or to dry, high-oxygen conditions of the later Cenozoic, two carbon-concentrating mechanisms have repeatedly evolved, the crassulacean acid metabolic pathway (CAM) and C₄ photosynthesis [65,66].

A third mechanism, the lycopsid photosynthetic pathway (LPP), occurs in living freshwater species of Isoetes, and likely characterized tree-like lycopsids of Late Paleozoic swamplands [60], relieving somewhat the carbon-transpiration trade-off and enabling rapid growth. One of the most useful proxies for inferring paleophysiology has been established in land plants. Experiments have demonstrated a fundamental link between the density of veins (total vein length per unit leaf area) and photosynthetic capacity [67–70]. Before the mid-Cretaceous (110–100 Ma), photosynthetic capacity was evidently low, as indicated by low vein densities on fossil leaves. Thereafter, with the evolution of angiosperms (especially dicots), it increased three- to fourfold as conducting structures became smaller [67,71]. This transition began when CO₂ levels were high but continued as those levels reduced during the Cenozoic [67], in part because angiosperms and, to a lesser extent, gymnosperms achieved active control over stomatal opening and closing [72–74].

Physiologists tend to evaluate plant performance with factors such as temperature, precipitation, soil moisture, and mineral content, and atmospheric gas composition. However, plants also respond to herbivory. Caswell and colleagues [75] suggested that innovations such as CAM and C₄ photosynthesis were favored as adaptive responses to insect herbivory because the

photosynthetic machinery is situated well beneath the leaf surface. Nevertheless, the LPP of the Late Paleozoic evolved at a time before the widespread appearance of herbivores. A role for herbivory should also be considered in the evolution of high leaf-vein densities. In any case, proxies for physiological performance, such as the presence of carbon-concentrating mechanisms and leaf-vein density, must be evaluated carefully with respect to both abiotic factors and biotic agencies, such as herbivory and competition. Similar concerns apply to aquatic photosynthesizers, for which proxies of performance have yet to be developed. Experiments show that planktonic Cenozoic diatoms and coccolithophorids need more light and a higher supply of land-derived nutrients compared with more ancient phytoplankton groups [76].

These new groups have prospered as increased mountain building and the expansion of grasslands fertilized the ocean [76–79]. In attached seaweeds, rapid nutrient uptake and transport is indicated by a highly branched morphology and, in species with large blades, a complex 3D surface [80,81]. Mapping of these potential proxies for performance on algal phylogenies can indicate how performance has evolved over time and the extent to which performance is related to CO₂ levels and to escalating herbivory in the sea [82–84].

Concluding Remarks

The most cogent reason to study paleophysiology is to understand how organisms of the past dealt with circumstances that had much in common with those projected for the future. By examining patterns of extinction and survival during past times good and bad, we can gain insight into what worked and what did not. Importantly, fossils offer a range of phenotypes and physiologies that are rare or absent in the modern biota. By sampling them and inferring their performance levels, we have available to us adaptive possibilities that are inaccessible among living species.

Table 1. Summary of Proven or Promising Approaches for Inferring Paleophysiology

Process or group	Approach
Accretionary growth	Rate of spiral expansion of shell
	Convexity of valves
	Complexity of apertural rim
Muscular movement	Muscle mass:total body mass ratio
Tolerance of extremes	Mapping tolerance on phylogeny
Biomineralization	Markers for different sources of carbon
	Markers for microbial activity at different pH
	Effect of organic layers at different pH
Photosymbiosis	Exposure of tissues to light
	Isotopic fractionation due to photosynthesis
Vertebrate metabolism	Histology related to bone remodeling
	Presence of turbinates in nasal cavity
	Temperature-sensitive isotopic fractionation
	Diversity of melanosomes
Land plants	Stomatal density and metabolic control
	Leaf-vein density
	CAK and C ⁴ morphological indicators
All processes	Mapping performance on phylogeny

A particularly important question is how future changes affect species with different ecological roles, from primary producers to apex predators (see Outstanding Questions Box). Did (and do) systematic differences in tolerance, activity, and metabolic flexibility exist among producers and consumers, and how did (and will) physiological traits affect the structure and sustainability of ecosystems? Answers require that we think of organisms not as abstractions or mere markers of past or current environments, but as working wholes adapted to their physical and biotic surroundings (Table 1).

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Outstanding Questions

Can shell form in bivalves and brachiopods, especially valve convexity, be used as a proxy for growth rate and metabolic rate? Validation of such a proxy, for which preliminary evidence exists, will require controlled experiments with living bivalved animals.

Can muscle mass relative to body mass be used as a proxy for metabolic activity in fossil mobile animals, such as cephalopods and vertebrates? Such a proxy would require measurements of locomotor-muscle attachment to skeletal elements, and be verified by experiments and measurements on living animals.

Can phylogenetic analysis be used to infer thermal and other stress tolerances of fossil organisms? Can potential proxies for such tolerances be developed that are observable in fossils? This is important because past conditions and extremes may resemble some future circumstances.

Can proxies of photosynthetic capacity comparable to leaf-vein density in land plants be developed for attached aquatic plants and algae? This is important because there is evidence pointing to increases in photosynthetic capacity over time in land plants, and some phylogenetic evidence pointing to a similar conclusion in seaweeds.

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