Predation to climate change: what does a fossil shell tell us?

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Paleobiology is a growing field where researchers are primarily interested to reconstruct the past biosphere using a truly interdisciplinary approach. The effect of biotic and abiotic agents of natural selection influencing an organism's ecology and evolution is a question that intrigued ecologists and paleobiologists alike. Study of such interaction in deep time using the marine fossil record presents some unique challenges. In this article, I have tried to share my personal account of such challenges and subsequent developments where I was involved as a researcher working on this topic.

Keywords: Fossil, mollusca, paleoecology, paleoclimate.

Introduction

ON his historical trip to Galapagos islands, one of young Darwin's favourite read was a book that came out just the year before. It was Charles Lyell's *Principles of Geology*. The key aspect of the book was the concept and importance of time. Lyell emphasized that large changes could be brought upon on the surface of the Earth by very slow natural changes accumulated over enormously long span of time. Large mountains could be levelled off by work of wind and river over millions of years. Being an avid naturalist, Darwin was moved by this idea and spinned it towards animal kingdom. He started to wonder what will happen to organisms if they accumulate very small, heritable changes through generations for a very long time. As we all know, this simple question eventually led to one of the most profound scientific ideas of 19th century, namely 'evolution through natural selection'.

The relationship between biology and geology did not end there; it started before Darwin and continued long after. Starting from 17th century, we find geologists digging out old lives in the form of fossils to understand how sediments turn into rocks. In the 18th and 19th century, we find paleontologists studying fossil forms and often using them as time markers. The 20th century saw the rise of a new breed of researchers, paleobiologists, who are interested in fossils not just as time markers, but as windows to understand the biosphere of long lost ages.

As a paleobiologist, my interest is in some of the very old questions that intrigued Darwin. What are the natural triggers of evolution? The answer simply points to the two existing types of triggers: biotic (such as predation, competition) and abiotic (such as change in substrate, nutrient, temperature). Although simple, this question troubled researchers for ages. Primarily, because of the disconnect between ecological and evolutionary time-scale. Are the triggers that affect a population in an ecological time-scale (decades) likely to leave an impression in evolutionary time-scale (millions of years)[1]? Now, this question is quite difficult to answer by studying only living organisms. Evolutionary paleoecology addresses this question by studying such ecological processes and evaluating their evolutionary response in deep time.

Molluscan fossil record

Just like any other discipline, we need a model group that can be studied for answering the questions of interest. Because it involves fossils, we need a group that has a high potential to be fossilized. Contrary to popular beliefs, dinosaurs are not very good when it comes to paleoecological study that demands large data. Being terrestrial organisms, they are less likely to get preserved. Even when they do, the numbers are too low to be studied at a population level. We want a group that would come in large batches to give us meaningful data about their population. Marine fauna is usually better preserved compared to their terrestrial cousins because they suffer less disturbance due to quick burial inside sediments under water once they die. The water column and sediment blanket above their dead body work as shields to protect them from natural vagaries. Among marine organisms, molluscs (such as clams, snails, squids, etc.) are one of the most abundant groups. Majority of them have hard mineralized shells which make them durable. They also have a long evolutionary history dating as far back as ~540 my. They occupy a variety of ecological niche and play important role in the trophic structure. The added advantage of choosing mollusc as a model group is the fact that many of the members of this group still survive today. So, we can study and experiment with the live

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molluscs to understand the response of their fossilized great-grand-parents.

Biotic interaction in the fossil record

Everything said and done, the key issue to recognize biotic interaction in the fossil record remains challenging even for a popular group like mollusc. Let us take the case of one important biotic interaction: predation. Many groups prey upon other groups by swallowing them whole; naturally, this leaves almost no evidence of predation in the fossil record. There are instances where the predator was 'caught-in-the-act' while preying upon an animal. These unusual preservations are very rare and cannot be used for a quantitative study. So we should again look for a record of predation that is common yet informative. Shell crushing predators, such as crabs, often attack molluscs. If they are successful, they completely crush the shell. If they are not, which is not very uncommon, they end up damaging only a part of the shell. Because molluscs grow by adding new materials to their existing shell throughout life, they often regrow the shell around the injury leaving a 'repair scar' denoting the experience of that near miss. When fossilized, these shells along with the 'repair scar' represent unsuccessful predation events. The record gets even better with another type of predation where carnivorous snails (gastropods) drill their hard-shelled prey (such as snail, clam) and consume the soft part. In such drilling predation, after a lethal attack, the prey is left with a shell marked by a 'drill hole' completely penetrating the shell; an 'incomplete drill hole' is created when the attack is unsuccessful (Figure 1). The beauty of this record is in its informativeness. The drilled shell provides us with the identity and size (and therefore growth age) of the prey. The drill hole shape and size tell us the same about the predatory group. The exact relationship between predator size, and the drill hole it can create, has been worked out using their live counterparts[2,3]. These experiments also illustrate how much time would it take for a predator to complete the task of drilling. This basic information about the predator and its prey helps us to build a 'cost-benefit model' that evaluates the net energy gain for a specific predator-prey pair. Using predator-prey pairs from ancient ecosystems, we can then try to evaluate if the predators developed a specific choice of prey (in terms of species, size) or if their choice is evolving through time. In a study of Miocene (~20 my) marine assemblage from Kutch, we showed that the predators were choosing their bivalve preys non-randomly to maximize the net energy gain[4]. At times, they become cannibalistic when their preferred group is not abundant[5]. Occasionally, the predators show an interesting behaviour that seems like a deviation from their success; that is when they produce a lot of incomplete drill holes. This pattern was initially thought to be a classic case of co-evolution where the prey is putting up an evolutionary resistance by getting thicker and hence causing the predator to fail[6]. This view, however, is not always supported by data as the shell thickness increase was not significant. A closer look at the system revealed a complicated dynamics. We find that the predators do not just fail, they choose to fail[7]. However funny it may seem, failing often is the best scenario to ensure bigger gains. These predators live above or just below the sediment surface under the sea. But when they hunt, they come to the sediment surface and often spend a considerable amount of time manipulating the prey. This is the most vulnerable time for a driller because it is a 'sitting duck' to its own predator, such as a crab. Abandoning a prey midway into a drilling attack means a chance for the driller to escape its own predator: a dinner is better to skip if that costs someone's own life. Using drill hole and repair scar data, we demonstrated that such behaviour is indeed common in ecosystems as old as 5 my (ref. 8). Although, we have found such behaviour long ago, there are other characters that evolved fairly recently[9]. Some anti-predatory strategies, that used to be effective defences for the prey, loses its effectiveness through time. Using a variety of drill hole data from groups with different habitats, we demonstrated how some of the life modes, that were effective defence for prey previously, have become obsolete in modern times[10]. It leads to the development of newer strategies in prey and such reciprocal evolution between predator and prey is still in progress.

Archive of abiotic triggers

Shifting gears from biotic interaction, we now look at important abiotic interactions. It has been documented that with change in climatic condition, marine groups may change their life habit and size[11]. If we want to observe such changes through time, we need to find a way to reconstruct past climate along with response of the animal witnessing the change. The best scenario would be if we could reconstruct it from the same animal, more precisely, the same individual. It sounds too good to be true; but that's what clams are. As I mentioned earlier, clams grow by adding new shell materials every season throughout their life. They use the dissolved calcium carbonate from the sea water to do it. Geochemically, they carry distinct signature of sea water in their shell of every season they saw during their lifetime. Even after death and through fossilization, many of them carry that signature intact. These are archives of past climate that can be reconstructed. What does the geochemical signature tell us? The composition of the shell can change with climate in two ways: (a) if the ratio of elements/isotopes in sea water changes with climatic shifts; and (b) if the intake of specific element/isotope by the organism is a function of ambient temperature. Using this principle, it is possible to

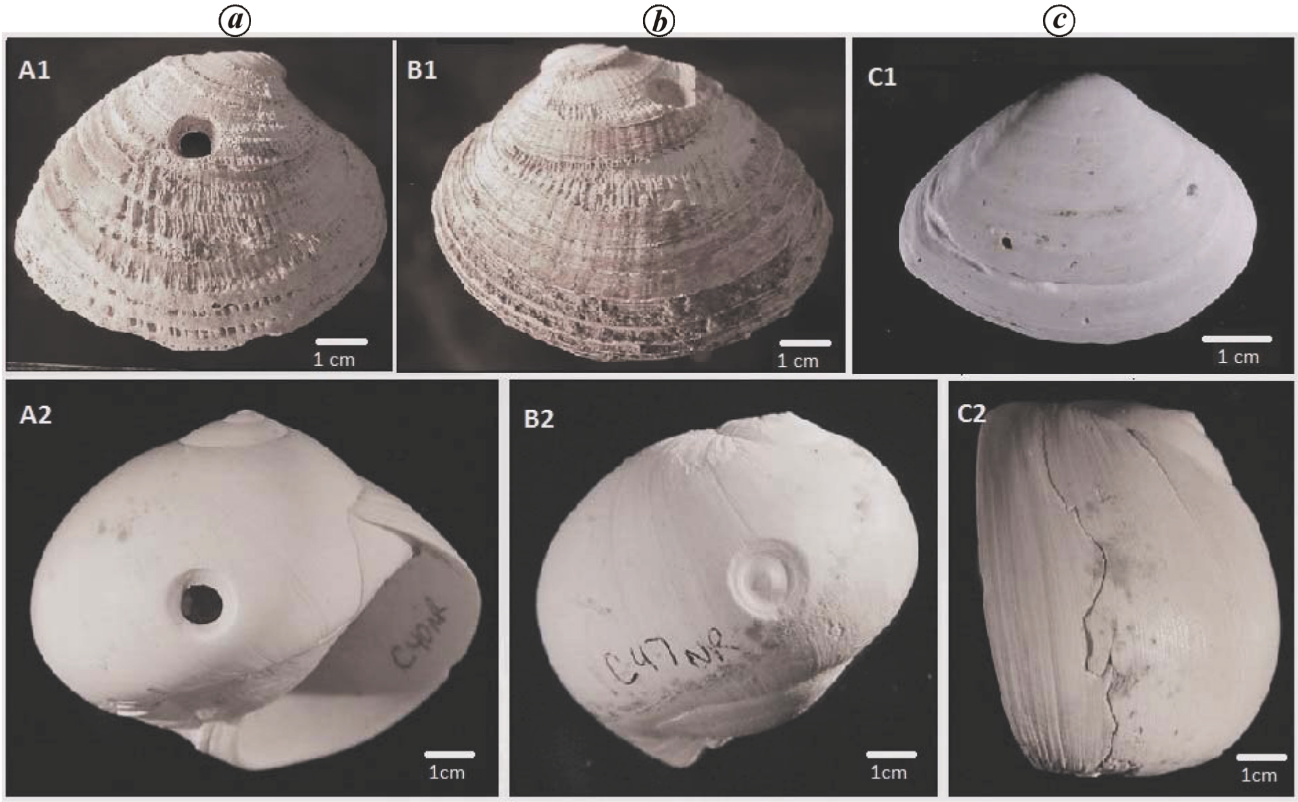

Figure 1. Record of predation in fossil shells. The top panel represents the predation marks in clam shells (bivalves) and the bottom panel represents scenario where the prey is a snail (gastropod). ***a***, Successful attack by a carnivorous snail resulting in a complete drillhole on prey shell. ***b***, Unsuccessful attack by a carnivorous snail resulting in incomplete drillhole on prey shell. ***c***, Unsuccessful attack by a shell-crushing predator resulting in 'repair scar' as the prey shell regrew its shell after the injury.

reconstruct the past climate with reasonable accuracy from a clam shell. It is also possible to do it at seasonal level by sampling the growth bands of fossil clam[12]. Let us take an example of a common paleoclimatic proxy: the oxygen isotopic ratio. The oxygen stable isotope ratio is one of the most widely used paleoclimatic proxies. It comes in three stable isotopes (^{16}O, ^{17}O and ^{18}O) that shows different proportion in natural Earth material due to fractionation (process that partitioned the isotopes) and mixing (processes that assimilated the isotopes). Fractionations could be of two kinds, isotope-exchange reactions and kinetic effects. Molecules with heavy isotopes tend to be less reactive because they have slightly higher covalent bond strength and lower vibrational frequencies as compared to the lighter ones. Consequently, evaporation – a natural fractionation process – slightly favours ^{16}O. This, in the long run, may change the isotopic ratio of sea water between times of glaciation and deglaciation. During glaciation, the ice sheet starts to expand from the poles. Ice sheets are expected to be rich in ^{16}O (isotopically depleted) because they are generated from high-latitude water vapour, that is itself depleted through evaporation and condensation during its long journey from the ocean to the pole. Therefore, the glaciation would leave the ocean isotopically enriched[13]. This is one instance when the original isotopic composition of sea water would change due to climatic shift and would be reflected by the shell composition of the animals that were living at the sea. However, this is not the only reason why we may expect to see difference in isotopic ratios in an organism due to climatic fluctuation. There are organisms which show differential preference for isotopes as a function of temperature even though the sea water composition remains the same. Mollusc is one such group that shows varying oxygen isotopic ratio in their carbonate shell depending on the temperature of precipitation[14]. The sea water composition through times of glaciation and deglaciation is relatively well constrained. Using that information, we can use the isotopic ratio of mollusc shells to reconstruct the paleoclimate. Although discussed specifically about clams, there are skeletons of other marine organisms that can be used in a similar way.

Response to abiotic triggers

Groups respond ecologically to their ambient physical environment, often by changing their size, shape or

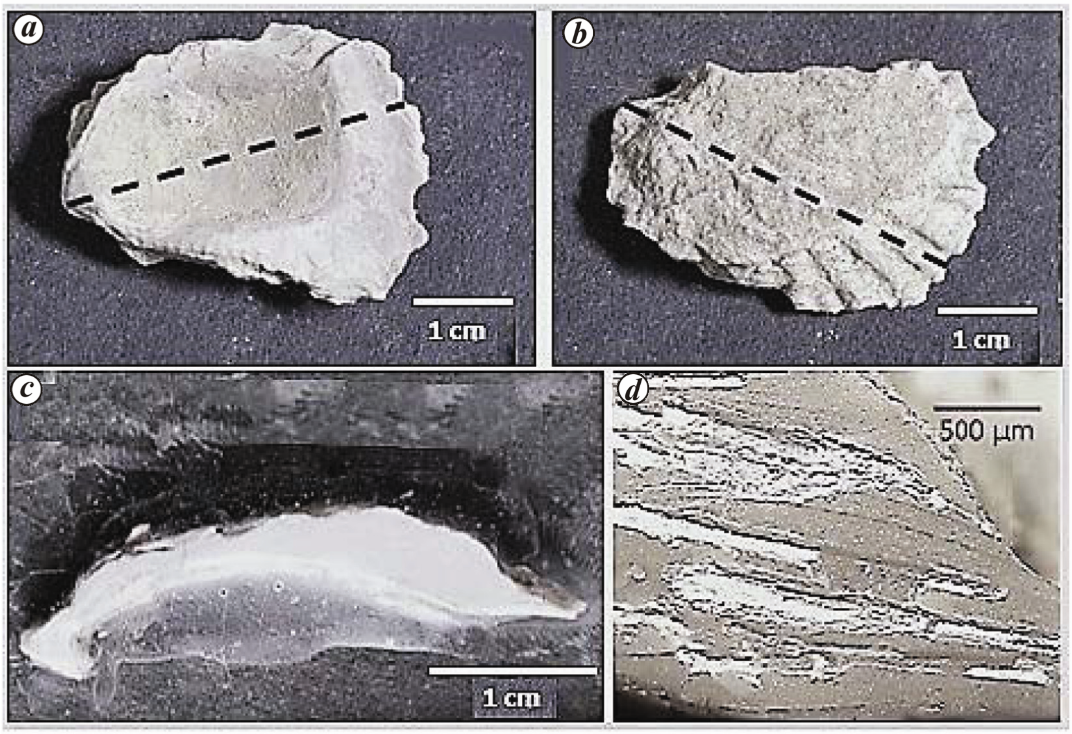

Figure 2. Processing fossil shells for paleoclimatic analysis. The top row shows a fossil clam shell. ***a***, internal view; ***b***, external view. The dashed line marks the line along which a cross-section is prepared; ***c***, A mounted section of the above shell; ***d***, A photomicrograph of the section showing annual growth bands of the shell. The white parts are the places from where we took out powdered samples by microdrilling for relevant geochemical analysis.

community composition. This pattern is very obvious for terrestrial organisms, but not unheard of among marine groups. The drastic effect of recent climatic shifts on polar marine biota is obvious. A relatively unappreciated aspect is the effect of climatic shifts on tropical marine ecosystem. While, on one hand, tropical climatic shifts are not as drastic as polar regions (even during warming), on the other, the tropical biota is very sensitive to the slightest change (unlike their temperate cousins). So, it is not obvious exactly how would a tropical ecosystem behave in the face of a climatic perturbance. To evaluate the effect on tropical marine biota, we decided to study a 20 my old marine ecosystem of India, Miocene of Kutch.

To study this ecosystem, we, the members of paleontology research group at IISEE Kolkata, literally had to walk on the sea – an ancient sea bed exposed in the barren lands of Kutch, preserving hundreds of clams, snails and other sea creatures. After days of painstaking hammer and chisel work, we took out fossils and brought them to our laboratory. Few of us studied the groups for their identity, size, shape and finally recreated the details of their community structure. The others made sections of the clam shells and took micro-samples from specific areas of growth bands through a computerized sampling apparatus. The powdered micro-samples were then sent to the geochemical laboratories for analysing their elementary/isotopic characteristics (Figure 2).

Using oxygen isotopic ratio as a paleoclimatic proxy from clams of Kutch, we found a significant change in climatic signal around 20 my; the climate warmed up resulting in an ecosystem reshuffling. Our ongoing research shows that the dominant molluscan groups before the warming event, such as oysters, took a back seat and less conspicuous groups like scallops came to the lead[15]. Moreover, we found a significant size decrease in all species of clams that coincided with the warming[16].

Doubts

Doubts are an important component of scientific journey. That is what makes us cautious and keeps us vigilant. Apart from all the reconstruction discussed before, we also do ‘doubt’ our own data – the formal name for it is ‘evaluating taphonomic bias’. Taphonomy is the study that focusses on the process of fossilization and hence can raise serious ‘doubts’ about the validity of paleobiological data in representing biological truth. The underlying assumption for any paleobiological reconstruction is that the fossils represent the true biological community, may be incompletely (random subset), but not with any bias (non-random subset). Consequently, it is absolutely necessary for us to be certain about the quality of the record. We approach this problem by running experiments with recent shells to simulate the fossilization process and check the features that would indicate 'taphonomic bias'[17,18]. Once we identify such criteria, we try to build a numerical scheme to quantify levels of taphonomic alteration. This, in turn, helps us to identify the fossil assemblages that has undergone severe taphonomic alteration and should be removed to ensure the unbiased nature of sampling required for any paleoecologic study.

Looking forward

Interaction between organism and its environment (biotic and abiotic) is an old topic and has become increasingly more relevant with changes in global ecology due to human intervention. The future of this theme is in its interdisciplinarity which was appreciated by Darwin some 150 years ago. Now, paleobiology, is not just at the juncture of biology and geology; it involves almost all other disciplines (physics, chemistry, mathematics) disguised under different names such as biomechanics, isotope geochemistry, and climate modelling. However, even with all these changes one feature still remains the same; that is the fact that our data comes from fossils. Unfortunately, in India, we do not have large research museums and hence very limited scope to archive such valuable and slowly diminishing treasure for future researchers. Often valuable specimens, collected during a paleontologist's tenure, are neglected and lost after the person-in-charge retires from duty. Without good preservation practices, we are adding another level of taphonomic bias and permanently crippling our ability to deduce the true nature of paleobiological record. Hence, the need of the hour is a large research museum for paleontology with modern curatorial facilities. It is important to note that for paleobiologists, the best way to look forward is to look back – to look back at the billion-year long record of finest natural experiments.

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ACKNOWLEDGEMENTS. I would like to thank my mentor, collaborators and students without whom this journey would not have been possible. Majority of the work was conducted at the University of Michigan, IISER Kolkata and University of Vienna which provided the necessary infrastructure. The research was funded by government and non-government funding organizations in USA, India and Austria.

doi: 10.18520/cs/v112/i07/1489-1493