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CHAPTER

14

Armor: Why, When, and How

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"Der Welten Kleines auch ist wunderbar und groß, und aus dem Kleinen bauen sich die Welten"—Gottlieb Christian Ehrenberg (1795–1876), motto of his Ph.D. thesis and the inscription on his gravestone.

Armor implies physical defense against attack by other organisms and is hence distinct from mechanical structures that confer protection or provide support against nonbiological environmental stressors. A comparison between armor-plated, military and streamlined, civilian vehicles illustrates this difference. Human history teaches us that the arms race is a powerful driving force in the evolution of technology. This principle—the evolving interaction between attack and defense mechanisms and techniques—also applies to Darwinian evolution, except that natural selection takes the place of intelligent design.

The fitness of an individual organism is expressed in the degree of its ability to gather resources and avoid becoming a resource itself—bottom-up and top-down selection, respectively. In both cases, the organism is competing with its neighbors, either for resources with those of the same trophic level or for avoidance of becoming a resource with those sharing the same enemy ranging from specific pathogens and parasites to predators. The co-evolution of specific attack and defense systems is well documented in terrestrial and benthic biota (Ehrlich and Raven 1964; John *et al.* 1992; Rausher 2001).

In contrast, planktologists have traditionally focused on bottom-up competition within the growth environment and neglected organismal properties that promote survival in the mortality environment, defined by Smetacek *et al.* (2004). Chemical defense systems are currently attracting attention (Cembella 2003), but mechanical defenses are still poorly appreciated. Indeed, the relationship between form and function in protistan plankton remains largely mysterious (Sournia 1982).

In this chapter, we provide a brief history of the conceptual framework of plankton evolutionary ecology to explain why the role of defense in the evolution of unicellular plankton has been neglected so far. The aim of this historical overview is also to point out what can be learned from studying the arms race: the other side of the coin. Given the range of attack techniques to which protists are exposed—from viruses to zooplankton—we define armor as all forms of mechanical defense against pathogens, parasites, and ingestors. These in turn will range from slimy or tough cell walls that hamper purchase, bar entry, or withstand puncturing to long spines that deter ingestion. Following a brief comparison with terrestrial systems we expand on the argument, first broached by Smetacek (2001), that evolution of eukaryotes in the plankton is driven by the arms race. To this end, we survey the range of attack systems evolved by pathogens, parasites, and predators in the plankton, align them with their respective defense systems, and speculate on their evolutionary history. In the final section, we examine how the various types of armor (cell walls, scales, frustules, and colony skin) of selected groups provide protection against specific forms of attack.

I. WHY ARMOR

Early life forms assembled organic molecules from the environment to build themselves and fuel their growth. Evolution at this stage will have been driven by resource competition and death caused by resource deprivation: ultimately, the energy required to maintain cellular structures. Dead organisms will have represented a new type of resource whose utilization could be hastened by deployment of exo-enzymes. The arms race began when living organisms were killed by exo-enzymes—the transition from scavenger to predator. The origin of protective layers of slime and, ultimately, cell walls, that is, armor, was an inevitable result. Indeed, the universality of cell walls in unicellular plankton might well be a reason why their role in selection has been taken for granted and hence overlooked.

To understand the role of armor in individual selection, one needs to observe its performance under various forms of attack in the mortality environment. In the case of larger organisms, the relationships between form and function can be assessed by visual observation and tested with straight-forward experiments. In contrast, interactions among unicellular organisms are difficult to observe because microscopes, in contrast to telescopes and binoculars, do not reveal the required breadth and depth of focus. Because nobody has watched protistan interactions in the wild, our assumptions of plankton behavior are based on inference colored by the concepts applied.

A. History of the Concept "Armor" Applied to Plankton

Like any concept transplanted from the realm of human sensory experience to a realm outside of it (in this case the pelagial or pelagic environment inhabited by the plankton), the word "armor" carries with it roots, the subliminal connotations that influence the ramifications of the concept in its new, theoretical environment. We illustrate this effect by contrasting the connotations of the English word armor with its German counterpart "Panzer." Whereas armor is associated with steel,

whether the coat of mail worn by knights or the projectile-proof plates of military vehicles and ships still in use today (dictionary definition), Panzer has broader connotations reflected in its wider usage: Panzernashorn: one-horned rhinoceros, Schildkrötenpanzer: the shells of a tortoise, but also Panzerglas: bullet-proof glass and simply Panzer: tank (armored vehicle).

So it is not surprising that the 19th-century German-speaking scientists, who were the first to systematically study protists, freely used the word Panzer to describe protistan cell walls that their English-speaking colleagues substituted with the more ambiguous "shell." In English "armored plankton" does have the ring of scientific hyperbole if not overkill. In the few instances where armor has entered English terminology, for example, dinoflagellates, the connotations are of ornamentation rather than defense. However, the pioneers of protistan ecology clearly had defense on their mind, otherwise they would have chosen other widely used German terms with differing connotations: *Gehäuse* derived from *Haus* (house), which implies protective structure in a broader sense, that is, also against the physical environment (as in snails), or *Außenskelett* (exoskeleton), which implies a shape-giving, supportive function (as in arthropods) but does not exclude defense.

The impression of the early researchers who interpreted apparently tough outer walls as defense is exemplified by Ehrenberg's (1838) description of diatoms as Panzertierchen (armored little animals) implying that their silica shell protected them against a range of potential predators. In his Latin description of the taxon "Bacillaria" he also used "lorica" (cuirass or corselet worn by Roman soldiers), the French description contains the word "carapace."

Defense is defined by attack. However, attack and defense systems were not studied systematically by any of the early microbial naturalists. Methodological constraints were one of the reasons; another, the rise of taxonomy accompanied by its increasing attention to details of the armor as criteria to differentiate species. Not surprisingly, the large armored forms were the first to receive attention by taxonomists and the numbers of species required specialization. Because species have to be defined on the basis of objective criteria, taxonomists reveled in the custom of using dead languages to coin new names and concepts bereft of subjective roots. This sterile jargon is aimed at curbing imagination instead of stimulating it. Ernst Haeckel is an outstanding example of this trend: He described hundreds of Radiolaria species (Haeckel 1862) and was apparently so overwhelmed by the sheer diversity of forms that he was unable to imagine an equivalent range of functions to which these forms might be attributed.

The way out of the dilemma was to declare that there was no function, that the forms were produced by an underlying natural law that automatically generated pattern expressed in the variety of shapes. In a textbook of general zoology, Haeckel (1866) introduced this concept and termed the mysterious driving force the morphogenetic basic law (*Grundgesetz*), which he compared to an organic crystallography. Haeckel was a bold thinker looking for rules to organize the bewildering diversity of organisms being described at the time. He was the champion of Darwinian evolution in Germany and ferociously antireligious. Nevertheless, his concept of an internal programing of organic matter that manifests itself in the shape of whole organisms is ultimately the internalization of intentional design. Natural selection is the quality control of this exuberant, prodigious shape maker. Because random mutation within the genome was not known at the time, Haeckel can be forgiven for focusing on appreciation rather than explanation of planktonic forms. Haeckel's famous and influential coffee table book *Art Forms of Nature* (1904) was strongly influenced by *A Handbook of Ornament* (Meyer 1888), which probably strengthened the perception that biogenic forms are often "artistic" rather than functional (Figure 1).

However, the etymology of "ornamental forms" reflects its deeper roots. Ornament is derived from the Latin ornamentum, meaning "equipment, trappings, embellishment." Ornament's original function was understood to exceed mere decoration and to serve as a way of equipping a person for ceremony or battle. Similarly, the Sanskrit term for ornament, alamkara, encompasses meanings that include invigoration and making one fit.

Haeckel's influence was so pervasive that attributing functions to the diversity of planktonic forms appeared a hopeless task (Smetacek *et al.* 2002). This was in contrast to invertebrate biologists who took delight in relating form to function in their graphic descriptions of the feeding behavior of the various types of meroplanktonic larvae (Hardy 1956). The last systematic attempt at relating form and function in unicellular plankton is that of Sournia (1982), who gave up in despair and appealed to planktologists to ask their children for clues. But were not these the early innocent observers exemplified by Ehrenberg who looked at the plankton with childlike eyes and whose visionary descriptions (Ehrenberg 1838) were later buried in the plethora of overwhelming detail?

A different note was struck by Hensen (1887), who coined the term plankton and also launched biological oceanography on the agricultural paradigm. He insisted that diatoms were not part of the food chain leading to fish because they consisted of little more than the worthless silica ("wertlose Kieselerde"), that is, they were all shell with little content and not worth eating. This can also be interpreted as a form of mechanical defense in which volume and not necessarily strength of the coating is significant.

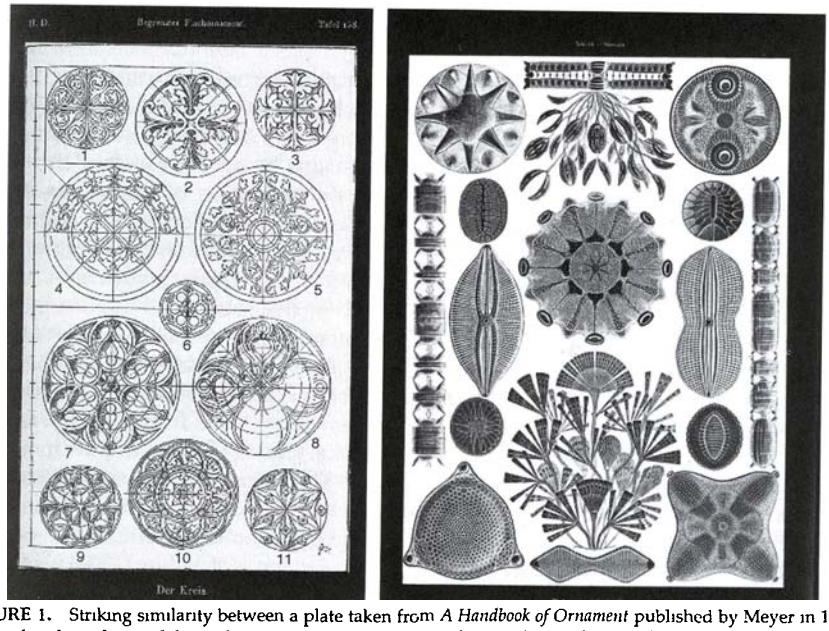

FIGURE 1. Striking similarity between a plate taken from *A Handbook of Ornament* published by Meyer in 1888 and a plate from the much better known Haeckel's *Art Forms of Nature* (1904) One is left with the impression that planktonic shapes are mere ornament.

His belief was based on general observations of dense diatom blooms subjected to little grazing pressure and his claim of the scarcity of diatoms in the copepod guts he examined.

Such a radical view provoked a number of studies that showed that diatoms were indeed eaten by a broad range of organisms (Smetacek *et al.* 2002). The accent of these studies was on proving that diatoms were not only edible but good food to boot on which a number of organisms thrived. Interestingly, the term grazing, with its connotations of sheep grazing on the lush grass of a meadow, was applied to copepod feeding. So phytoplankton, particularly diatoms, became the pastures of the sea, described with terms like yield and crop, all concepts that thrived in the fertile ground of the agricultural paradigm established by Hensen.

By the middle of the 20th century, the agricultural paradigm with its diatom-copepod-fish food-chain conceptual framework had developed into the cornerstone of biological oceanography (Raymont 1963) till it was side-tracked by discovery of the microbial "loop" (Pomeroy 1974; Azam *et al.* 1983). In the 1970s, ultrastructural studies of the mouthparts of the copepods revealed the presence of numerous chemoreceptors, which allowed a new insight into the potential of selective feeding of zooplankters (Friedmann and Strickler 1975).

During the 1980s, the application of high-speed cinematography revealed that copepod feeding movements were faster than the human eye could follow. The footage demonstrated that copepods actually fed selectively on a broad range of particles and exhibited complex handling techniques depending on the shape and size of the prey (Alcaraz *et al.* 1980; Paffenhöfer and Lewis 1990). The complex feeding behavior of the ubiquitous dinoflagellate genus *Protoperidinium* was another major discovery of the period (Jacobson 1999). These observations of selective grazing showed that there was ample scope for the evolution of defense mechanisms in the plankton but the implications were not immediately realized by mainstream pelagic ecology.

B. Why Should Protists and the Pelagial Be Different?

1. *The Terrestrial Analogy*

Biological oceanography was launched on a terrestrial paradigm at a time when agricultural thinking with its promise of easy quantification held sway. The aim of agriculture is to maximize production of desired properties (increase yield) and minimize that of undesired ones. In practice, crop defenses, both mechanical and chemical, are bred out by domestication because their function is fulfilled by fences and pesticides. The focus of bio-oceanography has accordingly been on the production and fate of biomass, that is, on the primary metabolites, reflected in the much greater effort spent on studying the growth as compared to the mortality environment (Smetacek *et al.* 2002).

To appreciate the efficiency of any defense, one has to first understand the form of attack against which it evolved. In the macrophyte realm, the fact that a plant, or a part of it, is eaten by some animal or infected by some pathogen or parasite does not mean that this is accomplished easily or that the plant is not effectively defended against a host of other potential enemies. Clearly, mechanical defenses such as the cuticles of leaves protect against desiccation, but they also deter the mycelia of parasitic fungi and the piercing mouth parts of many, but not all, insects and they are poor protection against ungulate grazing. The same can be said of the silica phytoliths of grasses and bamboos that aid in stiffening the plant (skeleton function) but also deter a host of herbivores including many, but not all, ungulates. Clearly, appropriate measurements can be made to discern when the degree of toughness of a protecting agent goes well beyond the requirements of a life-supporting function (preventing evaporation or maintaining

optimum rigidity against fluctuating environmental pressure) and becomes part of a life-protecting function, that is, defense. In terms used previously, when does a water tank become a Panzer?

In the pelagic realm, any photo-autotrophic population with a large number of small cells will be more competitive in resource acquisition than a species with equivalent biomass comprising fewer, hence larger, cells. This is a fact dictated by the physicochemical environment via the surface to volume ratio (s/v). So the evolution of eukaryote phytoplankton can only be explained in the light of the mortality environment where survival of both genomes, that of the photoautotrophic endosymbiont as well as its exosymbiont ingestor, results in a new organism with a novel combination of properties and with a smaller s/v ratio. However, growth rates of the autotroph in an endosymbiotic relationship will be lower than that of its free-living cousins not only because uptake of dissolved nutrients will be hampered by the host cell but also because a significant proportion of photosynthetic products will be diverted for its reproduction.

A possible exception would be under nutrient-limiting conditions if the host cell provisions its endosymbionts with nutrients derived from digestion of ingested particles. Such a mixotrophic relationship, although widespread, does not explain the dominance of eukaryote phytoplankton under the nutrient-replete conditions in which blooms develop. The more obvious advantage accruing to the endosymbiont is protection from ingestion by the predatory cousins of the ingesting cell, implying reduction in mortality rate of the endosymbiont (Smetacek 2001). In this connection we consider it more appropriate to refer to the form-giving organism of the endosymbiotic relationship as the exosymbiont rather than the host cell as the latter term has connotations of a parasitic or temporary condition rather than an integrated, mutually beneficial symbiosis.

Another reason why the evolution of defenses in the marine plankton has not received the attention it deserves is based on a widespread belief that an arms race cannot evolve among protists because the target of evolutionary selection is the individual cell. This is a serious misconception: in an asexually reproducing organism, the target of natural selection is the sum total of all the cells comprising the clone (Mayr 2001). In protistan plankton, the individual is a cloud of cells. So there is ample scope for predators to sample their food, learn to select easy-to-handle cells, and avoid others, thus driving evolution of mechanical and chemical defenses in populations of their prey species. So there is no reason why an arms race, equivalent to that in biomes dominated by multicellular plants, should not also be raging in the plankton.

C. Form and Function in Sessile and Drifting Photoautotrophs

The diversity of forms present in protistan plankton has always amazed the eye of the terrestrial beholder, because we are used to plants that come in standard, understandable shapes dictated by the physical environment and constrained by phylogeny. Thus, land plant lineages evolved trees in characteristic shapes but with a common principle: competition for light in the air and water and nutrients in the ground. The gravitational field coupled with wind energy selected the architecture and material properties of terrestrial plants (roots, trunks, and crown, cellulose fortified with lignin, respectively) as an optimal solution. The degree of freedom of shape ranges from that of the unbranched palm tree, the symmetrically branched conifer, to that of the standard branched tree. The phylogeny and function of each of these morphotypes are not only easily understood by us, we also use the tree as an abstract symbol to depict conceptual, organizational frameworks. Armor, in the form of thorns, tough cell walls, or thick bark, is clearly

of secondary importance in determining the overall shape. Even German-speaking botanists did not use the term Panzer when describing land plants.

The shapes of marine macrophytes differ, with the exception of sea grass, from those of land plants, but again, the range of shapes is restricted (from ribbons to filaments) and reflects the environmental energy of the habitat: the gradient from exposed rocky shores to secluded coral reefs. Interestingly, vascular plants have not succeeded in recolonizing the sea except for sea grasses, which seem to have colonized a habitat (sandy coasts) not occupied by macroalgae. The latter did not develop a root system to "hold on" to sandy beaches because nutrients are taken up by the photosynthetic tissue directly. This also applies to sea grasses, whose roots primarily function as holdfasts in soft sediment and secondarily for taking up interstitial nutrients. Although macrophytes, including sea grasses, occur along the entire range of nutrient concentrations prevalent in the sea, sophisticated structures for increasing dissolved nutrient uptake do not seem to have evolved, in contrast to the manifold mechanisms such as cilia and pumps developed by zoobenthos to collect suspended particles. Apparently there is no optimal-solution shape dictated by the physical environment for taking up dissolved nutrients or gases at low Reynold's numbers but just a rule: the greater the s/v ratio, the more efficient the uptake of both photons and molecules.

For phytobenthos organisms below the Kolmogorow scale of turbulent diffusion (< ca. 1000 μm), mechanical stress exerted by shear becomes irrelevant, and shape should no longer matter as long as it does not interfere with holding on to the substrate. The various protistan photoautotrophic lineages represented among the benthic microbiota do not appear to have evolved adaptive shapes that clearly differentiate them from phytoplankton. Nevertheless, the preponderance of pennate diatoms in the phytobenthos does suggest that their streamlined morphology is particularly well suited to life on or within sediment and obviously connected to their motility; so it is surprising that the same shape, including the raphe that enables locomotion on the surface of particles, is also widespread in pelagic pennates. On the other hand, various centric diatom species have also adapted to life on, or in close association with, the benthos as in mud flats and in the surf zone. The other protistan group that thrives on the sediment surface is Foraminifera. The flattened shells of benthic forms are distinct from those of their more spherical pelagic counterparts, but it is of interest to note that only calcifying and agglutinated heterotrophic protists have colonized the benthos. Silicifying heterotrophs such as Radiolaria are absent even in the deep sea where competition with diatoms for silicic acid should not occur. The significance of this absence is worth pondering.

It follows from this brief comparison of sessile and free-living plants that a relationship between form and function aimed at maximizing light and nutrient harvesting is no longer apparent at the protistan-size scale. In the picoplankton-size range occupied by prokaryotes, cell shape is more or less spherical or rod-shaped, the result of optimal packaging rather than a response to the environment. Diversity of shape increases rapidly in the nanoplankton-size range and reaches its maximum in the micro-size range occupied by bizarrely shaped dinoflagellates, radiolarians, and diatoms. Interestingly, in groups with autotrophic and heterotrophic representatives, in particular dinoflagellates and ciliates, the nutritional mode is not reflected in morphotype, suggesting that the latter serves a function other than resource uptake. Thus, exosymbionts have retained their shape even after changing their life style. Survival in the mortality environment, rather than competition in the growth environment, seems to play the crucial role is determining shape of protists in contrast to that of higher organisms.

As pointed out previously, a school of thought, spearheaded initially by Ernst Haeckel and more recently by Stephen Jay Gould, holds that thinking up a function for every type of form—the "adaptionist approach" ("if this organism is the answer, what is the question?")—is a wild goose chase. The supposedly nonfunctional, roughly triangular wall space between adjacent arches of the San Marco cathedral in Venice (spandrels) have been used as an analogy (Gould and Lewontin 1979). Spandrels do have a mechanical function, although it is not optimized for weight reduction. In addition, they were retained for decoration and their shape will have been dictated by the particular style of architecture in vogue rather than mechanical considerations. They are clearly the product of intentional design that becomes intelligible in its historical context. However, in connection with natural structures, Darwin was of a different opinion: "Natural selection is continually trying to economize in every part of the organisation." "Thus, as I believe, natural selection will always succeed in the long run in reducing and saving every part of the organisation, as soon as it is rendered superfluous" (Darwin 1859). The implication is that natural selection is parsimonious and that the evolution of form is ruled by the role of its function in maintaining fitness of the individual and ultimately the species.

D. Attacking Organisms/Attacking Tools

To appreciate the efficiency of any form of defense one has to first understand the form of attack—whether mechanical or chemical—against which it evolved. The size of the attacker relative to the prey organism is also crucial in the unicellular world, so we follow familiar usage and differentiate attack systems in the three size categories: pathogens, parasitoids, and predators. All three categories have in common that they must gain access to the plasma of their prey, whether mechanically or via enzymes. However, the techniques employed are very different, as will be the defenses against them. In the following, we present a brief description of the mortality environment sensu Smetacek *et al.* (2004) in which phytoplankton have to grow.

1. *Pathogens*

Although the presence of pelagic pathogens has been known for a long time, interest in their occurrence and function has blossomed only fairly recently (Suttle 2005). However, most of the interest is focused on viruses; reports on pathogenic bacteria are few (Stewart and Brown 1969; Nagai and Imai 1998; Córdova *et al.* 2002). There is, however, no reason why they should not pose an equivalent threat to protists as they do to multicellular organisms.

It is now well established that viruses and heterotrophic nanoflagellates (HNFs) together prevent bacterial populations from reaching concentrations much above 10^6 cells/ml (Pernthaler 2005). This is a reflection of viral infection potential in the pelagial, implying that other organisms, in particular those that routinely attain high densities, such as bloom-forming phytoplankton, are better defended than the bacteria. However, the ability to ward off viral attack appears to vary considerably among phytoplankton lineages, although more dedicated studies (with publication of negative results) are required before firm statements can be made.

Rampant infection of coccolithophorids and decimation of their blooms by viruses have been reported (Suttle 2005). However, large-scale infection of a diatom bloom has yet to be reported and only two viruses have been isolated so far from diatoms. Both are exceptionally small and infectivity was species-specific and in one case clone-specific. The high degree of specificity indicates that diatoms as a group are well defended against viruses. The possible nature of the defense can be deduced from another

bloom-forming group—colonial species of *Phaeocystis*. Hamm *et al.* (1999) have shown that colony shape is maintained by an inelastic but plastic skin with a pore diameter of less than 4 nm, which is highly permeable to dissolved substances. The cells inside the colony are never observed in contact with the skin, which raises some intriguing questions as to how the skin expands with growth of the colony. But that is another matter; the point here is that the cells cannot be contacted by viruses, which is why viral infection of colonial cells has not been observed, although it is common among solitary flagellates (Jacobsen *et al.* 1996). So only the colonial stage of this genus forms blooms that rival the biomass attained by diatoms.

The fact that both diatoms and *Phaeocystis* colonies can build up blooms in a variety of environments stretching from the coast to the open ocean and from the tropics to the poles suggests that they are not adapted to a specific range of light or nutrient environments. It is probably also not a coincidence that diatoms and *Phaeocystis* colonies reach high biomass levels within sea ice. The skin then takes the shape of the brine channel within which the colony grows. Because the stiff diatom frustules cannot adapt to the spatial constraints within the sea ice, small-celled species predominate. These "sea-ice species" also thrive in the water column following ice melt so it does not appear that they have adapted their physiology to the specific conditions prevalent in either habitat. It is tempting to suggest that immunity against viral attack, hence reduction in mortality rate, is the common property enabling biomass accumulation to bloom proportions in these species and that the diatom frustule serves a similar role in warding off viral infection as does the colony skin.

Viruses can only generate small forces. Smith *et al.* (2001) have shown that DNA confinement can build up an internal force to ~50 pN; this force may be available for initiating the ejection of the DNA from the capsid during infection. In addition, the contraction of the tail sheath of bacteriophages generates a force that suffices to puncture bacterial cell walls. However, most viruses need a direct contact to the cell membrane in order to infect a cell. This may be possible if phytoplankton organisms have only organic covers directly adjacent to the protoplast or if biomineralized covers have temporary loopholes, such as shown for coccolithophorids (Bratbak *et al.* 1993).

2. *Pelagic Parasitoids*

As in the case of pathogens, planktonic parasitoids have been known for a long time but their role in pelagic ecosystems has been underrated so far. The term is widely used in limnology (Sommer 1994) and is derived from terrestrial ecology, where it is applied to the special type of predation where a small organism feeds on a much larger one while growing or multiplying concomitantly. The parasitoid either forcibly enters its prey and eats it from inside or settles on its surface and feeds on the prey plasma through a tube. In either case, force is required to puncture the prey and the size of the parasitoid sets an upper limit to the force it can generate. Parasitoid attack can be warded off by strengthening the cell wall although the degree of toughness required will be far below that required of a defense against larger predators. The fact that naked species such as amoebae are rare to absent in the marine plankton is indicative of the ubiquity of the threat posed by parasitoids. To exert force on the cell surface of a much larger organism, the parasitoid has to first gain purchase on it. As in the case of pathogens, this can be deflected by a layer of mucus adhering to the cell wall. However, ultimately, effective protection will depend on the strength of the armor relative to the force the parasitoid can generate.

Parasitoid–prey relationships have been reported from a number of organism groups including dinoflagellates that feed on nauplii and ciliates that prey on euphausiids.

Interestingly, parasitoid attack of *Phaeocystis* colonies has yet to be observed, indicating that the mechanical properties of the colony skin provide perfect protection. The best known parasitoids from the pelagic realm are nanoflagellates ("zoospores") from several lineages that feed on large diatom cells (Kühn 1995; Tillmann and Reckermann 2002). Most parasitoids feed only on one or a few diatom species, indicating co-evolution of armor and attack techniques based on the mode of entering the frustule (Kühn 1998). This implies that all diatom species not attacked by a given parasitoid species are effectively protected against penetration by it. No cases of puncturing the silica frustule have been reported, suggesting that even the thinnest frustules are resistant to parasitoid attack. Rather, parasitoids "squeeze" into the frustule through specific sites: either between the girdle bands or through pores in the valves (Figure 2). This implies that the surface of the silica frustule is an effective armor against this class of organisms and it is only the chinks in the armor that render them vulnerable.

In contrast to viral attack, there are reports of mass mortality of diatom blooms due to parasitoids that, because they superficially resemble the ubiquitous bacterivorous HNF, are overlooked in the free-living stage and only recorded when feeding on diatom cells. The literature is anecdotal, but where they have been systematically surveyed over the annual cycle, many species are reported to have recurrent seasonal cycles geared to those of their prey (Drebes 1974). The fact that blooms can be decimated by parasitoids indicates that their growth and infection of new cells can potentially keep up with that of the prey. Therefore, because most diatom blooms are not accompanied by mass parasitoid infection, we infer that these organisms are generally kept under control together with the HNF by grazers such as ciliates and zooplankton larvae. Absence of a frustule would shorten handling time (finding the chink and squeezing through it), thereby increasing parasitoid growth rates and their likelihood of overtaking, hence decimating, growing diatom populations. We suggest that the obligate requirement of diatoms for silicon reflects their vulnerability to pathogens and parasitoid attack, which can be met by a minimum frustule thickness.

Large armored dinoflagellates such as *Ceratium* and *Alexandrium* that also form blooms appear to be even less susceptible to parasitoid attack than diatoms, as, to our knowledge, there are no reports of decimation of a dinoflagellate bloom comparable to the reports for diatoms. Parasitoids of these species have been described (Drebes

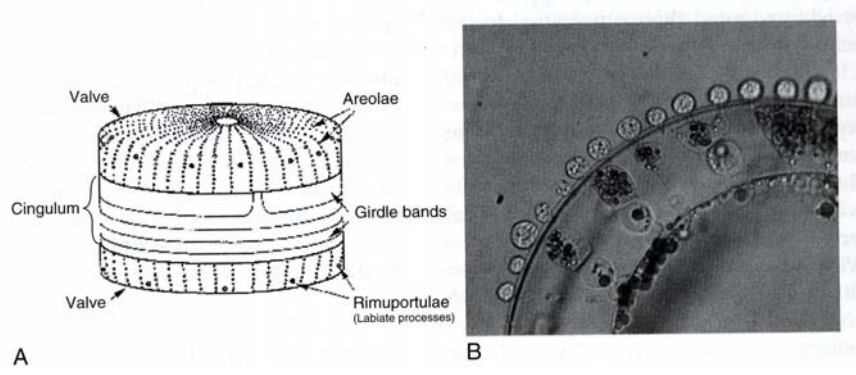

FIGURE 2. **(A)** Potential sites of infection on the surface of a diatom frustule. **(B)** Numerous cells of the parasitoid *Pirsonia diadema* feeding on the diatom *Coscinodiscus wailesii* (Kuhn 1995). (See color plate)

1979), but the rate of infection must be low, suggesting that the cellulose plates of dinoflagellates and their mode of attachment are superior to those of diatoms. The superiority must come at a price: cellulose armor will be more expensive in energy terms than silica, so diatoms can maintain high growth rates at low light levels.

E. Ingestors or Predators

All the regular herbivores, including protistan ingestors of similar size or larger than their prey, are included here. The largest are centimeter-sized euphausiids and the even larger Peruvian anchoveta, and the smallest are in the same size range as their prey. The difference from the previous categories is that prey shape, and not just its size and surface properties, matters. We argue that the range of shapes in armored phytoplankton larger than 10 μm represent responses to specific types of ingestors. The armor impregnable to small ingestors is mere crispness to the gizzard of a krill. However, the nonselective feeding pressure exerted by large, mobile ingestors is by nature patchy because they feed on swathes of the environment: A dense krill swarm might ingest almost all the potential food in its path but it is only several meters deep and so covers only a portion of the water column. A lot of potential food escapes, so selection exerted by nondiscriminatory filter feeders is weak when compared with the impact of small, more uniformly distributed ingestors. However, not all ingested cells are digested and growth experiments have shown that individual cells of a range of taxa survive euphausiid gut passage (Fowler and Fisher 1983).

Protistan predators share the water column with their phytoplankton prey, actively search for food by swimming with flagellae or cilia, and have growth rates comparable to those of phytoplankton. Their selective pressure will hence be potentially large. Because of their larger size, they can exert more force than the parasitoids and more elaborate armor is required to deter ingestion. Phagocytic protists have developed a range of techniques to overcome prey defenses (Tillmann 2004). Some species of dinoflagellates have a powerful peduncle with which they pierce their prey and suck in the contents (Jacobson 1999). Species of soft-bodied ciliates appear to be their preferred food, and we know of no reports of large peduncle-feeders preying on diatoms. Apparently, the silica frustules withstand puncturing or crushing by organic-tipped weapons of protists. The skin of *Phaeocystis* colonies appears to be equally effective.

However, the contents of ingested diatoms can be digested without apparent damage to the frustule, as demonstrated by a broad range of diatom-ingesting dinoflagellates. The spines of diatoms deter ingestion but can be overcome in the pallium-feeding mode. The prey item, chains, spines, and all, is covered with a feeding veil (pallium), which is subsequently retracted by the predator leaving behind empty frustules. This spectacular, modified form of ingestion has a major drawback: The deployed pallium will be vulnerable to attack, so prey handling time is crucial. Protuberances of the cell wall will increase the time required to envelope the prey and hence slow growth rates. Although pallium feeders are ubiquitously distributed, they are preferentially grazed by copepods and hence only attain large population sizes sufficient to control blooms under exceptional circumstances.

Not surprisingly, many phagocytic protists (tintinnid ciliates, armored dinoflagellates, Radiolaria, Acantharia, and Foraminifera) also carry lightweight armor based on similar construction principles as in the case of phytoplankton. Some of the protists use phytoplankton shells to construct their own armor (Young and Geisen 2002).

Copepods are the dominant grazers in the ocean in terms of biomass but also impact because they occupy an intermediate position between the large, nonselective,

swathe-feeding euphausiids and salps and the selective protists. They tend to feed selectively, and the different species have clear preferences (Koehl 1984). All have powerful mandibles lined with elaborate teeth reinforced with silica with which they crush their prey, including diatom frustules (Figure 3). Clearly these have co-evolved with diatoms (Beklemishev 1954), and a broad range of feeding techniques and abilities are represented in marine copepod assemblages. Thus, feeding experiments with two small, coastal copepod species (*Acartia clausi* and *Temora longicornis*) have shown that, whereas both could successfully tackle chains of the spiny genus *Chaetoceros*, only *Temora* was able to bite out chunks of the equally large frustules of the genus *Coscinodiscus* and suck out the plasma (Jansen 2006). Cells of the armored dinoflagellate *Dinophysis* also appeared to survive copepod gut passage and were the main constituent of the feces of copepods feeding on a natural, summer phytoplankton assemblage (Wexels Riser *et al.* 2003). It should be pointed out that the contents of copepod feces only reflect undigested food items, which explains why diatom frustules, whether intact or crushed, appear so prominently in them.

The coastal copepods *Calanus helgolandicus* and *Temora longicornis*, when offered a culture of the heavily silicified oceanic diatom species *Fragilariopsis kerguelensis*, fed voraciously but only cracked less than half of the ingested cells (Jansen 2006). The cells within whole frustules in the feces appeared to have survived gut passage as indicated by vital stains. Large copepods such as *Rhincalanus gigas* and *Calanus similimus*, that co-occur with *F. kerguelensis*, manage to crush a much larger percentage of ingested cells; nevertheless, many still appear to survive gut passage (Schultes 2004). The remarkable mechanical strength of the frustules of this diatom has been demonstrated, using micromanipulators and finite element crash models, by Hamm *et al.* (2003). Thus, grazing by the selectively feeding protistan and copepod assemblages will result in distribution of pressure over a wide range of armor types, as reflected in the concomitantly

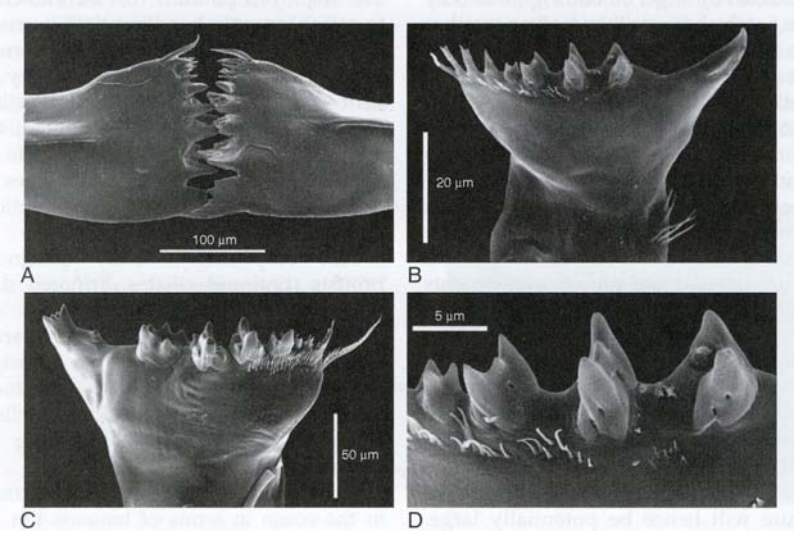

FIGURE 3. Copepod mandibles: In vivo position of the gnathobases of *Methidia gerlachei* (A), and diverse specific morphologies of *Calanoides acutus*, (C), and *Stephos longipes*, overview and detail (Michels 2003).

occurring diversity in natural phytoplankton assemblages.

A very effective armor-crushing mechanism is undoubtedly the euphausiid gizzard, which is lined with comb-like teeth reminiscent of the mandibles of copepods (Figure 4). However, it is not known whether these, too, are reinforced with silica. The crushed contents of euphausiid feces bear witness to the efficiency of this gastric mill, but, nevertheless, intact individuals of various armored species are commonly observed in krill feces. On the other hand, salps have not developed crushing mouth parts or gizzards but nevertheless indiscriminately ingest phytoplankton assemblages. However, their efficiency of digestion has not been systematically demonstrated and live *Synechococcus* cells have been found in their feces (Pfannkuche and Lochte 1993). In the Southern Ocean, the inverse correlation between high concentrations of salps and diatoms has been attributed to avoidance rather than grazing pressure. Smetacek *et al.* (2004) have argued that the long barbed spines and needle-shaped cells of dominant diatoms characteristic of the Antarctic Circumpolar Current are adaptations to deter salp feeding.

It follows that, as can be expected from any arms race, a variety of attack systems will co-evolve with an equal variety of defense systems. Given the heavy grazing pressure prevalent in the pelagial, one can assume an equivalent selection for defenses, whether by deterring ingestion or surviving gut passage. No single armor type can provide universal protection against the armies of pathogens, parasitoids, and ingestors operating in the water column.

II. WHEN

It is highly likely that the origins of armor date back to the early Proterozoic when prokaryotes developed cell walls to protect themselves against chemical attack by other prokaryotes even prior to the evolution of phagocytosis. Indeed, a durable cell outer layer is a prerequisite for the evolution of endosymbiosis, as otherwise the endosymbiont could not survive within the exosymbiont. As mentioned previously, the various instances where new phytoplankton lineages were started when an efficient photosynthesizer sought shelter in, or was taken over by, a well-protected exosymbiont resulted in species radiations, which had profound implications for ocean and hence planetary biogeochemistry (Knoll 2003).

The advent of mineral armor probably extends well back into the Precambrian, but during the Cambrian Explosion the

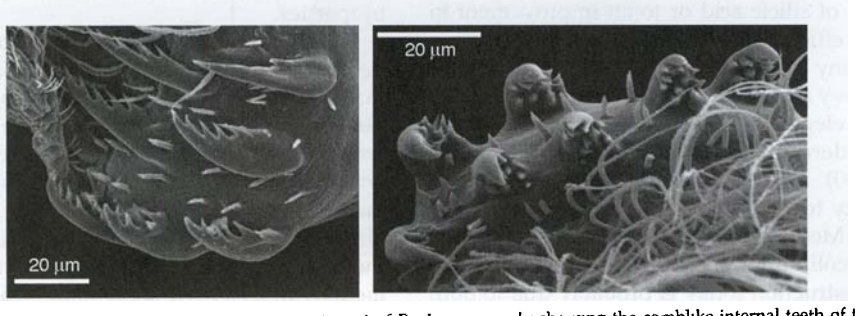

FIGURE 4. View of the interior of the gizzard of *Euphausia superba* showing the comblike internal teeth of the gastric mill adapted to crush diatom frustules. (J. Michels, unpublished).

evolutionary arms race intensified as evidenced by the prominence of mineral armor in the fossil record. As the compressive strength of armor increased, crushing and piercing tools or weapons increased in efficiency concomitantly. However, mineral armor is not necessarily superior to organic armor, as demonstrated by the presence of both calcareous and organic types in dinoflagellates and prymnesiophytes. In fact, calcifying dinoflagellates were prolific in the Cretaceous but are represented by only a few species today that are of minor importance. Dinoflagellates with cellulose armor plating are the dominant types today. Similarly, coccolithophorids are very prominent in chalk deposits from the Cretaceous, whereas the highly effective organic skin of *Phaeocystis* is reported to have evolved comparatively recently (about 30 million years ago [Ma] [Lange *et al.* 2002]).

The case of silica armor is most illuminating in this respect as it demonstrates that it is not just the presence or absence of minerals that is crucial but, in particular, the geometry and architecture in relation to the life cycle. Thus, silicoflagellates with an internal skeleton of silica are reported to have played a more important role in Mesozoic plankton than the diatoms (Parsons *et al.* 1977), although the origin of the latter goes back to the Jurassic. There has been speculation regarding the success of diatoms during the Cenozoic, exemplified by the massive deposits of diatom silica during the Neogene. Whether this is due to a greater supply of silicic acid or to an improvement in the efficiency of the silica frustule is unclear. In any case, Mesozoic diatom frustules look heavy and crudely constructed compared to the elegant lightweight construction of most modern diatoms (Gersonde and Harwood 1990). A similar development from heavy-duty to lightweight calcareous scales from the Mesozoic to Cenozoic can be observed in coccolithophorids. This trend to lightweight construction today is probably due to both sophistication in herbivore mouth parts and a shortage of the building material.

III. HOW

In this section we examine some aspects of physical barriers, that is, "armor" in its broadest sense, in terms of material properties and construction principles. Thus, a coat of mucilage is probably the simplest and perhaps earliest form of armor as it can ward off various attack systems from those of viruses to ingestors and continues to be deployed across all size ranges from bacteria to fish and amphibians. Many phytoplankton species secrete vast amounts of mucus or "exopolymer particles" (Decho 1990) as defense against grazing (Malej and Harris 1993). However, mucus is structurally unspecific ("messy") and may have unfavorable side effects, such as supporting aggregation and sedimentation of algae (Passow 2002). Possibly the major disadvantage of mucus is that it has to be produced continuously as it sloughs off at the outer surface and is hence metabolically more costly than a rigid armor that does not have to be renewed in order to be effective.

Ideally, efficient armor needs to combine optimal stability with a minimum of weight, so it is not surprising that the armor but also endoskeletons of modern plankton exhibit the typical properties of stable lightweight constructions developed by engineers. Because material cross-section and (external) pressure both scale with the square of the length scale, stable lightweight constructions are characterized by typical, well-matching geometries and material properties.

Although the overall geometric properties of phytoplankton are well described, mainly by light and electron microscopy, the material properties of phytoplankton armor are not well known. Several properties are crucial for understanding the use of specific materials as armor. The geometries of stable lightweight constructions may vary, but they all comply with relatively few, fundamental rules. Here we show some basic principles of lightweight engineering that are reflected in the structures of many plankton

shells. Gordon (1978) and Mattheck (2004) have provided introductory information on the mechanics of structural engineering.

A. Material

A very clear concept in solid mechanics is that of stiffness of a given material defined by the modulus of elasticity or Young's Modulus E or Y. It describes the deformation (strain e) of a material as a function of a certain stress S. This can be experimentally determined from the slope of a stress–strain curve (Figure 5).

$$Y = \frac{stress}{strain} = \frac{F/A}{\Delta l / l_0} = \frac{Fl}{A\Delta l_0}$$

In brittle materials this function is almost linear (elastic region of Figure 5), but in many materials, such as metals or elastomeres, it contains or is a nonlinear function (plastic region in Figure 5). The higher E becomes, the stiffer is a certain material. Typical values are 2 GPa for polymers, 20 GPa for bone or hardwood, 70 GPa for glass, and 200 GPa for steel.

The ultimate strength of a material is defined by the highest stress a material can resist without breaking (see Figure 5). The values of maximal compressive stress and tensile stress may differ, so that the ultimate tensile strength of a material may have different values from the ultimate compressive strength. Although some metals and ceramics may reach strengths of well over 1000 MPa, high-strength steels range between 400 and 600 MPa. A similar value has been calculated for the silica of diatoms (Hamm *et al.* 2003). In contrast, most polymers have values of less than 100 MPa.

Toughness results from strength and stiffness. It is defined as the amount of energy that a material can absorb before rupturing and can be quantified by calculating the area (i.e., by taking the integral) underneath the stress–strain curve (see Figure 5). The modulus of toughness is measured in units of joules per cubic meter (J/m^3); however, this is not often used to describe material properties.

$$U_e = \int \frac{YA}{l_0} dl = \frac{YA\Delta l^2}{2l_o}$$

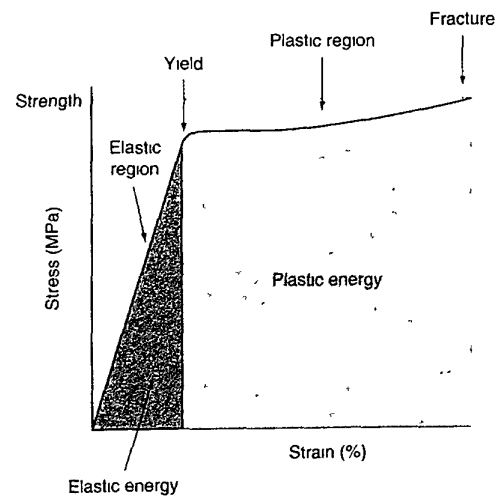

FIGURE 5. Stress–strain diagram for a material subject to a classic tension test

Typical tough materials include many metals and polymers, because they can dissipate a lot of energy due to a large degree of plastic deformation before failure; brittle materials include glass/opal and ceramics and most inorganic crystalline minerals.

It seems paradoxical, at first sight, that many phytoplankton groups use apparently brittle materials such as silica (i.e., opal) or calcite (coccolithophores) to create armor. On the other hand, biomineralized materials are, in fact, almost always composites (Jackson *et al.* 1990), in which small amounts of organics improve the strength and toughness of the dominating mineral by a large factor (e.g., up to 3000 in the case of nacre compared to aragonite; Okumura and de Gennes 2001). There is evidence that biomineralized phytoplankton shells such as diatoms, in analogy to nacre, are also made of functional composites (Hamm *et al.* 2003).

B. The Geometry

In addition to the material properties, the geometry of a structure defines its use as mechanical protection. Certain geometries (e.g., sharp angles, notches, and crack tips) create stress concentrations (Figure 6). If the stress exceeds the strength of a material, failure occurs. If the crack length cannot be shortened, it is necessary to reduce stress concentrations by blunting crack tips. This is expressed by the simplified formula:

$$s\left(1+2\sqrt{\frac{L}{r}}\right),$$

where L is the length of the crack, and r the radius of the crack tip. Examples for stress reduction can be seen in many pennate diatoms, which need a slit (a crack) in their shell for locomotion. The tips of these structures are always blunted, bent, and/or reinforced (see Figure 6).

The stiffness contributed by the geometry results from the value of the second moment of area (also called moment of inertia) It measures the efficiency of a shape in respect to its resistance to bending. If a beam or a shell is bent, the external regions of the structure are more strongly deformed than are the inner regions. A certain plane of the structure, which passes through the centroid, is not deformed at all and therefore does not help the structure to resist deformation; it is, therefore, called "neutral axis or fiber." For a light but stiff structure, it is necessary to move the material as far away from the neutral axis as possible, which results in i-beams, honeycomb sandwich constructions, and corrugated materials in the technical world and

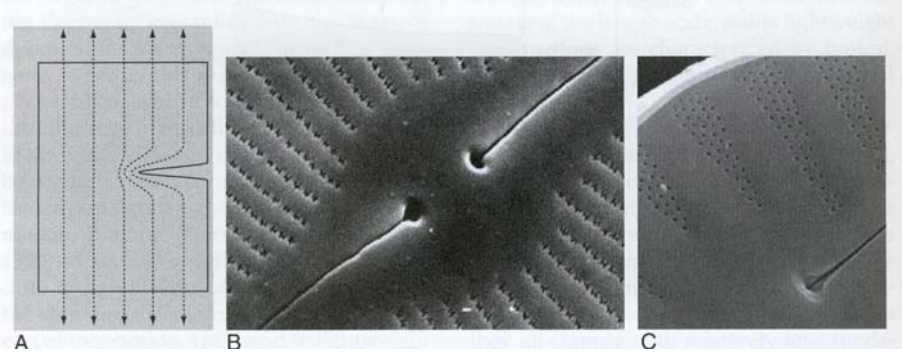

FIGURE 6. Sketch displaying stress concentration around a crack (from Gordon 1978) and the "blunted" ends of the raphe of two pennate diatoms Scanning electron microscope (SEM) pictures from C Kages/F Hinz (See color plate)

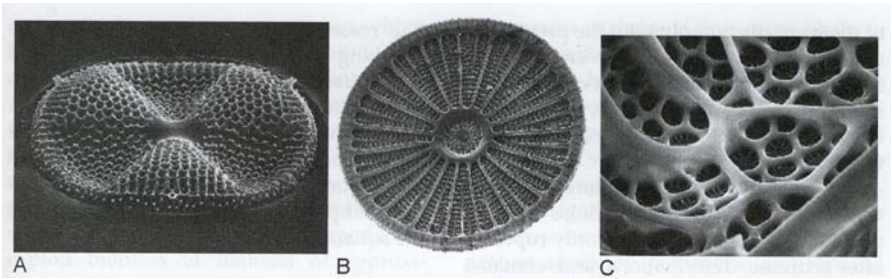

FIGURE 7. (A, B, C) Frustules of the marine diatoms *Actinoptychus*, *Arachnoidiscus*, and *Isthmia* (detail), respectively, displaying different ways of building a stiff lightweight construction by generating high moments of inertia at different scales Note the corrugated surfaces, ribs, and honeycomb structures and the fractal character of the *Isthmia* shell Parts (A) and (C) from C Kages, (B) from F Hinz

analogous structures in the shells of unicellular organisms (see Figures 1, 7, and 8). The formula for the uniaxial moment of inertia is:

$$I_y = \int_A Z^2 dA$$

The units are thus m^4, and increasing the thickness of a beam or a shell in the direction of the bending force results in an exponential improvement of its stiffness.

The axiom of equal stress describes another principle of efficient engineering: A structure is always only as strong as its weakest member, for example, a girder that is so thin that stress values within it exceed that of the ultimate stress will break (Mattheck 2004). On the other hand, "lazy" structural members in which stress values are low are not functional but costly because they have to be built and may be a disadvantage to an organism if it needs to be light to compete within its ecosystem. A homogeneous distribution of stress within a structure is, therefore, besides a high moment of inertia, a sign for an efficient use of the construction material.

C. Lightweight Constructions of Phytoplankton Armor

Examples of protist armor show that the principles of stable lightweight constructions are realized in many different ways. All

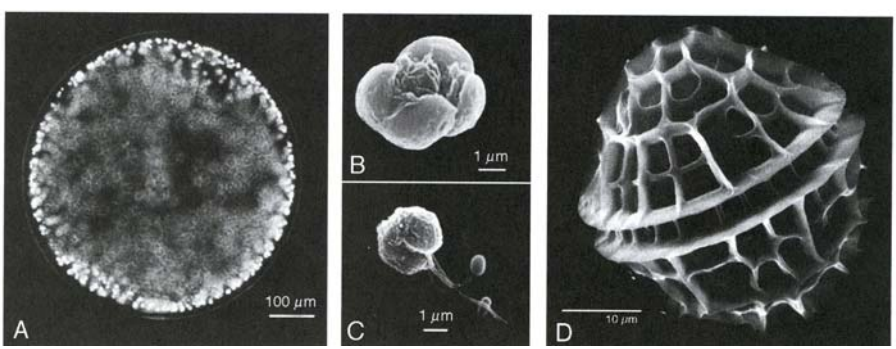

FIGURE 8. Organic covers Left: *Phaeocystis* colony (A), naked colonial cell (B), and free-living flagellate (C). Right The stiff, lightweight cellulose armor of a dinoflagellate *Protoceratium spinulosum* (D). Part (D) from Hallegraeff (1988). (See color plate)

of them strictly comply with the previously mentioned laws of good engineering Although very little is known on the material properties of protist armor, the available data indicate that natural selection has led to powerful solutions

An example for tough, tensile armor was found in *Phaeocystis* colonies that are surrounded by a skin, which only ruptures after extreme deformations and contains only pores smaller than 4 4 nm—an effective barrier against viruses (Hamm *et al* 1999, Figure 8) The blooms of *Phaeocystis* colonies quickly break down when the colony skins lose these properties, which usually happens in conjunction with nutrient depletion This approach of a tough, tensile, and collective armor is successful but not often realized in autotrophic marine protists We suggest that tensile covers do not enable structural differentiation, *Phaeocystis* colonies and other phytoplankton colonies with tensile covers, such as *Volvox* or *Coelosphaerium*, look very much alike—they resemble inflated objects The rapid disintegration of such structures under unfavorable growth conditions suggests that they cannot be used for less productive stages

More durable and more versatile in their forms are the thecae of dinoflagellates first described in detail in monographs published by Stein in 1878–1883 The thecae, or armor, of dinoflagellates is made of cellulose-like polymers, and their forms suggest compressive strength of this material (see Figure 8) It is known that many dinoflagellate cysts, which can be composed of the very refractory sporopollenin or even calcite, are resistant to bacterial attack and thus well preserved in the fossil record (Evitt 1985)

The highest diversity and the most obvious function as armor can be found in the silica shells, the frustules, of diatoms Diatoms often combine several principles of lightweight constructions such as I-beams, honeycomb sandwich constructions, corrugated forms, or supporting ribs in a single shell at different size scales (see Figure 7) The reason for this is, probably, that the attacking organisms likewise use tools of very different sizes to crack or puncture the shells A fractal appearance of some diatom shells, that is, similar structures repeated at different size scales (see Figure 7), may also result from the fact that material cross-section and pressure on a shell both scale with the square of the length scale

D. Spines and Large Size

Spines keep potential predators at a distance but, in addition, can injure the feeding/digestive system of organisms trying to feed on them Diatoms often possess extensive, highly structured (i e , barbed and latticed) siliceous spines, which are often hollow and harbor parts of the cytoplasm, including chloroplasts (e g , in *Chaetoceros*), but there are also chitinous, threadlike processes such as those of *Thalassiosira* The effect of spines as a deterring mechanism is difficult to quantify, but it is known that copepods bite off spines from diatoms individually before feeding on them Spines, which are not integrated within an exoskeleton but connected to an endoskeleton, such as found in silicoflagellates (e g , *Distephanus*), may be harmful to larger organisms (metazoans) but are inefficient against pathogens and small protists

Spines have often been interpreted as structures that reduce sinking velocity of diatoms, as they increase the drag of the cells considerably without adding much weight to them Although this function is plausible, it is only worthwhile on large, mechanically defended organisms, as reduction of size would have the same effect and could, in addition, increase the growth rate of a unicellular alga, as its smaller diffusive boundary layer would permit more efficient nutrient uptake

Large size in combination with a certain mechanical resilience can, in addition to offering other beneficial effects (Finkel 2001), definitely help in making an armor more efficient Thus, the costs for producing

a given thickness of armor decreases, within limits, with the s/v ratio. If predators have difficulties swallowing or engulfing a cell, they cannot use their enzymes as efficiently. However, large cells usually grow slower than small cells, and larger size in combination with similar shell thickness leads to decreased stability. Recent results have shown that, although some copepods can exploit biomass of diatoms of approximately their own size by fracturing the cells at specific sites, others, which are unable to fracture the shells, are completely excluded from grazing (Jansen 2006).

E. *Other Functional Explanations*

Several other explanations for presence and form of the shells of eukaryotes have been proposed. However, in our opinion, they do not provide an equally plausible and straightforward explanation on both materials *and* complexity of forms present in phytoplankton shells, as does selection pressure to develop stable lightweight constructions against physical attack by grazers.

The diatom frustule is far beyond the requirements of rigidity to support a vacuole, as demonstrated by the auxospore, which first forms a huge vacuole supported by thin scales within which the silica frustules subsequently develop. The idea that the honeycomb pattern of many diatoms may act as photonic crystals that concentrate light on the chloroplasts is not consistent with the fact that the chloroplasts in large diatoms with loculate areolae (pores surrounded by honeycomb structures) are evenly distributed directly at the proximate side of the shell, thus not where a focus would be. Still, the analysis of the optical properties of the patterned silica or calcium carbonate is needed. Optical effects such as iridescence have been observed in diatom frustules but are also present in mother of pearl inside the shells of many bivalves and gastropods, where an optical significance is not plausible. Iridescence caused by multiple reflections from multilayered, semi-transparent surfaces is thus more likely to result from mechanical necessities.

A proton buffering role of diatom shells to stabilize external carboanhydrase activity has been postulated (Milligan and Morel 2002), but it would, if efficient, explain the presence of silica but not its intricate forms. Also, a negative sorting effect of the silica pore structure of diatoms as an adaptation against attack by pathogens, as proposed by Hale and Mitchell (2001), is problematic, as the silica shells vary strongly in their types of external surfaces. Strong evidence for the hypothesis that phytoplankton covers serve as armor is given by the possibility to induce colony formation of *Phaeocystis* (Tang 2003) and a reinforcement of diatom shells by the presence of grazing copepods (Pondaven *et al.* 2007). Such induced responses are well described from freshwater and terrestrial systems.

IV. CONCLUSIONS

The potential of mechanical defense in unicellular organisms, especially those occurring in the plankton, is still underestimated. Most likely, this neglect is related to the small size of unicellular organisms, in spite of Feynman's remark that there is plenty of room (e.g., for sophisticated and complex structures) in the microscopic world and in spite of the current enthusiasm about nanotechnology. In order to link structural features of an organism to a function, knowledge of the physical and ecological context, and thus of the factors that cause significant selection pressure, is crucial. We have given an overview of the mechanical challenges faced by these organisms. The criteria typical for stable lightweight constructions are realized in many aspects of phytoplankton shells. Efficient implementation of lightweight principles are reflected in the fact that these biogenic constructions can be used to improve professionally engineered anthropogenic structures. The time is, therefore, ripe for reconsideration of the role of defense in the evolution of unicellular

organisms, in particular the plankton Given the panoply of attack techniques extending from viruses to fish to which protists are exposed, we have deemed it pointless to draw artificial boundaries and have accordingly defined armor with its German connotations as all forms of mechanical defense against pathogens, parasites, and ingestors. These in turn will range from tough cell walls that withstand puncturing to long spines that deter ingestion Armor evolves in response to a specific form of attack Indeed the co-evolution of attack and defense systems, encapsulated in the term evolutionary arms race, is an acknowledged driving force in natural selection of terrestrial plants, leading to speciation and ultimately shaping the structure and function of ecosystems Autotrophic marine protists will be shaped by the same processes

Acknowledgments

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