THE MICROSCOPE
Vol. 72:2, pp. 86–96, 2025
https://doi.org/10.59082/TPCI4745

CRITICAL **FOCUS**

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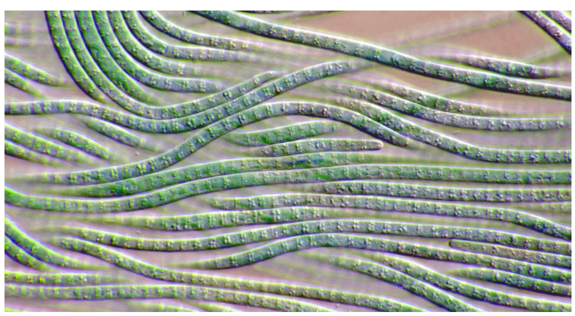
From Pond Life to Powerhouse

Algae don't officially exist. Yet we use agar from algae for our bacterial cultures; and now we are developing futuristic alginate substrates for printing tissues for surgeons.

We all know the algae, yet taxonomists do not recognize them as a legitimate group, even though algae are the single most important class of organisms on Earth. The oxygen on which we survive? Created by algae. The limestone which defines our landscape, and from which we have created our finest buildings, from the pyramids of Giza to the Empire State Building? Algae. What absorbs much of that extra carbon dioxide and helps to regulate the global climate? The algae. What gives birth to the food web of all life in the oceans, helps to purify water, produces biofuels, and is one of the fastest-growing health-food sectors in the world? Algae, of course. Every living creature on Earth depends upon green plants – and how did they become green? You guessed it.



Blue-green algae are currently designated as cyanobacteria, although bacteria do not photosynthesize. I prefer to know them as cyanophytes, since they fit every criterion for algae. This *Microcoleus* culture takes us back some 2 billion years, when the first photosynthetic cells had become established.

ALGAE AND DINOSAURS EMERGE

Algae were the first living organisms to capture solar energy. This process of photosynthesis dates back 2.7 billion years, it is something we fully understand, yet is one that we still cannot emulate (Ford, Brian J. "Are Cells Ingenious?" *The Microscope*, 52:3/4, pp. 135–144, 2004). As I remarked in that article, a little weed growing in the sidewalk can perform a reaction on which all life depends, yet which science cannot imitate.

The first prokaryotic algae were less than a micron in size, and now they range up to gigantic eukaryotic seaweeds tens of meters long. The earliest date from the Proterozoic Eon, and we can have an idea of them from species alive today. The prokaryotic *Prochlorococcus marinus* measures around 0.5 µm, while the eukaryotic *Ostreococcus tauri* is some 0.8 µm in size. Most bacteria are bigger. We can observe the remnants of those earliest life forms in stromatolites – mounds of algae and minerals that still survive in seas where salinity is raised.

During the Paleoproterozoic Era, oxygen levels may have crept up to 0.5%. It may seem like a minute component of the atmosphere, but that's more than ten times the amount of carbon dioxide we see today, and that's enough to support every plant in the world.

That was the first Great Oxygenation Event. The second came during the Neoproterozoic Era, 850 to 540 million years ago, when freshly evolved chlorophyte algae raised levels of atmospheric oxygen tenfold, approaching 5%. This triggered the dramatic increase in the evolution of abundant life of animals on land and vascular land plants that we know as the Cambrian Explosion.

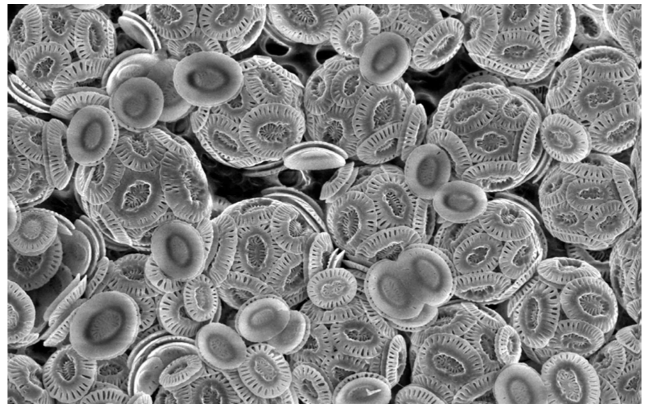
The proportion of oxygen in the air rose steadily, until present-day levels were finally attained during the late Paleozoic Era, specifically around the Carboniferous Period from 350–200 million years ago. Huge plants covered the swampy earth, pumping out oxygen every second of sunlight, and as they fell the dense layers decomposed and consolidated until only the carbon remained. The result? Coal. So luxuriant were the verdant forests, supported by levels of atmospheric carbon dioxide sometimes reaching twice today's values and oxygen levels that eventually climbed to 35%, that I concluded (some 50 years ago) that this would have stimulated the evolution of gigantism. The vast carboniferous forests would have flourished under a mantle of high levels of CO_2; the huge land sloths and colossal sauropod dinosaurs were the consequences of an atmosphere so rich in oxygen. It was a revolutionary idea (Ford, Brian J. *Microbe Power, Tomorrow's Revolution*, London: MacDonald & Jane's, New York: Scarborough Books, pp. 100–101, 1976).

So anxious are many people about a lack of oxygen due to industrial combustion that they have been buying oxygen cylinders to top up supplies. Yet we are breathing the same O_2 that the dinosaurs did. It's a constant presence. If you burnt every combustible substance in the world it would only lower the levels of atmospheric oxygen from 21% to 20.87%. You'd not notice the change.

ALGAE AND GEOLOGY

The look of the landscape is often marked by rounded limestone hills: the Indiana Limestone so widely used for buildings, the creamy Lompoc Deposits in California – some 10% of the American landscape is composed of limestone. I was born in rolling limestone hill country of the Cotswolds in England, and the Ozarks and the Edwards Plateau are remarkably similar. Think of Ha Long Bay in Vietnam; the drama of the Yucatán Peninsula, Mexico; Mammoth Hot Springs in Yellowstone National Park; those towering White Cliffs of Dover, England … all were created by algae.

Chemically, limestone is calcium carbonate



Chalk is a common form of limestone composed of fossilized coccoliths, protective disks of calcite, CaCO3 that were secreted by haptophyte algae some 80 million years ago. Some 50 million gigatons of carbon have been sequestered by algae, releasing the 21% atmospheric oxygen that we breathe today.

($CaCO_3$) that is usually present as calcite, although aragonite (a polymorph of $CaCO_3$) may also be found. The chemistry can be summarized thus:

$$Ca^{2+} + 2HCO_3^- \rightarrow CaCO_3 + CO_2 + H_2O$$

The CO_2 propels photosynthesis. We are left with limestone that contains some 60,000,000 gigatons of carbon. Roughly the same has been stored in the deep marine sediments, almost all of it by algae. That is some 99% of all the carbon on the planet, safely locked away and out of harm.

ALGAE POWER THE WORLD

One of the most astonishing sites in Los Angeles is one that is easy to overlook. Tourists revel in the Hollywood Walk of Fame and the Universal Studios Tour*, while scholarly visitors are captivated by the Getty Center and the Griffith Observatory, yet all the while we can witness where the city was born.

La Brea Tar Pits are an extraordinary phenomenon everybody should see – crude oil and asphalt are continually oozing from the ground as it has done for tens of thousands of years. In 1769, the Franciscan friar Juan Crespi explored the Los Angeles basin and recorded the "springs of pitch" that sprung from the ground. Local tribes, notably the Chumash and Tongva people, were utilizing the fresh, warm asphalt to

*Did you know that this is how the silent movies obtained much of their finance? It wasn't just through showing films in theaters. They had bleachers erected around locations and charged the public to watch the filming. We think that these studio visits are a recent development, but they date back to the first movies ever made.

The tar pits and oil wells at La Brea in the 1880s provided fuel and asphalt to surface the highways for the new city of Los Angeles. Prehistoric animals – mammoths and saber-toothed cats – became trapped some 25,000 years ago, and their skeletons are now on display in the La Brea Tar Pits Museum. The oil derived from diatoms.

waterproof their homes and canoes.

The oozing petrochemicals proved to be valuable to the European colonizers, who used it to caulk their vessels, to roof their buildings, and to burn as fuel. The natural asphalt from the tar pits is what surfaced the highways.

And it all came from algae. The area was once covered with shallow tropical seas (as was much of the world: Ford, Brian J. "Aquatic Dinosaurs Under the Lens," *The Microscope*, 60:3, pp. 123–131, 2012). This was the perfect environment for diatoms to flourish, and led to the great quarries of diatomite at Lompoc. Diatoms use their captured solar energy to store food reserves, and these are laid down as oil droplets within the cell. During the Monterey Formation of the Miocene from 23–5 million years ago, the oil from within each single cell became the Salt Lake Oil Field. Our crude oil has powered the world, and it all originated from tiny diatoms.

When levels of CO_2 reached 3,000 ppm in the early Cretaceous, ambient temperatures rose to some 25° C and there was no ice at the poles. Vast soupy blooms of algal coccolithophores clouded the seas and laid down calcium carbonate as layers of chalk that could be thousands of feet thick, so levels of CO_2 were regulated. By the end of that era, global temperatures had subsided below 20° C and, by the time humans first evolved, average temperatures were around 15° C. It has increased by 1.2° C in my lifetime, indeed the temperature has risen 0.5° C in the 15 years since I began this column…no wonder we are worried. Climate has always changed – but not this fast.

ALGAE AND THE BUILT ENVIRONMENT

Look around you. It's a world of concrete skyscrapers, magnificent classical constructions and brick buildings. None would exist without algae. Ten per cent of all our buildings are made with limestone – created from the fossilized remains of microscopic algae. Concrete comprises a good 40% and it could not exist without cement. The chemistry is based on the heating of limestone to 1600° F (900° C) which splits off the CO_2 – the reverse of how the limestone was formed:

$$CaCO_3 \rightarrow CaO + CO_2 \uparrow$$

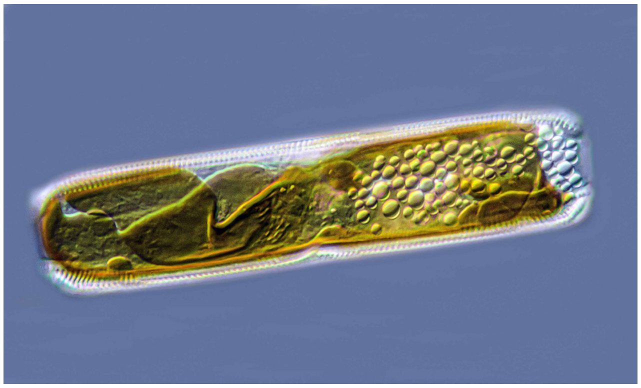
The resulting CaO (quicklime) is further heated to 2700° F (1500° C) to combine with compounds from clay or shale including silica and alumina. The resulting mix is cement. The resulting blend of cement and aggregate, when mixed with water, cures to form complex compounds like calcium silicate hydrate, which slowly absorb atmospheric CO_2, so a gradually increasing proportion of the cement turns back to the calcium carbonate with which we began. Some of the heat energy from the calcination is released as concrete sets and it becomes warm to the touch.

Apart from the buildings made with limestone, more than one-third are constructed of concrete. Concrete in cities is everywhere you look, and even brick buildings are held together with mortar made with limestone cement. Hardly anybody pauses to reflect that we owe it all to the algae.

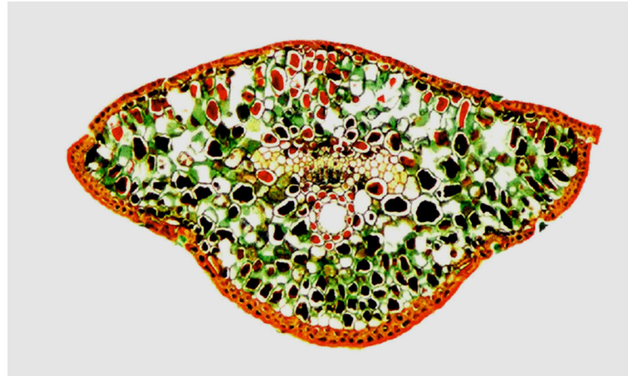
CELL WITHIN CELL

You may already be considering that I am making a great play for the importance of algae, while sidestepping the crucial significance of green vascular species – the plants we see every day. These capture solar energy and fuel the life we see around us. Farmed crops comprise the vegetables and cereals in our daily diet, while the meat we eat comes from domesticated creatures that consume plants. Carnivorous animals may be thought of as exclusively eating flesh, but the meat-consuming wolf or mountain lion favor the abdomen of their prey, and that is where the vegetation of a herbivorous diet is to be found. An exclusively carnivorous predator consumes herbivores, so green vascular plants are at the base of every one of these food chains.

Solar energy is captured by plants through chlorophyll, a complex chemical compound first recorded



Diatoms are among the algae that store their excess energy as oil droplets (visible on the right of this photomicrograph by Rob Berdan). In time, pressure and heat converted the oil to beds of crude that can be extracted and refined into a range of petrochemicals from gasoline to pharmaceuticals.



A redwood leaf section imaged by Alana Chin at Cal Poly Humboldt University, California. The chloroplasts began as independent algae, so a *Sequoia* could be thought of as algae adapting themselves to escape from a watery environment, to a safe and secure base from which to tower over the countryside.

by the French philosopher Antoine Lavoisier in his posthumous book *Mémoires de Chimie* of 1805. In Germany, Hugo von Mohl provided us with the first clear description of these distinct structures within plant cells in 1837, but not until 1883 did they acquire the name chloroplasts in studies published in Germany by Andreas Schimper. He was intrigued by their origin, and it occurred to him that they might have once been free-living algae.

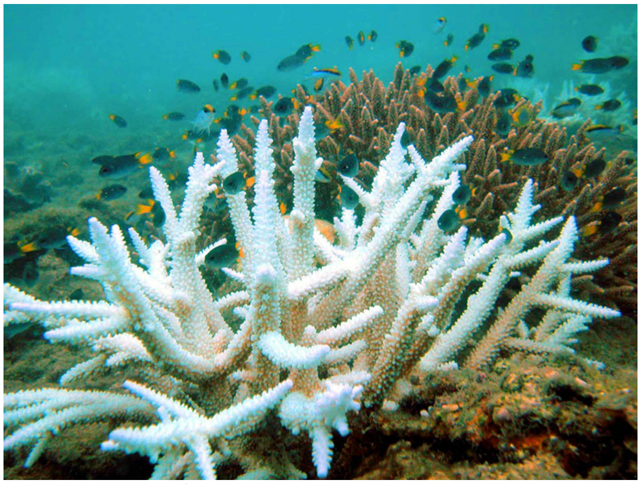
His astonishing proposal received support from Konstantin Mereschkowsky, a prominent Russian microscopist, who showed that chloroplasts divided just as any microbe would divide, and he drew comparisons between these apparently endosymbiotic algal cells and those that cooperated with fungi to produce lichens. In 1905, he put his research together for a paper published in Germany: *Über Natur und Ursprung der Chromatophoren im Pflanzenreiche* (On the Nature and Origin of Chromatophores in the Plant Kingdom) and his novel notion of symbiogenesis created a ripple of controversy.

The notion that organelles within the eukaryotic cell might have derived from free-living microbes emerged again from a French physiologist named Paul Portier, who postulated that mitochondria had originated as symbiotic bacteria that survived within the host cell. He described his theories in *Les Symbiotes*, published in 1918. Portier tried unsuccessfully to isolate mitochondria as bacterial cultures, but contemporaries dismissed his ideas. It fell to Ivan Wallin, a biologist at the University of Colorado, to conjure up the same idea independently. He saw symbiogenesis, rather than Darwinian evolution, as a driver of evolutionary advance.

Symbiogenesis is now said to be the brainchild of Lynn Margulis. She was a great friend, and Margulis would have been quick to point out that symbiogenesis was not her idea. Margulis showed that chloroplasts and mitochondria contained their own DNA, like independent microbes. Their double-membrane structure showed they'd once been ingested, and the simple ribosomes echoed those of bacteria. In 1967, she published *On the Origin of Mitosing Cells*, citing the prior investigations by Schimper, Mereschkowsky, Portier and Wallin. This time the evidence was overwhelming, and it is because of Margulis that symbiogenesis was at last accepted by the academic establishment.

GIGANTIC PLANTS

The tallest living tree is the Coast Redwood *Sequoia sempervirens*. In 2006, Hyperion was measured at 379.7 ft (115.7 m) in Redwood National Park, California. It's currently the tallest tree in the world, and grows in a secret location. A mature *Sequoia* may have 10 million separate leaves, each comprising about 10,000 individual cells, and if there are some 10 chloroplasts in each cell, the entire mature tree could harbor 10 trillion individual chloroplasts. It is customary to regard them as the solar-powered generators within each cell, driving the tree's metabolism. My way of looking at the chloroplasts is different: to me they are opportunistic algae that have taken advantage of the protection offered by a leaf, and have a secure, moist environment in which to live. This evolutionary adaptation means that algae, rather than drifting aimlessly in water, can now inhabit dry land, in communities towering far higher than all other forms of life, some 350 ft (more than 100 m) above the landscape. We see each tree as a



Flourishing coral reefs have been built up over centuries by polyps relying on their algal symbionts. Rising sea temperatures are killing the algae, and without their input of carbohydrate from photosynthesis, the colony cannot survive. Vast areas of reef are left bleached in consequence.

single green plant; to me they are ingenious communities of single cells that have conspired to colonize the countryside.

TRUTH ABOUT CORAL

It's fifty years since I first flew to Australia and the tropical city of Townsville. I remember it so well – the swooping flying foxes, timid koalas that crept like sloths among the eucalypts, possums that stole fruit from gardens (but were fast asleep by dawn) with cockatoos and lorikeets swooping through the bush, which I kept assuming were escapes from a zoo.

When we went diving over the Great Barrier Reef, the colored corals were unforgettable – vivid green staghorn, bright blue soft corals, occasional deep pink Acropora and vivid orange plate corals. It was as if a rainbow had been captured in rocky sculpture. Parrotfish and Wrasse vied with Butterflyfish and Grouper and I still have the slight scar on my arm from a Surgeonfish that I had speared for lunch. I had it dangling and, in a final act of defiance, it thrashed out and its razor-sharp caudal spines caught my forearm.

I was last there a few years back, and everything had changed where we dove. Many of the corals were dead, bleached bright white like bones on a beach – because of global warming. The midsummer sea temperature had been 1° C higher than normal. Online resources will tell you that corals are polyps, marine invertebrates of the class Anthozoa within the phylum Cnidaria, that form skeletons of calcium carbonate to create reef structures in tropical and subtropical oceans, their color deriving from symbiotic algae.

But the polyps will not survive on their own. The algae are zooxanthellae, mostly dinoflagellates like *Symbiodinium*, and they obtain a secure home from the polyp, along with essential nutritional supplies (like phosphorus and nitrogen). In return the polyp derives energy-rich organic compounds from the photosynthetic algae, such as glucose and essential amino acids. It also needs the carbon dioxide that the algae release each day, indeed, they produce more than 80% of the nutritional needs of the reef.

The coral polyps obtain calcium (Ca^{2+}) and carbonate ions (CO_3^{2-}) from the seawater, along with bicarbonate ions (HCO_3^-), almost all of which are derived from the algae. The key reaction is:

$$Ca^{2+} + CO_3^{2-} \rightarrow CaCO_3$$

The calcium carbonate is laid down in the form of aragonite and, although it is secreted by the calicoblastic cells within the polyp, it depends for its formation on the production of carbonate by the algae.

The algae and the polyps are truly interdependent. Neither can survive without the other. Describing the coral reef as a community of polyps is misleading; it is a communal system of polyps and algae. The Great Barrier Reef has lost half its coral within the last 30 years, entirely through the warming of the sea. The polyps have hardly noticed the change, but the algae cannot endure the rise in temperature. Once the algae go, the life of the coral is finished.

FROM DOG LICHEN TO PETER RABBIT

Lichens are a symbiotic union between ascomycete fungi like *Cladonia*, *Parmelia*, or *Usnea* and green algae such as *Chlorococcus*, *Trebouxia*, and *Trentepohlia*. Occasional lichens have also been discovered in which the fungus is a basidiomycete, and blue-green algae like *Nostoc* or *Scytonema* are sometimes seen as symbionts.

Lichens were known to the ancients. Theophrastus mentioned lichens as "mosses" around 300 BC. The medieval herbalists used lichens medicinally, and they were described as algae by Carl Linnaeus in his *Species Plantarum* of 1753. The Swiss microscopist Simon Schwendener was the first to propose that lichens are not single organisms in 1869, for he recognized for the first time that they were a curious concatenation of fungi and algae from which he coined his dual hypothesis. The view became popular that the fungus was parasitic upon the alga, but Beatrix Potter, whom

The yellow lichen *Xanthoria parietina* was recorded by Carl Linnaeus in 1753. The plant is symbiotic between the ascomycete fungus that gives it its name, and the alga *Trebouxia* (which is ignored by taxonomists) that contains parietin, a yellow anthraquinone photosynthetic pigment.

we know as the author of the Peter Rabbit books though was also an expert microscopist, wrote that she had had "the idea of lichens" in 1896 (Ford, Brian J. "Forgotten Women Who Lit the Way," *The Microscope*, 68:3/4, pp. 139–150, 2020). To Potter, the fungus and alga grew together for mutual benefit, and that's how we understand them today.

The fungus gains an immediate supply of metabolites from its algal partner, and glucose from photosynthesis becomes its principal energy resource. The algal partner gains protection through its existence within the protective thallus, which shields it from desiccation, ultraviolet radiation, and physical damage. The fungus absorbs water and minerals from the environment, and these become available to the alga, which lacks specialized structures for uptake. The mat of fungal mycelium that forms the thallus provides a stable substrate for the alga to grow, anchoring it to surfaces like rocks or bark where free-living algae would struggle to survive.

This symbiotic relationship allows both partners to colonize diverse and extreme habitats, including arctic tundra and desert outcrops, where no other plant life could thrive. Their mutualistic relationship is so effective that lichens are often pioneer species in colonizing barren environments. I have seen them thriving on bare granite in the arctic, and on rocky outcrops in the scorching Sahara Desert. Lichens populate almost 10% of the Earth's surface, and the creation of soil is the legacy they bequeath that allows successive species to colonize areas that would otherwise have remained barren.

Classifying lichens was always problematic. They were traditionally given species names, like the yellow specimen *Lichen parietinus* which was named by Linnaeus in 1753. The genus derives from the Greek λείχην (leikhēn) via the Latin *lichen*, referring to slowly spreading growths (lichen planus, in current usage, is a skin condition). The specific epithet that Linnaeus chose, *parietinus*, derives from the Latin for a wall, *parietis*, since the spreading yellow growth is frequently seen on walls.

Botanists cannot resist changing Latin names, often unnecessarily, and in 1860 Theodor Fries, a Swedish investigator devoted to lichens, created a new genus so Linnaeus's choice of nomenclature was replaced with *Xanthoria parietina*. And herein lies a problem – a scientific name had been assigned to an entity that is not actually one species, but two. Indeed, they are completely unrelated life forms, a fungus and an alga. The matter was settled in 1905 at the Vienna Congress of the International Code of Botanical Nomenclature (ICBN), who officially declared that in future, all lichens would be identified by the fungus only. So *Xanthoria parietina* would henceforth be the name of the ascomycete fungus while its essential partner, the alga *Trebouxia arboricola* without which the lichen would not exist, is simply written out of the equation and ignored. Once again, as with the corals, the alga is ghosted even though it is an equally important partner.

GIANT AMONG CELLS

Most typical plant cells measure about 20×50 μm. Textbooks and online resources love to tell people that cells are invisible to the naked eye, although you can see a human ovum, and larger plant cells are just about visible without a lens. Some are larger than others; the staminal hairs of *Tradescantia virginiana* have cells that look like minuscule beads in a necklace, and you can clearly see those without a microscope.

But it is the algae that set the record. *Valonia ventricosa*, the bubble alga, produces prodigious multinucleate cells up to 2 inches (5 cm) in diameter. This is a single cell bigger than a golf ball. To the alga, the advantage of this coenocytic mode of growth is that it eliminates the expenditure of energy through cell division and allows the easy transport of metabolites through cytoplasmic streaming. Although *Valonia* cells are the largest rounded cells in the sea, algae like *Caulerpa* develop complex branching structures from a single coenocytic cell. Since this avoids the time taken in cell division, rapid growth is possible and *Caulerpa* can spread at a surprisingly high rate – *C. taxifolia* can grow an inch a day (2.5 cm) and, in the Mediterranean Sea, has formed growths covering more than 75,000 acres (30,000 hectares) where it is widely regarded as an invasive species. *Valonia* has remarkable resilience to physical stress and can survive rough waves. It is known as the "green grape of the sea." The time it saves in undergoing mitosis means that it can quickly overtake an aquarium. These algae are record-setters in more ways than one.

ALGAL ODYSSEY

In Antarctica, I hopped ashore from my Zodiac rubber craft and scrunched up the black, icy rocks towards the glacial snowfields above. And there was a sight: the snow was green. Patches of the icy layers were unmistakably colored – not a pale, marine greenish hue, but the color of a freshly watered lawn. The vivid coloration shows growths of a chlorophyte alga, *Chlamydomonas nivalis*. It does not merely survive in snow but cannot exist in warmer habitats. The biflagellate cells are typical of the genus, about 20 µm in diameter, and they can form resistant spores if temperatures drop and traces of liquid water are no longer available.

Although the vivid green is often observed, the algae can produce a carotenoid pigment astaxanthin later in the life cycle, which turns snow red. Aristotle recorded colored snow around 340 BC and John Ross reported it from the Arctic during his expedition of 1818. The species responsible was originally named *Protococcus nivalis* when discovered in alpine snow by a German microscopist, Friedrich Traugott Kützing in 1836. It is not uncommon; there are typically at least 1,000 areas of colored snow around the Antarctic Peninsula during the summer months. The flourishing verdant growths in such inhospitable conditions are highly counter-intuitive.

Yet, I have found algae in deserts. Genera including spheroidal *Chloroidium*, elongated *Cylindrocystis*, characteristically spiky *Scenedesmus*, oval, yellowish *Myrmecia* and *Chlorosarcinopsis* which forms cuboid groups (like the bacterium *Sarcina*) are commonly found in the most extreme desert environments. All are chlorophytes, and I have seen them as a greenish blush on rocky outcrops after rainfall in Arabian desert environments and the Sahara, also thriving in desert crusts in Australia. They are well known in Arizona, California, and Nevada. These species thrive in the extreme heat of the Mojave, for example, which is the least likely environment in which you'd expect to find them. They secrete extracellular polysaccharides

It was a surprise to scramble ashore in Antarctica and be confronted by bright green snowfields. The chlorophyte *Chlamydomonas nivalis* is specifically adapted to an icy environment and will not survive in a temperate habitat. The alga was first observed in the alps and is also found in polar regions.

which protect them during desiccation, and some can burst back into life and resume photosynthesis within a minute of experiencing droplets of rain – this in a habitat where the summer ground temperature can exceed 180° F (80° C) and real rainfall is rare. From the blistering cold of the polar regions to the arid desert crusts…algae are truly astonishingly adaptable.

GREEN GOLD

As we have seen, nature has been quick to harness the power of the algal world. In recent decades, we have begun to learn ways in which algae could be harnessed to benefit human society. Algae are cultivated as a renewable feedstock for biofuels, offering a sustainable alternative to fossil fuels due to their ability to produce high yields of lipids, carbohydrates, and proteins without competing with food crops. It has even been proposed that algal cultures could be used to generate oxygen for space travelers undertaking extended journeys, perhaps to Mars.

Many of the species like *Chlorella vulgaris* and *Nannochloropsis oculata* that are rich in lipids can now be cultured in photobioreactors. Recent advancements in genetic engineering have increased lipid content by up to 60%, offering annual yields of 20,000 gallons of biodiesel per acre (almost 200,000 liters per hectare) which far exceeds extracting biofuels from soybeans or corn.

Many algae store their energy as carbohydrates rather than oil droplets. Some, like *Scenedesmus* and *Porphyridium* contain more than 50% polysaccharides by weight. The resulting carbohydrates can be fermented to liberate ethanol or methane. There are even species like *Chlamydomonas reinhardtii* that generate hydrogen through photolysis, and pilot projects in Japan are currently reporting yields up to 30% of the theoretical maximum. This would provide genuinely clean automotive fuel for hydrogen-powered cars. The Japanese lead the world in Hydrogen Fuel Cell Electric Vehicles (FCEVs) and over 25,000 Mirai automobiles have been sold since the model was introduced a decade ago.

Much emphasis is placed on the fact that tailpipe emissions from an FCEV are entirely clean – nothing but pure water. It sounds too good to be true and, of course, it is. The liquid hydrogen that powers their cars is delivered to Japan in pressurized tankers from Australia, where it is produced from lignite by heating to 2,700° F (1,500° C) in superheated steam and oxygen. Pure hydrogen is released, but the process produces more than ten times as much CO_2 as H_2 along with sulfur dioxide (SO_2), nitrogen oxides (NOx), and highly polluting particulates and volatile organic compounds. The Japanese can use their FCEVs, happy in the knowledge that they produce nothing but water as they drive, and entirely ignorant of the fact that they have exported massive amounts of air pollution to Australia, some 5,500 miles (9,000 km) away.

Algae could solve the problem. *Chlamydomonas reinhardtii* is key to the biological production of hydrogen. Culturing the algae requires a growth medium rich in nitrogen and phosphorus, so runoffs must be avoided; but the resulting biomass could be processed into nourishing cattle feed. They will burp methane, of course…

Not all the potentially useful algae are microscopic. The Sea Lettuce *Ulva lactuca* can be cultured in enriched seawater. It produces up to 100 gallons (400 liters) of ethanol for every ton of dry biomass, while anaerobic digestion can efficiently convert it to methane. Here is the possibility of generating biofuels on a commercially large scale, and all from algae. The blue-green alga *Spirulina platensis* has become increasingly popular as a health food in recent years, and useful supplements can be extracted from the cultures, including omega-3 fatty acids and phycocyanin. The global market for algal supplements is currently estimated at $1.5 billion. It is increasing all the time. The polysaccharides that can be extracted from *Ulva lactuca*, and from other algae including *Porphyridium cruentum* are being used to create biodegradable plastics. Commercial trials in Europe already suggest that these could be extensively used for product packaging within the next few years.

One of the most eye-catching areas of current research is the possibility of bioprinting living organs. A substrate for cell attachment that permits the diffusion of nutriments is being used in attempts to regenerate epidermis, bone, and vascular tissues, and these porous materials are based on alginate-nanocellulose obtained from cultures of algae. They are already being used to comprise the scaffold for bone tissue engineering.

If one day we are successfully to bioprint entire organs, like liver or kidney, hydrogels from algae could support vascularization and cell proliferation. There is even talk of 4D bioprinting, where the printed structure changes with time and responds to external stimuli like pH or temperature. If the future of organ transplantation is organ printing, then the future is algae.

Algal products are already widely used. The agar in our petri dishes is a polysaccharide from rhodophyte algae, traditionally *Gelidium*. The discovery of what was originally called agar-agar is said to have been that of a Japanese innkeeper, Minoya Tarozaemon of Kyoto, in 1658. It gradually became known in SE Asia as a thickener for foods and was proposed for making a growth medium for bacteria by Fanny Hesse in 1881. Her husband, Walther Hesse, was a research microbiologist at Robert Koch's laboratory and the Germans were frustrated by the fact that gelatin media, their customary means of growing bacteria, became liquid at around body heat (98° F, 37° C) – the ideal temperature for culturing pathogens. Fanny helped in his work, and an acquaintance from the Dutch East Indies mentioned her preference for using agar. It solidified, like gelatin, near body temperature – but, once set, it did not melt again when warmed. It had to be heated almost to boiling point (185–194° F, 85–90° C) before it liquefied, so it was ideal as a growth medium for bacteria. Fanny prepared some experimental plates for her husband to try, and nutrient agar instantly became a success in microbiology laboratories around the world. Many other of our daily reagents have an unusual history (Ford, Brian J. "Microscopy's Ingenious Legacy," *The Microscope*, 70:4, pp. 163-176, 2023; https://doi.org/10.59082/QGBV8515). Currently, *Pterocladia capillacea* is most widely grown for agar production, while *Gelidiella acerosa* is cultured in India and Indonesia though has a weaker gel. These forms of agar are used to thicken and stabilize foodstuffs; our laboratory agar is still produced from Gelidium.

It is an important ingredient – 20,000 tons of agar, worth $300 million, are sold annually. The industry is changing, though; *Gracilaria* is being more widely used for the industrial production of agar for the food industry, and other rhodophyte genera like *Pterocladia* have their own devotees. Gels from other algae include alginates and carrageenan, which are important thickeners and stabilizers in products like ice cream and yogurt. Carrageenan alone accounts for 40% of global hydrocolloid use in food. Enjoy your ice-cream; it's the algae that are the key.

SEAWEED BY THE TON

If you visit the Scottish island of North Ronaldsay, you will find that sheep are the principal product. It is a small island, measuring only about 3 × 1.2 miles (5 × 2 km), and is surrounded by a stone wall. You might imagine that they'd need a wall to keep the sheep in, but that's not the reason it was built. The wall is to keep the sheep out.

They are not allowed on the island, but instead of grazing on the grassy sward, they subsist entirely on seaweed. The sheep traditionally grazed on dry land and, when grass was in short supply, also on the beach. In 1832, the decision was reached to confine them to the shore, so that the wall was constructed, winding for 13 miles (20 km) around the ragged coast and measuring six feet tall (almost 2 meters). From then on, the sheep fed exclusively on the extensive beds of seaweed, mostly the kelp *Laminaria digitata*. Their meat has a distinctive, gamey flavor. It's unique. And all because the sheep feed on nothing but algae.

Laver Bread, *bara lawr* in the ancient Welsh language, is a traditional food in South Wales, made from the rhodophyte *Porphyra umbilicalis* that grows on rocky shores. It is boiled, rolled in oats and fried for breakfast in bacon fat. Rhodophytes have long featured in dishes such as the Japanese *nori* or Korean *miyeok*.

Piled high and left to ferment, seaweed provides an excellent soil conditioner, rich in biostimulants and fertilizer used to enhance the health of soil and crop growth. The wrack *Ascophyllum nodosum* is commonly harvested, and *Sargassum* seaweed dressing is said to improve plant growth, stress resistance, and crop yield by 10–20%. Seaweed supplements such as *Ulva* and *Gracilaria* are even being fed to livestock and are said to reduce methane emissions from cattle by up to 20%. Global seaweed feed production reached 50,000 tons in 2025. These algae are big business, and bigger every year.

WHAT IS AN ALGA?

They are characterized by a lack of vascular tissue, and the ability to perform photosynthesis. The green chlorophytes include many microscopic forms that rely mainly on chlorophyll, while the phaeophytes (typical seaweeds) supplement this with the carotenoid fucoxanthin which imparts the classical brown color. Fucoxanthin absorbs light in the blue-green to yellow-green range (450–540 nm) so they can still photosynthesize in deeper waters where those wavelengths predominate. Finally, the red Rhodophyte algae primarily photosynthesize with phycoerythrin, a maroon pigment that absorbs the green wavelengths that other green plants reflect. Only dim, greenish light can penetrate to the depths where rhodophytes predominate and they have evolved to absorb these wavelengths.

Yet algae don't have an official scientific group name. We are used to the categories of living organisms – domain, kingdom, phylum, etc. – and the algae don't fit into any of them. They are unique. The green algae are included in the kingdom Plantae, some (like *Euglena*) are clustered under the kingdom Protista, while the phaeophytes and rhodophytes have been granted separate kingdoms of their own. The name algae is an informal term for this curious assemblage of aquatic organisms.

Yet they have more in common than disparity: they are the only plants that lack roots. They have a unique anatomy that may feature a thickened basal region, or thinner spreading photosynthetic lamina, but they lack stems or leaves. None of the algae, no matter how highly evolved, has any form of vascular tissue. Unlike all other plants, algae never form embryos during reproduction. The rhodophytes have a complex triphasic lifecycle involving passive spermatia, carpospores, and tetraspores that are dispersed by water currents. No flagellated cells have ever evolved anywhere within the group, and reproduction subsists in releasing non-motile cells in the hope that they waft towards their target. It is an entirely hit-and-miss procedure, with far more misses than hits.

The algae could have been classified as something like the Algophyta, if those anatomical features had been the chosen criteria. Even in the 1970s, they were considered a single group, until Robert Whittaker at Cornell University proposed his Five-Kingdom System in 1969. He introduced the kingdoms of the Monera, Protista, Fungi, Plantae, and Animalia and lumped the algae, with their unspecialized anatomy, mostly in his kingdom Protista. Some were assigned to the Plantae, but that made no sense since the algae lacked the roots, stems, leaves, and vascular tissues, all of which are diagnostic of higher plants. Sometimes the Phaeophyceae and Rhodophyta were grouped by taxonomists with the Protista (which makes no sense at all) or as separate divisions of their own. No matter how you look at it, the algae are a distinct category. Taxonomists like to force every living thing into specific categories, associated with a convenient dichotomous family tree, so they can be neatly classified. Algae don't fit these arbitrary schemes. Face it – the algae are rebels.

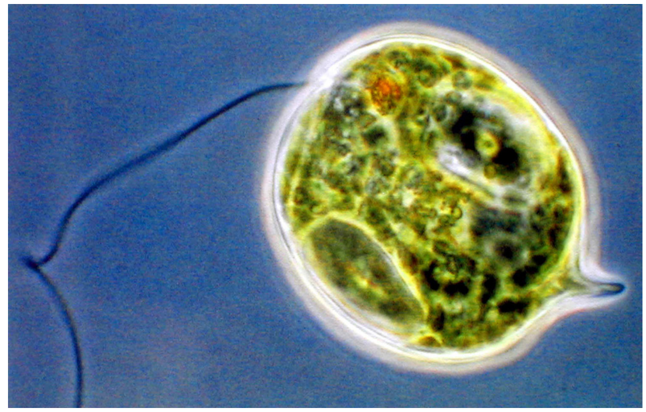
CURIOUS CONUNDRUMS

Everyone knows of the dreaded red tide. Those are massive, seasonal blooms of marine dinoflagellates like *Alexandrium* that produce lipid-soluble toxins which can accumulate in marine food chains, and which cost the fishing industry $100 million every year.

People also know of the deadly blue-green algae that occur in fresh water and kill cattle. Genera like *Microcystis* produce hepatotoxins that can contaminate stagnant ponds or irrigation water, leading to symptoms ranging from tremors and paralysis to death. In regions like the Midwest and Great Lakes, livestock losses cost over $2 billion annually. Cattle deaths alone cost hundreds of millions, and single incidents can cost $100,000 through the loss of livestock and the need for temporary relocation. Ask the public about algae and all you will hear is disaster, death, and destruction. Yet there are magical miracles to witness, and secrets to discover.

The colorless dinoflagellate *Noctiluca scintillans* is bioluminescent. When the water in which they occur is disturbed, they produce trailing flashes of lingering light. A ship sometimes leaves a glistening wake from these sparkling algae as it sails through warm seas. Green *Noctiluca* are sometimes found with photosynthetic endosymbionts. They can ingest *Pedinomonas noctilucae*, a small green alga that – instead of being digested – contentedly inhabits the central vacuole of the host and provides it with carbohydrate, while benefitting from the protection of the cell.

Euglena was once used in the management of pernicious anemia. At the Medical Research Council in the late 1950s, we grew cultures of Euglena gracilis in a defined medium devoid of vitamin B_{12} to which test samples could be added. After incubation under controlled light and temperature, the green color was assessed by spectrophotometry and a calibration curve with known B_{12} concentrations gave an immediate indication of the level of the vitamin in the sample. Although this seems crude in comparison with today's digital measurements, the method was sensitive to picograms per milliliter, so we found it uniquely valuable for clinical and nutritional studies.



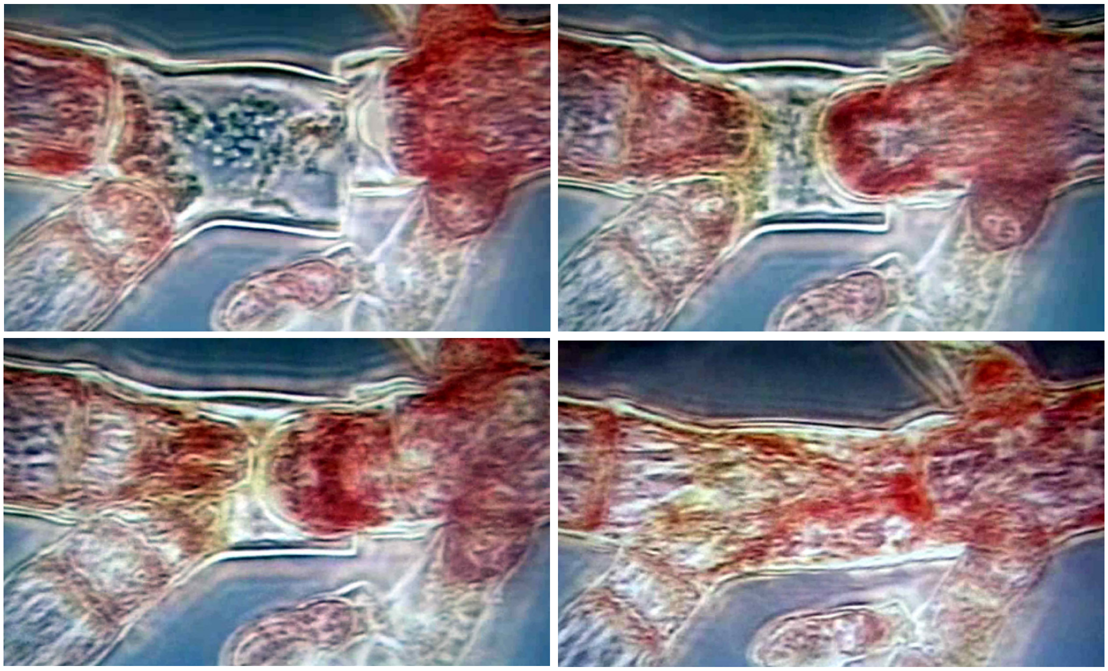
Red eyespots are characteristic of motile chlorophytes like *Phacus*, here beautifully imaged by the late Hilda Canter-Lund. They have been considered mere pigment particles, but electron microscopy reveals that they have a complex structure and are clearly important in navigating the algal environment.

Although *Euglena* is certainly an alga, it can survive in the dark as a heterotroph. And there is a species that is uncannily similar to *E. gracilis* though it cannot photosynthesize. This is *Astasia longa*, a protozoan with an exclusively heterotrophic metabolism. It has all the features of *Euglena*, but without the chloroplasts, chlorophyll or plastid-associated genes. When I first encountered the euglenoid algae when at school, I was fascinated to see them described as algae in all the botany textbooks, and as protozoa in the books on zoology. It's a paradox that persists.

INTELLIGENCE IN LOWLY LIFE

Of all the macroscopic algae, the rhodophytes will have stood out because of their curious life cycle. They seem to represent a strangely lowly form of life. While the typical alga has motile zoospores, which swim actively towards the female and seek out the oospore, the rhodophytes are bereft of any such advanced feature. Their spores can sometimes show gliding movement, and a few produce trailing tails of cytoplasm, but flagella are absent throughout the entire phylum. Spores trickle into the water and lie there, drifting in a casual current on the off chance that male and female might fortuitously meet. Can we imagine anything more unrefined and basic?

Yet even such primitive forms of life can exhibit intelligence. I noticed a remarkable event recorded on 16 mm film by the late Jeremy Pickett-Heaps. We were working on marine algae in Australia when he showed me the sequence. I was spellbound, and stopped the film. A filament of *Antithamnion* had been mounted in seawater on a slide, and a single cell in the center was



Still frames from Jeremy Pickett Heap's 16 mm film. A single cell in a filament of the rhodophyte *Antithamnion* is destroyed with a steel needle (top left). Adjacent cells detect the damage, divide to re-occupy the empty cell walls (top right), and realign the severed edges (bottom left) before recreating cell wall material to seal the gap (bottom right). This is an extraordinary achievement for a rhodophyte.

sliced across. Much as you might expect, the cell contents diffused away leaving an empty cell wall broken into two portions, just like cracking open an egg. The severed cell was empty and devoid of contents. The filament had simply been cut in half.

Time-lapse revealed an astonishing response. The surviving, intact cells on either side of the cut sensed what had just happened. We do not know how. They worked out how to divide, and to slowly occupy the empty fragments of the destroyed cell, through mechanisms we do not understand. Bursts of cytoplasmic activity can be seen on Pickett-Heaps' film, as the adjacent cells respond to the trauma, we know not how. Within a few hours, the empty cell wall is repopulated. The broken extremities are meticulously re-aligned, and new cell wall material is secreted (through mysterious mechanisms we cannot model) until the breach is repaired. Within 30 hours, the cell has been revived, and the filament is once more complete. Nobody knows how.

The astonishing ability of these algae to repair themselves was first documented by the English phycologist Elsie M. Burrows at the University of Leeds in the 1950s. We now know that cellulose and sulfated polysaccharides are synthesized at the wound site, processes that are mediated by vesicles derived from the Golgi, and involve enzymes like cellulose synthase. Yet this convenient shorthand skates round an essential issue: the severed ends of an algal filament in nature would be far apart. If the filament were ruptured by falling rocks, or torn apart by a wave of water, stamped upon and snapped by a browsing dinosaur, or ripped by rapid currents…whatever the mechanism, the severed ends would end up far apart. The only place in the world where they can remain adjacent to each other is on the microscopist's slide. So this is an unprecedented situation, and not one for which evolutionary specialization can have prepared the rhodophyte. It is faced with an unprecedented situation and has to work out, for itself, what to do.

These are extraordinary revelations. Not only did the algae give the world the chloroplasts in every green plant, which fuel all life on the surface of the Earth, but they can feed us, care for us, monitor our environment and offer us astonishing new technologies for the future. They remain a group without any scientific credibility and one that confuses and perplexes us at every turn, yet they show clear signs of intelligence. Algae are an enigma to scientists, and a mystery to everyone else. Yet their role is unique and, if people don't know about them, I think it's time they did. ■