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the Northwest Territories in Canada and the Isle of Harris in Scotland.

Granite is one of the bedrocks of our planet, but it is relatively rare on the surface beyond a few outcrops. Instead, our largest areas of exposed rock are the sands of deserts and coasts; there, the sands range from volcanic black to the more common red-yellow, to blinding white sands made from coral, shell, or exposed salt.

Plants

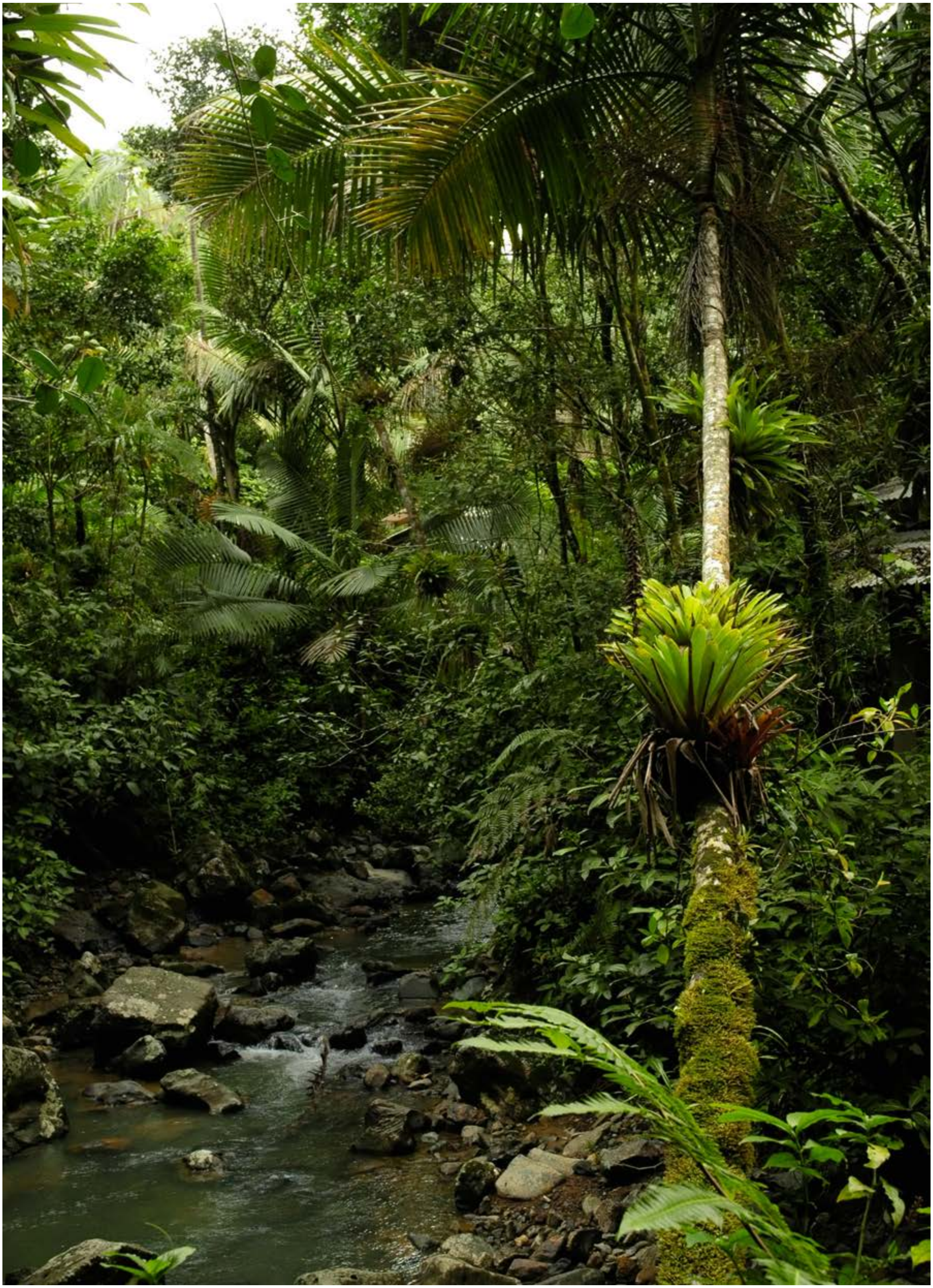
The Earth is primarily a wet, living world. At the polar icecaps, the color is white as the result of light being scattered by snow and ice, while the vast expanses of deep water are blue. Elsewhere, plants color the earth.

Almost every terrestrial region that is not covered with snow and ice has some foliage. Coastal oceans may also contain green chlorophyll in algae. Only the very harshest of deserts are totally devoid of plant life, and most of the world is covered with either forests or grasslands.

OPPOSITE: A stream running through the El Yunque rain forest in Puerto Rico.

OVERLEAF: Dunes in the Sahara desert, Merzouga, Morocco.

Whether tree, shrub, or grass, all plant life derives its color from one set of molecules—the chlorophylls. It is difficult to determine what was the key innovation that led to our planet being as densely inhabited as it is, but most biologists would likely choose the evolution of chlorophyll, since it is central to the ability of plants, and many other organisms, to use the energy of the sun and to produce oxygen. Chlorophyll absorbs the blue and red parts of visible light in the initial step of this "light harvesting" (see page 29), leaving green light to be reflected back. Not all plants are green, however, and even green plants do not appear green all the time. This is because plants contain varying amounts of chlorophyll, and also because they contain other pigments that serve other functions. In some cases, these pigments are quite obvious—for example, certain ornamental plants and some trees have purple or red leaves. In other cases, those pigments are hidden by the stronger effect of the chlorophyll, as seen in most deciduous trees. When the leaves die in the fall, the chlorophyll is lost, often revealing the remarkable red, orange, and yellow pigments that have been present within the leaves the entire summer, but previously unseen.



How Do Living Things Make Color?

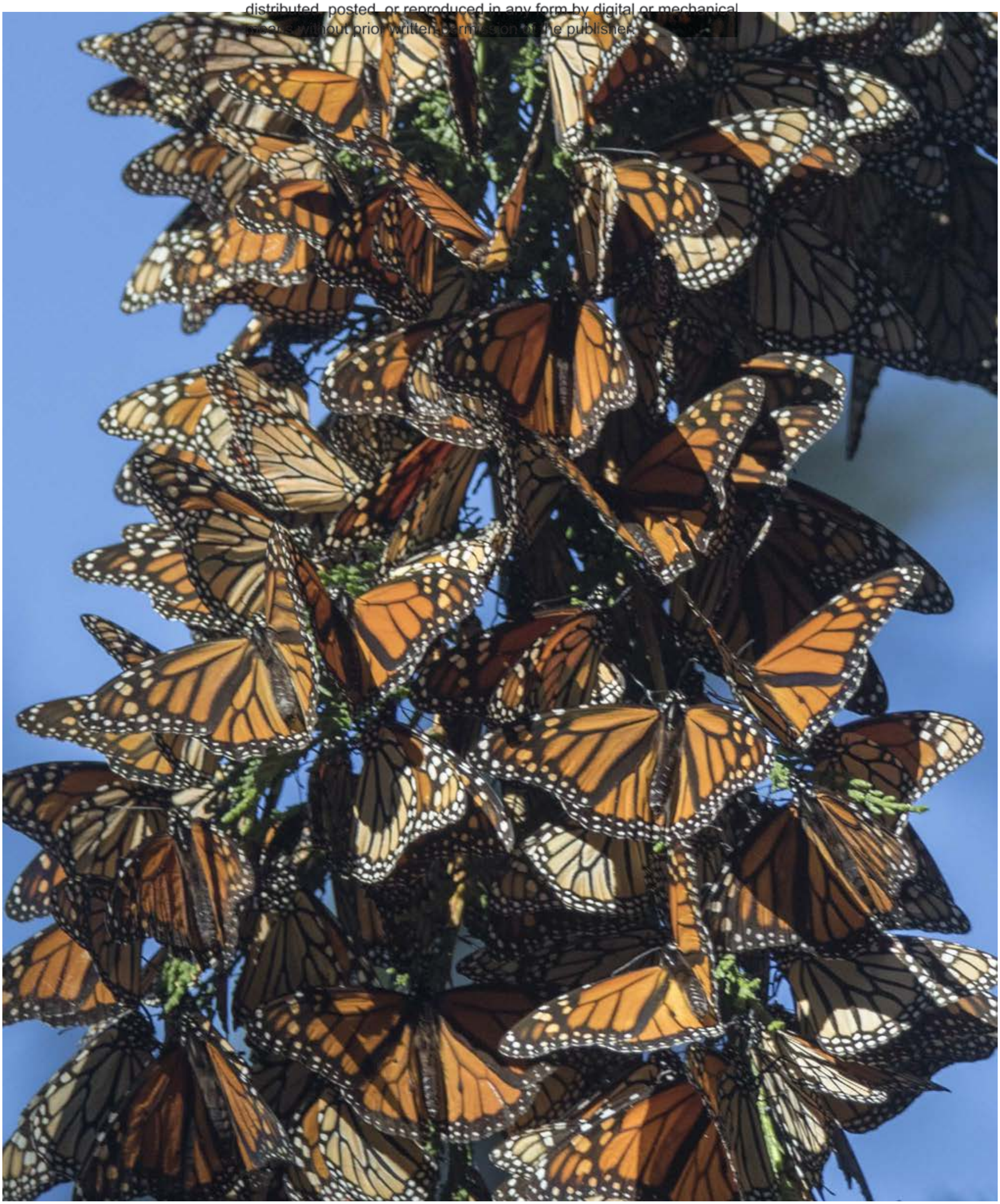
There are many ways to look colorful. Overwhelmingly, however, plants and animals rely on two very different mechanisms: pigments and structure.

Pigments are the most familiar producers of color in all living things. Pigments are based on atoms or molecules that absorb certain wavelengths of light, transmitting or reflecting the rest in a region of the spectrum that we perceive as color.

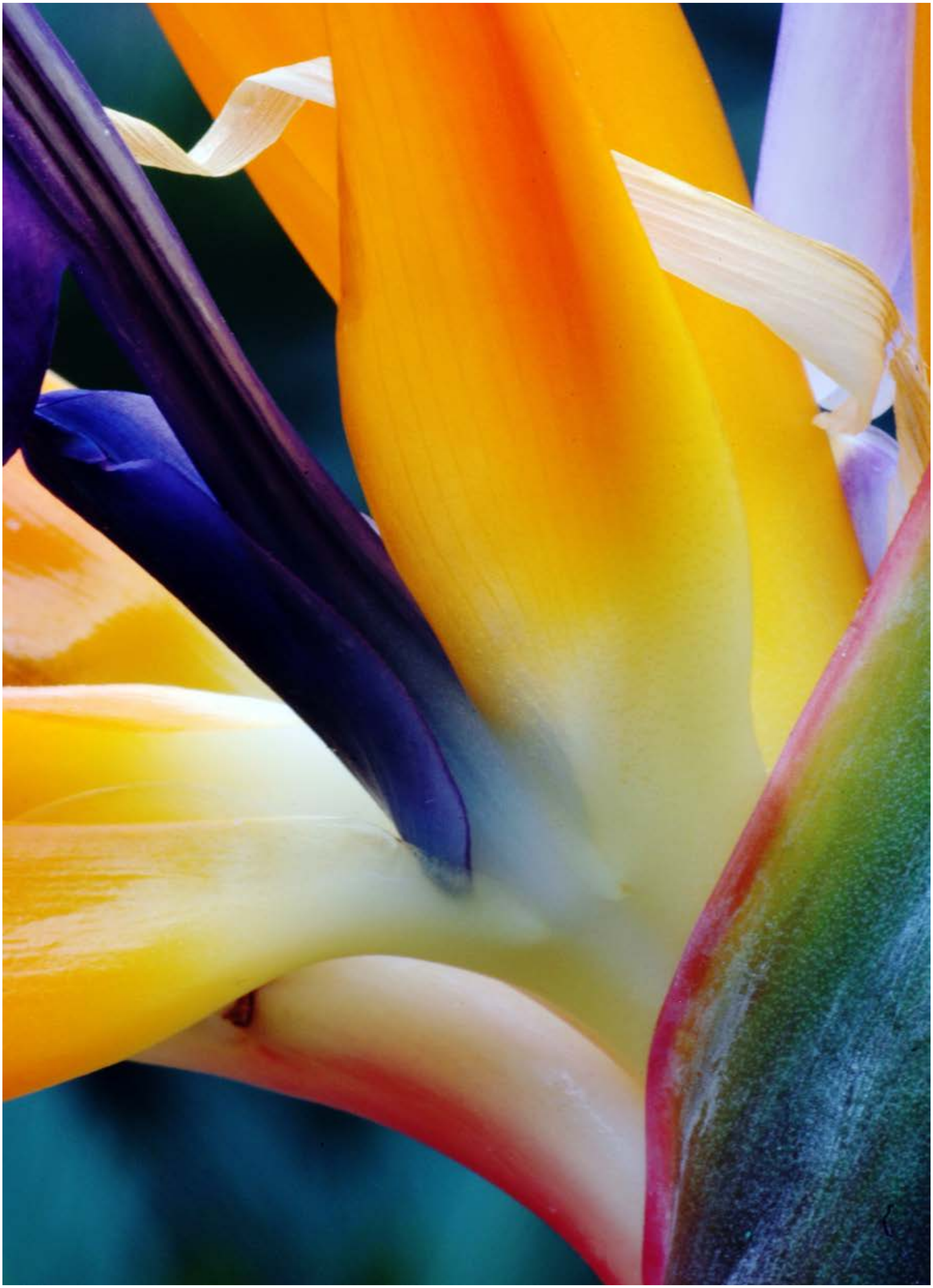
Pigments are ubiquitous in our world—they are used to color nearly every manufactured object that humans make, such as furniture, paints, appliances, cars, textiles, and so on. They are even used to color our own bodies in the form of tattoos or body paint. Many of these artificial pigments are inorganic molecules, such as minerals or artificial dyes, or even elements like copper or gold.

Animals and plants use neither of these, instead employing organic compounds they make themselves or sequester from their food. Sometimes these compounds include metal ions: examples are red hemoglobin in blood or green chlorophyll in plants. The basic organic structure of these, called a "porphyrin," is molecularly very similar in each case, but hemoglobin binds iron, making it red in color, while green chlorophyll has magnesium instead.

In most cases, pigments in animals and plants produce color by reflection, but transmission of color is also common. Structural colors are very different, relying on the geometry of components that are so small that they are on the scale of light waves. Humans use structural components to produce iridescent colors in polishes and they also occur by chance in the thin films formed by oil and other pollutants on the surface of water. Many animals and some plants make structural colors by scattering light (often appearing powder blue) or by controlling it with nanostructures called "photonic crystals."



A cluster of monarch butterflies, showing their orange ommochrome pigments highlighted by black melanin borders.



In addition to these two approaches, which create color by reflecting or transmitting light, a few animals make color by emitting light. Some are fluorescent, absorbing light of one color and re-emitting it as a different one; others are bioluminescent, making their own "cold" light biochemically (in contrast to the hot light of a fire or arc lamp). A very few fungi are phosphorescent, radiating light captured during the day later on at night in a spooky, ghostly glow.

Pigments and their diversity in plants

OPPOSITE: Bird-of-Paradise plant, possibly colored by green chlorophyll, orange carotenoids, and red or blue anthocyanins.

The beauty of the natural world is largely the gift of plants, which dominate the visual spaces of the terrestrial landscapes where most humans live, and provide the vibrant colors of kelp beds and coral reefs. Their beauty extends beyond this, though, because many animal pigments are either taken directly from the plants they ingest as food, or are modified from these plant pigments. Humans have long used plant pigments, such as annatto, saffron, or indigo, to color their textiles (and sometimes their bodies). The trade in such dyes is probably among the most ancient of human economies.

Plants are master biochemists, making their own colored pigments for photosynthesis, protection from damaging ultraviolet light (photoprotection), flower decoration (for pollination), and fruit enhancement (for dispersion). The chemicals they use for coloration are generally complex organic compounds, and commonly incorporate nitrogen and sulfur atoms in addition to the usual carbon, hydrogen, and oxygen. Chlorophyll adds magnesium to the mix. Few of the ways that plants use to produce pigments occur in animals, which explains why animals must ingest them for coloration.

Chlorophyll is a porphyrin. There are several types of chlorophyll, with different but similar molecular forms. Then there are pigments called "phytochromes," which plants use to measure the color of natural light and thus evaluate day length and season. Other familiar plant colors come from isoprenes, which form the colorful red, orange, and yellow carotenoids, and flavonoids, which synthesize the brilliant violet and red anthocyanins.

Unlike animals, which manufacture melanins to make black colors, plants have no specific black pigment. Instead, they use high concentrations of tannins or anthocyanins, or other less-well-understood mechanisms.

You might have noticed that none of these pigments produce blue! Faint blues can be derived from modifying some anthocyanins, but there are some other exotic blue-producing biochemical systems.

Pigments and their diversity in animals

The brilliant colors of many animals, including vertebrates such as birds, reptiles, and fish, and arthropods such as insects, are based on a widely shared palette of pigments.

Melanins are used to make black in almost all animals. Usually, yellow, orange, and red colors are derived from carotenoids, although other pigments can come into play. A derivative of melanin called phaeomelanin is used to make yellowish or reddish colors in many vertebrates. The red-winged blackbird displays all three of these popular pigments: melanin on most of the body, red carotenoid on the wing epaulets, and yellow phaeomelanin bordering the red patch.

OPPOSITE: A red-winged blackbird shows off its brilliant red carotenoid patch against its melanin-black body, highlighting it with a yellow phaeomelanin border.

Besides carotenoids, insects and crustaceans often use ommochromes, derived from the amino acid tryptophan, to make reddish or brownish colors. For example, the monarch butterfly has ommochrome-colored dark-orange wings, outlined by melanin. The white patches are structural colors, not pigmentary. Crustaceans regularly incorporate carotenoids into proteins to make complexes called carotenoproteins, which are blue or green. When a lobster is cooked, its blue carotenoprotein is denatured, revealing the red carotenoid color instead.

Other than the blues of crustaceans, blue colors in animals are almost always structural. Green colors, on the other hand, originate from a variety of sources. As Kermit the Frog noted, "It's not easy being green." Frogs use something called biliverdin, which results from the breakdown of hemoglobin. This is usually excreted, but here it is combined with a protein called serpin to make a pigment that circulates in the blood, coloring the skin green. (Hemoglobin itself is commonly used to produce red patches: often ones that appear and disappear rapidly like shy blushes.)

Sloths have green hair from chlorophyll, being symbiotic with the green algae living there. Parrots have pigments called psittacofulvins, which are yellow. When parrots look green, it is because they combine a structural blue with this pigmentary yellow—there is no actual green pigment.

Chlorophyll in Leaves and Plants

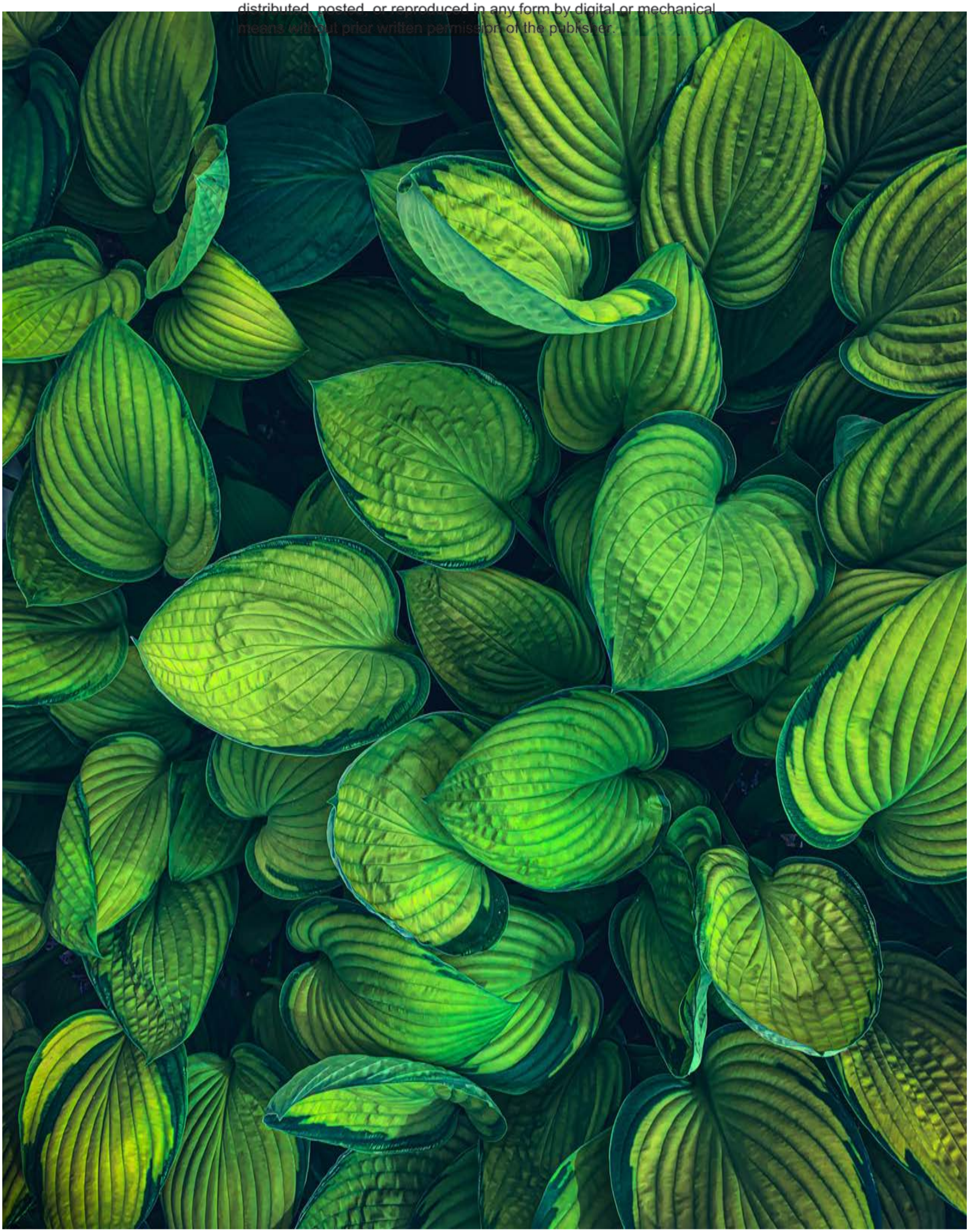
Why is chlorophyll the most important of all pigments? Putting it simply, the diversity of life that we know today would not exist without it.

Nearly all plant growth is fueled by chlorophyll's ability to capture the energy in sunlight and use it for chemical synthesis, ultimately forming nearly all the molecules of life. There are a few microorganisms that are able to survive on chemical energy in hot springs and deep-ocean seeps, and small communities of animals that feed on these microbes. Overall, though, chlorophyll-driven biology dominates life on Earth, and chlorophyll's reactive by-product, oxygen, fuels the high-energy lifestyles of complex animals.

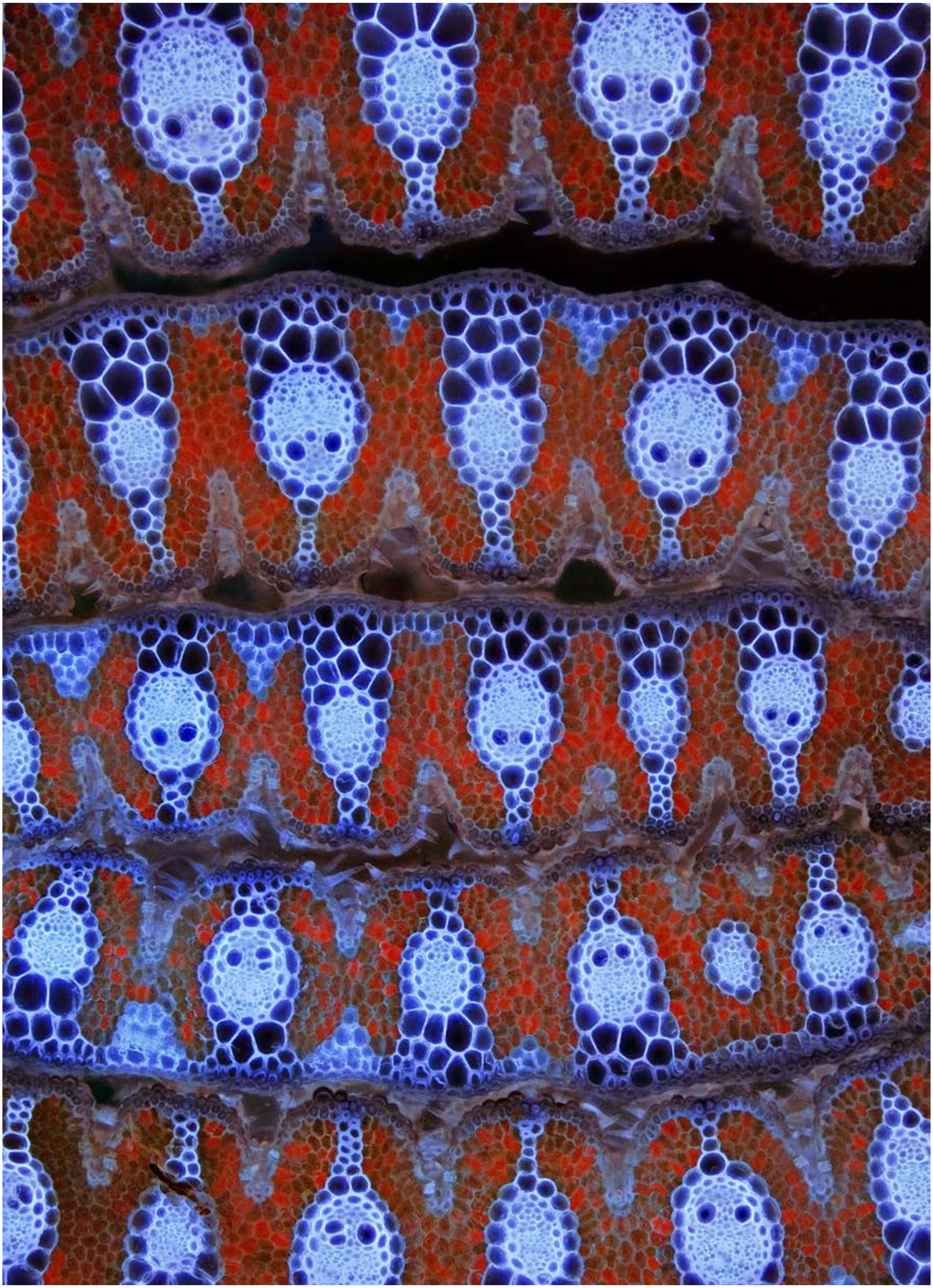
All the plants that we are generally familiar with produce two forms of this pigment—chlorophyll *a* and chlorophyll *b*. These are the two most abundant pigment molecules on our planet. Chlorophyll *a* is very ancient, first appearing billions of years ago. Chlorophyll *b* originated more recently, but is chemically nearly identical to its ancestor. Both are porphyrins containing a magnesium ion. There are other chlorophylls in some algae, but these do not appear in terrestrial plants.

Chlorophyll is green—the name means "green leaf." This color may seem ideal for capturing the high-energy solar radiation in the blue-green to green wavelengths in sunlight. However, being green means that chlorophyll does not absorb green, but instead reflects or transmits it. Instead, chlorophyll absorbs red and blue light best. Accessory pigments help by transferring some energy at middle wavelengths to chlorophyll, but the overall conversion of solar energy to chemical energy is surprisingly low—only about 1 percent. Fortunately, there is a lot of solar energy out there.

In addition to producing oxygen and providing energy for biosynthesis, chlorophyll is important because its action turns carbon dioxide into the organic chemicals needed for life, removing it from the air and fueling the major mechanism that offsets climate change. This is why the loss of chlorophyll via deforestation is having a major impact on Earth's weather and ecosystems.



Green leaves richly colored with chlorophyll.



Chlorophyll has another useful feature: it fluoresces light strongly at red and infrared wavelengths, which enables remote sensing of terrestrial and marine regions where photosynthetic plants are abundant.

Tuning chlorophyll

Chlorophyll is the only plant pigment that produces useful chemical energy from light, but it absorbs only part of the solar spectrum. As you would expect, the billions of years since chlorophyll *a*'s first appearance have provided plenty of time for adaptations to evolve that improve this critical molecule's performance. Pigments called accessory pigments harvest light from spectral regions where chlorophyll does poorly, and then transfer the absorbed energy to chlorophyll.

OPPOSITE: Red fluorescence from chlorophyll seen in a microscopic view of a pampas grass leaf lit by ultraviolet light. The "faces" are the leaf vascular bundles, with xylem vessels for "eyes."

Of the two chlorophyll pigments, only chlorophyll *a* actually converts light to chemical energy. Chlorophyll *b* is an accessory pigment that links to chlorophyll *a* and passes energy to it. The other major class of accessory pigments is made up of the carotenoids, which are chemicals that are present in chloroplasts together with the chlorophylls and that directly transfer energy to chlorophyll *a*. (Chloroplasts are the cellular components where chlorophyll allows plants to make oxygen and form simple organic chemicals.)

Carotenoids appear bright red, orange, or yellow; these molecules and their derivatives are taken from plants to make similar colors in animals. They are effective absorbers of blue-green and green light, and thus fill in the parts of the spectrum that the chlorophylls normally fail to capture. Other molecules, closely related to carotenoids, are the xanthophylls, which look brown or yellow.

Even though all these variously colored pigments are always present in leaves, they are so much less abundant than chlorophyll that we rarely see their colors. Their high concentrations in most leaves are only revealed when they are chemically extracted—or when the chlorophylls that overshadow them naturally degrade. Nature's beautiful gift of autumn foliage exists simply because the chlorophylls disappear rapidly as photosynthesis shuts down at the end of summer. Leaves then show their carotenoid content by displaying their oranges and reds, and their xanthophylls by becoming yellow. Those beautiful pigments have always been there, it is just that chlorophyll is so much more abundant that they were previously concealed. Despite their reluctance to display themselves, these pigments are essential for the success of plants.

Flowers and their pigments

Flowers are beautiful, ephemeral entities: they may sometimes be weird or alien, but are often awe-inspiring. Their shapes range from simple to fantastic, as do their colors and pigments.

Plant favorites are anthocyanins and carotenoids, each in a dizzying variety of types. The colors they produce range from blue-purple to orange-red in the case of anthocyanins, and from yellow to deep red in carotenoids.

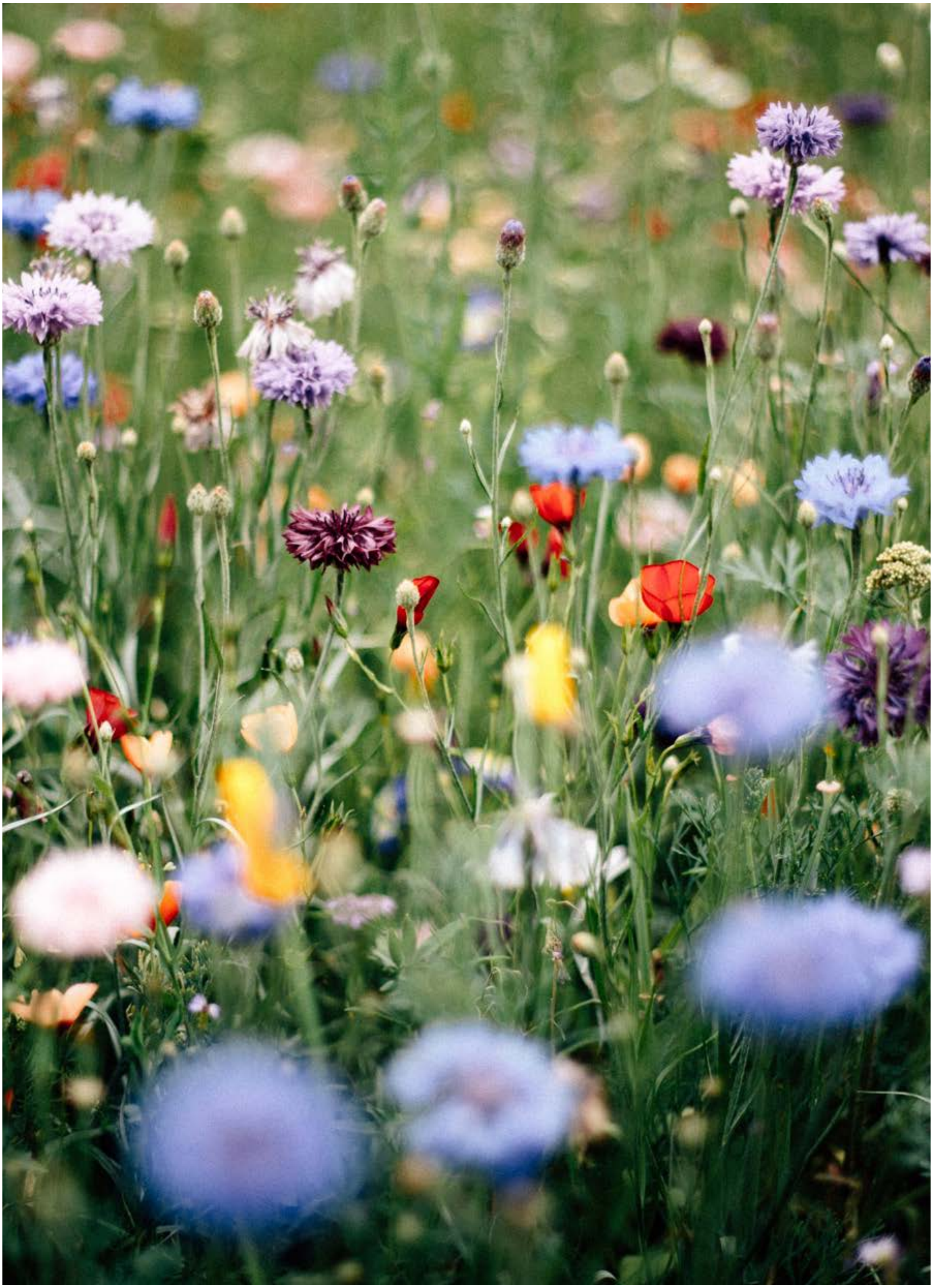
The variety of pigments is enormous, but a few names provide a bit of flavor. The anthocyanin pelargonidin is found in geraniums (genus *Pelargonium*). Mallows make malvidin and peonies make peonidin. Not all anthocyanins have such obvious names, however. Carotenoids are sometimes named by the colors they produce, such as aurone (golden) or xanthin (yellow).

Flowers first evolved only about 100 million years ago—relatively recently in geological terms—and often co-opt photosynthetic accessory pigments to make their stunning colors. Some flowers use only one kind of pigment, but most mix pigments to produce their stunning colors, often using both anthocyanins and carotenoids. The various yellows, oranges, and golds of marigolds are combinations of carotenoids, sometimes with a hint of anthocyanin. Hydrangeas make flowers with different colors based on the same anthocyanin pigment. The pigment is modified by aluminum ions, which are only freely available in acidic soils. That is why hydrangeas are blue in acidic soils, but are pink or red in alkaline ones. Depending on weather and growing conditions, hydrangeas can produce differently colored blooms on the same plant.

Not all flowers are colorful. The colorful ones exist to attract pollinators, especially insects like bees and butterflies, or nectar-feeding birds like hummingbirds, sunbirds, and honeycreepers. Over time, there has been a dance of adaptations, with animals evolving to better see flowers with abundant nectar, and plants adjusting to animals' vision to attract their pollinating ability. Some flowers even have ultraviolet colors, visible to their pollinators but not to us (see page 123).

OPPOSITE: Wildflowers displaying their showy assortments of pigments.

OVERLEAF: Lavender field at sunset, a sight not normal in the natural world but one that shows the human desire to amplify color sensation from flowers. In this case, smell sensations too.



Structural Color

Interactions of light particles (photons) with organized tiny features in organisms lead to interference phenomena that reinforce or obliterate specific wavelengths of light, producing brilliant structural colors in living things.

An oft-repeated statement is that "bluebirds are not blue," with the writer going on to explain that their color is an optical illusion. One could just as well say that goldfinches are not gold and scarlet tanagers are not scarlet—they too are optical illusions! The difference, however, is that complex organic pigments create red or gold colors, while blue colors generally arise from structure.

Structural colors are produced when light encounters repeated, fine-scale structures that constantly affect its speed of travel through a material.

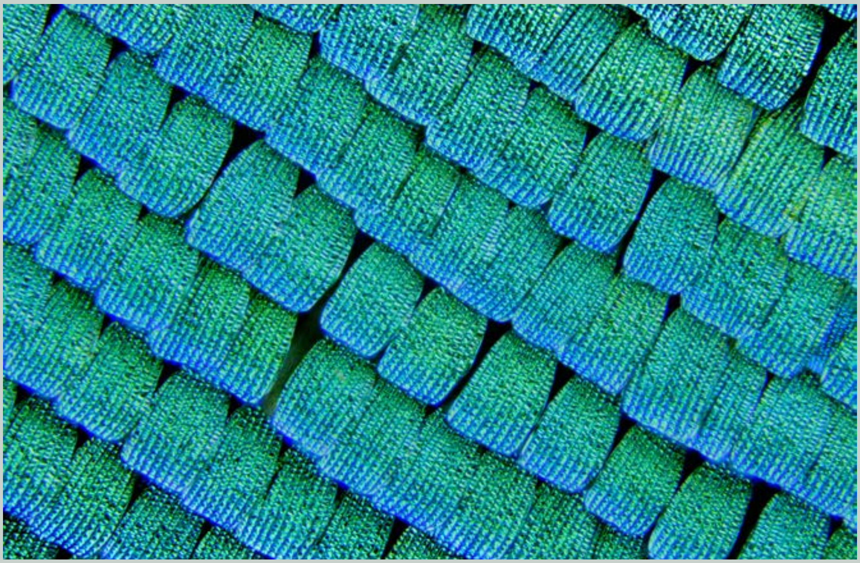
Some familiar colors are produced by scattering light. Essentially, incoming photons are redirected by interactions with miniscule particles. Scattering produces both blue skies and white clouds; the difference is that the molecules of gas in the open sky are much smaller than the tiny water droplets in clouds.

The colorful nanostructures in living things scatter light in a different way from atmospheric scattering. The scattering by living things is usually coherent, with all the outgoing light waves in lock-step. An example is thin layering of materials that affect how fast the light travels through them. If the layers are very regular, reflections are iridescent—their apparent color changes with the angle of view. Both plants and animals make iridescent colors, which are often brilliant and eye-catching.

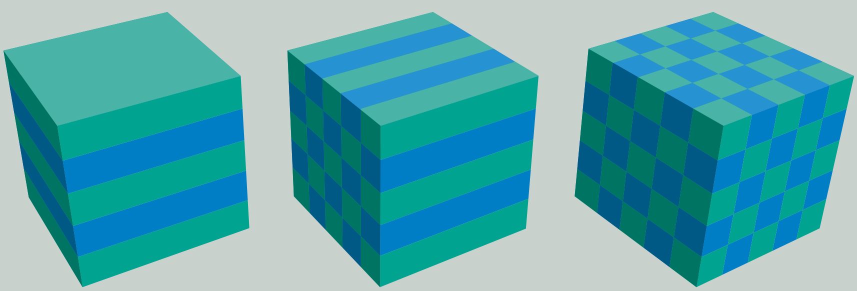
These thin layers are one type of photonic crystal: a term that sounds straight out of science fiction, but simply refers to nanoscale structures with a regular geometry. The scale of the structure and the optical properties of its arrayed components determine the wavelengths of light it transmits or reflects. Stacked layers only affect light that enters perpendicular to the surface of the stack, passing from one layer

A violet sabrewing hummingbird (*Campylopterus hemileucurus*), clothed in iridescent photonic colors.

Structural Colors in Butterfly Wings



Scanning electron micrograph of the photonic crystals in a butterfly wing.



Diagrams showing the structure of one-, two-, and three-dimensional photonic crystals, where the colors indicate materials of two refractive indices.

to the next, so they are considered one-dimensional. Two-dimensional and three-dimensional photonic crystals also exist. Almost all naturally occurring photonic crystals are built by living organisms, although a few minerals, like opal, also contain them.

Whenever you see a brilliant blue on a living thing, or an iridescent flash, or a bright metallic sheen, you can be confident that photonic crystals are responsible.

Structural colors in birds and insects

Biological systems routinely contain features with the intricate geometry required for structural coloration. Some of these intricate structures can even become fossilized, preserving the colors of long-extinct marine creatures and dinosaurs. Today, structural colors are flagrantly used by birds, insects, and countless other creatures.

Bluebirds are the classic example. As their feathers grow, cells in the vanes form strands of keratin. The dry, mature feathers contain a sponge-like mix of keratin and air pockets that have just the right dimensions to strongly scatter blue light. Because the keratin and air are arranged in a rather disordered array, termed "quasi-ordered," the color is scattered similarly in all directions. A layer of melanin under the keratin guarantees the purity of bluebird blue.

Some damselflies also use quasi-ordered clusters of particles in their epidermis to coherently scatter powdery blue or green coloration. Other damselflies take this a step further, creating photonic multilayers in the cuticle—their outermost covering—that reflect iridescent blue, green, or gold. Such iridescent colors are brilliant when seen from the right position. Butterflies also specialize in iridescence, frequently developing photonic structures to make stunning colors. A famous example is the blue morpho butterfly, whose wings are coated with sculpted photonic scales. The ridges on these scales look like Christmas trees when viewed in cross section using an electron microscope. This structure reflects a deep blue blaze almost entirely in one direction that flashes as the butterfly beats its wings. The signal is visible from hundreds of yards away, an important use of color for the butterflies and now also useful in our own medical world (see page 262).

Hummingbirds are also masters of iridescence. The colors of the male's throat (or gorget) are famous for their jewel-like brilliance when seen at a certain angle. In fact, most feathers on hummingbirds contain photonic crystals based on layers of flat, hollow structures. Even the green females have iridescent feathers, glistening in the sun.

Structures producing iridescence exist throughout living things, ranging from bristle worms, spiders, beetles, and bees to squid, fish, and many other kinds of animals and even plants. Animals often exploit them to make brilliant, highly directional, pure-colored signals that can be aimed at any desired viewer.

Structural colors in primates

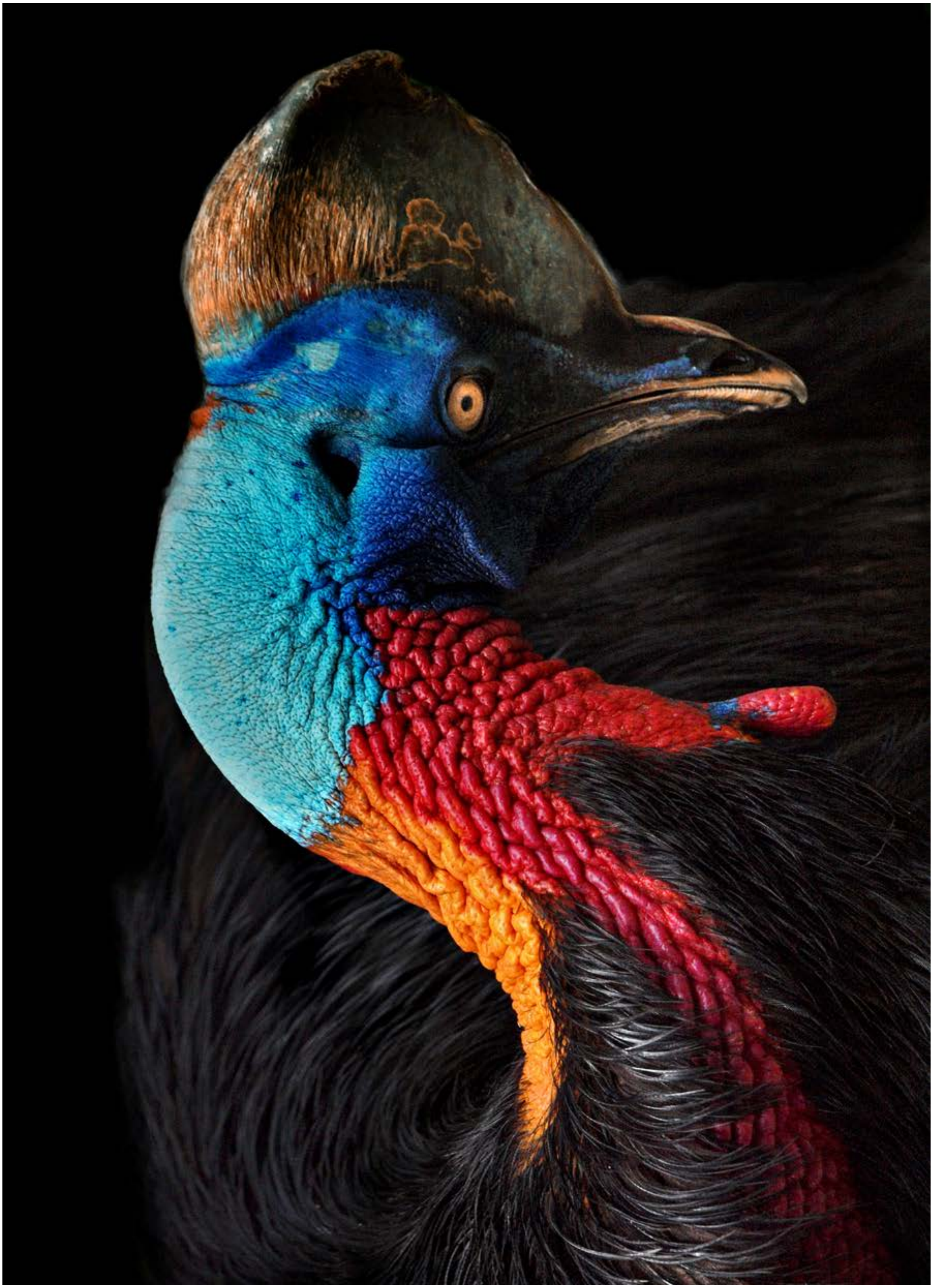
OPPOSITE: Rear view of a male black-faced vervet monkey (*Mandrillus sphynx*), showing its blue testicles colored by coherently scattered light.

A memorable sight on an African safari is a retreating male vervet monkey. Against its gray fur, its strikingly blue testicles are unmissable. How can a mammal produce such an uncommon color?

After all, mammals are not typically colorful creatures. The yellow stripes of tigers and red coats of foxes blend into nearby vegetation when viewed by their mammalian prey. But among primates there are golden tamarins, ruddy orangutans, red howler monkeys, blushing macaques, and dramatically red-faced uakaris. Any red skin patches are due to a plentiful blood supply, while the reddish or golden pelts probably result from deposits of phaeomelanin (the same thing that gives rise to red hair in people).

Blue patches occur on bare skin in male vervets, male mandrills, and golden snub-nosed monkeys. No non-primate mammal uses pure blue coloration—blue whales are really blue-gray. The fine hairs of some populations of wildebeests and of the Maltese tiger can take on a bluish sheen; this is probably due to weak diffraction of blue light. Ironically, the actual blue monkey is only faintly blue in certain lights, probably for the same reason.

So, how does a primate become blue? And why? Just like the blue of a bluebird, the blue of a primate is a structural color. The mechanism is analogous to that producing blue feathers in bluebirds—quasi-ordered arrays of tissue. In the case of primates, the array consists of parallel collagen fibers in the dermis layer of the skin. This structure coherently



ABOVE: The blue face of a male mandrill (*Chlorocebus pygerythrus*). The hue is a structural color produced by coherent scattering.

OPPOSITE: The male cassowary (*Casuarius casuarius*) advertises his presence in the rainforests of Australia with a head of contrasting colors. The blue is made by a structural light scattering mechanism similar to the mandrill.

scatters blue light. Since the array is not a true photonic crystal, being rather disordered, the color is not iridescent, appearing the same from any direction.

We can only surmise why this happens, which is that it is likely a strong sexual signal in male mandrills, with their blue patches on the face and rump. The same probably holds for vervets. In the snub-nosed monkeys it seems to be a species characteristic, since all individuals have the same appearance.

Primates have the best color vision of all mammals, which surely explains their frequent use of bright colors as signals. Our own primate vision lets us experience these colors just as they appear to our near cousins.

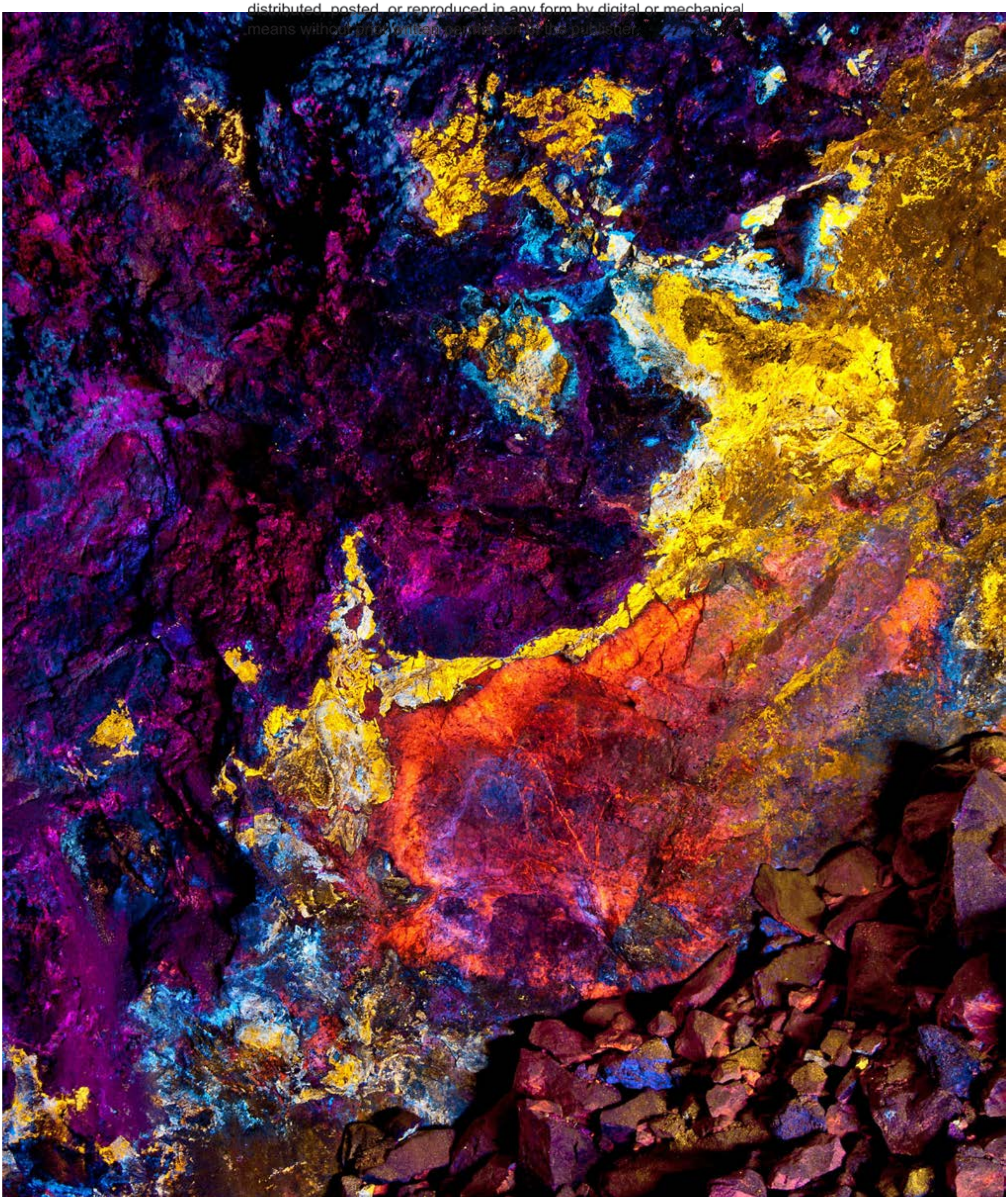
Fluorescence

To humans, fluorescence can look as if a material is glowing. The color you see may not be what you would expect, however, and certainly never very bright.

With the exceptions of some rare (and dramatic) conversions between energy and matter, energy is turned into other forms of energy. In the case of pigments, this means that all light that is absorbed by the surface of a colored organism is converted to other forms of energy.

When the light is extremely bright—for example, a laser—its energy can partially be turned into sound, ringing the tissue like a bell. For the most part though, the light is converted into heat. This is why black shirts and cars get hot on a sunny day, and why cell phones get so hot in the sun that they shut down. However, in certain cases, some of the light energy that is absorbed by a pigment is actually re-emitted as light. When the light is re-emitted so slowly that it lasts for many minutes after the original light has been shut off, it is referred to as phosphorescence. This is what may make your watch dial, the stick-on stars on a child's bedroom ceiling, and the eerie fungus glowing in the forest all glow in the dark (see page 155).

Fluorescence is when some light is re-emitted but only when the original light is present. Fluorescence has a number of special properties. One is that because only part of the energy of the original light—the excitation—is re-emitted, it must only contain colors (wavelengths) that have less energy. This means that fluorescence is always towards the redder end of the spectrum than the excitation light; typically it is just one color away, so ultraviolet excitation typically leads to blue fluorescence, blue leads to green, and green leads to red. However, it can sometimes be very far from the color of the excitation light. Secondly, fluorescence is typically not what is called an "efficient" process. This means that it is normally much dimmer than the excitation, sometimes 50 to 100 times dimmer. For this reason, we can usually only see it if the excitation light is blocked with a filter. With this light blocked, however, fluorescence can make it appear that the substance is glowing, which can be quite beautiful.



Minerals fluorescing in a tunnel lit by UV light: sphalerite is yellow, calcite is red, hydrozincite is white. Photographed at the Copper Queen Mine in Bisbee, Arizona.

Discoveries in fluorescence

Recent advances in fluorescent imaging, which shine a bright UV or blue light on an object and then block the eye from seeing that light, have shown that fluorescence is common in nature. It is seen in many minerals, especially the mineral fluorite, which is named for its strong and beautiful fluorescence under UV light. Fluorite's fluorescence is usually a deep blue, but can be nearly every color of the rainbow, depending on the impurities within the mineral. The geology sections in many museums contain exhibits of fluorescent rocks, where the light emission is triggered by a button that turns on a UV or deep blue light.

OPPOSITE: Desert hairy scorpion (*Hadrurus spadix*) in eastern Oregon, USA, fluorescing under UV light.

Fluorescence in biological tissue is a more recent discovery, and is common wherever pigments are used. This is because pigments absorb light, which is the first step in creating fluorescence. Certain common and important biological molecules fluoresce. For example, the keratin that makes up our hair, fingernails, and parts of our skin fluoresces green, while chlorophyll, which is found in nearly every plant and a number of other organisms, fluoresces red. Indeed, almost every major group of animals and plants have fluorescent pigments. Scorpions strongly emit blue-green light when excited by UV light, which has been used to find them at night, but is almost certainly not useful for the animals themselves. The common nature of fluorescence has also generated a fair bit of excitement among scientists and has led to the hypothesis that fluorescence serves a visual purpose.

We must be careful, however, in ascribing a function to a given example of fluorescence. As discussed, fluorescence tends to be weak. It also often requires excitation from parts of the sun's spectrum that are not very bright to begin with, such as the UV region. For these reasons, fluorescence is usually much harder to see under natural lighting conditions than it is in a laboratory, or at night where very bright excitation lights can be used together with filters to maximize the effect. The glow from scorpions, for example, which is so striking under UV lamps at night, is not even noticeable during the day, because even though more UV light is present, the blue emission is overwhelmed by the natural blue daylight.

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