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Glow, Big Glowworm

It behooves parents to respect their offspring, particularly when the youngsters are hungry

by Stephen Jay Gould

Small misunderstandings are often a prod to insight or victory. For such a minor error with major consequences, Laurel and Hardy got into terminal trouble with the toymaster in *March of the Wooden Soldiers*—they got fired for building 100 soldiers six feet high, when Santa had ordered 600 at one foot. But the six-footers later saved toyland from the invasion of Barnaby and his bogeymen.

In insects that undergo a complete metamorphosis, cells that will form adult tissues are already present in the bodies of larvae as isolated patches called imaginal disks. For many years, I regarded this term as one of the oddest in all biology—for I always read "imaginal" as "imaginary" and thought I was being told that this substrate of maturity really didn't exist at all.

When I learned the true origin of this term, I realized that I had not only misunderstood but had made an absolutely backward interpretation. I also discovered that my resolution had taught me something interesting—about ways of looking at the world, not about any facts of nature per se—and I therefore judged my former error as fruitful.

Linnaeus himself, father of taxonomy, named the stages of insect development. He designated the feeding stage that hatched from the egg as a larva (the caterpillar of a moth or maggot of a housefly), and he called the sexually mature adult an imago, hence imaginal disk for precursors of adult tissues within the larva.

The etymologies of these terms provided my insight—a larva is a mask; an imago, the image or essential form of a species. Linnaeus, in other words, viewed the development of insects as progress toward fulfillment. The first stage is only preparatory; it hides the true and complete representation of a species. The final form embodies the essence of louseness, thripsness, or flyness. Imaginal disks, by both etymology and concept, are bits of higher reality lurking within initial imperfection—no sign of "let's pretend" here.

Most impediments to scientific understanding are conceptual locks, not factual lacks. Most difficult to dislodge are those biases that escape our scrutiny because they seem so obviously, even ineluctably, just. We know ourselves best and tend to view other creatures as mirrors of our own constitution and social arrangements. (Aristotle, and nearly two millennia of successors, designated the large bee that leads the swarm as a king.)

Few aspects of human existence are more basic than our life cycle of growth and development. For all the glories of childhood, we in the West have generally viewed our youngsters as undeveloped and imperfect adults—smaller, weaker, and more ignorant. Adulthood is a termination; childhood, an upward path. How natural, then, that we should also interpret the life cycles of other organisms as a linear path from imperfect potential to final realization—from the small, ill-formed creature that first develops from an egg to the large and complex fruition that produces the egg of the next generation.

How obvious, in particular, that insect larvae are imperfect juveniles and imagoes are realized adults. Linnaeus's etymology embodies this traditional interpretation imposed from human life upon the development of insects. When we combine this dubious comparison of human and insect life cycles with our more general preference for viewing developmental sequences as ladders of progress (a prejudice that has hampered our understanding of evolution even more than our resolution of embryology), insect larvae seem doomed to easy dismissal by an aggregation of biases—etymological, conceptual, and parochial.

If we turn to two leading works of popular science, published five years after Darwin's *Origin of Species*—one on life cycles in general, the other on insects—we obtain a good sense of these traditional biases. A. de Quatrefages, great French student of that economic leader among insect larvae, the silkworm, wrote in his *Metamorphosis of Man and the Lower Animals* (1864) that "larvae . . . are always incomplete beings; they are true first sketches, which are rendered more and more perfect at each developmental phase."

An Introduction to Entomology, by William Kirby, rector of Barham, and William Spence, wins first prize among British works of popular science for popularity, for longevity (its first edition appeared in 1815), and for prose in the most preciously purple tradition of "nature writing," as satirized by example in James Joyce's *Ulysses*: "Note the meanderings of some purling rill as it babbles on its way, fanned by the gentlest zephyrs tho' quarrelling with the stony obstacles, to the tumbling waters of Neptune's blue domain . . . ." To which, Stephen Daedalus replies: "Agonizing Christ, wouldn't it give you heartburn on your arse." And for which (among other things) *Ulysses* was once banned from the United States as obscene—although I would sooner exclude that purling rill than a heartburn on any part of the anatomy.

In their first post-Darwinian edition (1863), Kirby and Spence make no bones about their preference for well-formed imagoes and their distaste for grubby larvae (a redundancy for emphasis of my point—grubs are larvae, and we owe this adjective to the same prejudice):

That active little fly, now an unbidden guest at your table, whose delicate palate selects your choicest viands, one while extending his proboscis to the margin of a drop of wine, and then gaily flying to take a more solid repast from a pear or peach; now gamboling with his comrades in the air, now gracefully currying his furled wings with his taper feet, was but the other day a disgusting grub, without wings, without legs, without eyes, wallowing, well pleased, in the midst of a mass of excrement.

The adult, they write, is called an imago "because, having laid aside its mask [larva], and cast off its swaddling bands [the pupal cocoon, or chrysalis], being no longer disguised [larva] or confined [pupa], or in any other respect imperfect, it is now become a true representative or image of its species."

The burden of metaphor becomes immeasurably heavier for larvae when Kirby and Spence then drag out that oldest of all insect analogies from an age of more pervasive Christianity—the life cycle of a butterfly to the passage of a soul from first life in the imperfect prison of a human body (larval caterpillar), to death and entombment (pupal chrysalis), to the winged freedom of resurrection (imago, or butterfly). This simile dates to the great Dutch biologist Jan Swammerdam, child of Cartesian rationalism but also, at heart, a religious mystic, who first discovered the rudimentary wings of butterflies, enfurled in late stages of larval caterpillars. Swammerdam wrote late in the seventeenth century: "This process is formed in so remarkable a manner in butterflies, that we see therein the resurrection painted before our eyes, and exemplified so as to be examined by our hands." Kirby and Spence then elaborated just a bit:

To see a caterpillar crawling upon the earth sustained by the most ordinary kinds of food, which when . . . its appointed work being finished, passes into an intermediate state of seeming death, when it is wound up in a kind of shroud and encased in a coffin, and is most commonly buried under the earth . . . then, when called by the warmth of the solar beam, they burst from their sepulchres, cast off their cerements . . . come forth as a bride out of her chamber—to survey them, I say, arrayed in their nuptial glory, prepared to enjoy a new and more exalted condition of life, in which all their powers are developed, and they are arrived at the perfection of their nature . . . who that witnesses this interesting scene can help seeing in it a lively representation of man in his threefold state of existence . . . . The butterfly, the representative of the soul, is prepared in the larva for its future state of glory; . . . it will come to its state of repose in the pupa, which is its Hades; and at length, when it assumes the imago, break forth with new powers and beauty to its final glory and the reign of love.

But must we follow this tradition and view larvae as harbingers of better things? Must all life cycles be conceptualized as ladders of progress leading to an adult form? Human adults control the world's media—and the restriction of this power to one stage of our life cycle imposes a myopic view. I would be happy to counter this prejudice (as many have) by emphasizing the creativity and specialness of human childhood, but this essay speaks for insects.

I will admit that our standard prejudice applies, in one sense, to creatures like ourselves. Our bodies do grow and transform in continuity. A human adult is an enlarged version of its own childhood; it retains the same organs, reshaped a bit and often increased a great deal. (Many insects with simple life cycles, or so-called incomplete metamorphoses, also grow in continuity. This essay treats those insects that cycle through the classical stages of complete metamorphosis: egg, larva, pupa, and imago.)

But how can we apply this bias of the ladder to complex life cycles of other creatures? In what sense is the polyp of a cnidarian (the phylum of corals and their allies) more—or less—complete than the medusa that buds from its body? One stage feeds and grows; the other mates and lays eggs. They perform different and equally necessary functions. What else can one say? Insect larvae and imagoes perform the same division—larvae eat and imagoes reproduce. Moreover, larvae do not grow into imagoes by increase and complication of parts. Instead, larval tissues are sloughed off and destroyed during the pupal stage, while the imago largely develops from small aggregations of cells—the imaginal disks of this essay's beginning—that resided, but did not differentiate, within the larva. Degenerating larval tissues are often used as a culture medium for growth of the imago within the pupa. Larva and imago are different and discrete, not before and shadowy versus later and complete.

Even Kirby and Spence sensed this true distinction between objects equally well suited for feeding and reproduction, though they soon buried their insight in cascading metaphors about progress and resurrection:

Were you . . . to compare the internal conformation of the caterpillar with that of the butterfly, you would witness changes even more extraordinary. In the former you would find some thousands of muscles, which in the latter are replaced by others of a form and structure entirely different. Nearly the whole body of the caterpillar is occupied by a capacious stomach. In the butterfly it has become converted into an almost imperceptible thread-like viscus; and the abdomen is now filled by two large packets of eggs.

If we break through the tyranny of our usual bias, to a different view of larvae and imagoes as separate and potentially equal devices for feeding and reproduction, many puzzles are immediately resolved. Each stage adapts in its own way, and depending upon ecology and environment, one might be emphasized, the other degraded to insignificance in our limited eyes. The "degraded" stage might be the imago as well as the larva—more likely, in fact, since feeding and growth can be rushed only so much, but mating, as poets proclaim, can be one enchanted evening. Thus, I used to feel sorry for the mayfly and its legendary one day of existence, but such brevity only haunts the imago, and longer-lived larvae also count in the total cycle of life. And what about the seventeen-year "locust" (actually a cicada)? Larvae don't lie around doing nothing during this dog's age, waiting patiently for their few days of visible glory. They have an active life underground, including long stretches of dormancy to be sure, but also active growth through numerous molts.

Thus, we find our best examples of an alternative and expansive view of life cycles among species that emphasize the size, length, and complexity of larval life at the apparent expense of imaginal domination—where, to borrow Butler's famous line with only minor change in context, a hen really does seem to be the egg's way of manufacturing another egg. I recently encountered a fine case during a visit to New Zealand—made all the more dramatic because human perceptions focus entirely upon the larva and ignore the imago.

After you leave the smoking and steaming, the boiling and puffing, the sulfurous stench of geysers, fumaroles, and mud pots around Rotorua, you arrive at the second best site on the standard tourist itinerary of the North Island—the glowworm grotto of Waitomo Cave. Here, in utter silence, you glide by boat into a spectacular underground planetarium, an amphitheater lit with thousands of green dots—each the illuminated rear end of a fly larva (not a worm at all). (I was dazzled by the effect because I found it so unlike the heavens. Stars are arrayed in the sky at random with respect to the earth's position. Hence, we view them as clumped into constellations. This may sound paradoxical, but my statement reflects a proper and unappreciated aspect of random distributions. Evenly spaced dots are well ordered for cause. Random arrays always include some clumping, just as we will flip several heads in a row quite often so long as we can make enough tosses—and our sky is not wanting for stars. The glowworms, on the other hand, are spaced more evenly because larvae compete with, and even eat, each other—and each constructs an exclusive territory. The glowworm grotto is an ordered heaven.)

These larval glowworms are profoundly modified members of the family Mycetophilidae, or fungus gnats. Imagoes of this species are unremarkable, but the larvae rank among the earth's most curious creatures. Two larval traits (and nothing imaginal) inspired the name for this peculiar species—*Arachnocampa luminosa,* honoring both the light and the silken nest that both houses the glowworm and traps its prey (for Arachne the weaver, namesake of spiders, or arachnids, as well). The imagoes of *Arachnocampa luminosa* are small and short-lived mating machines. The much larger and longer-lived larvae have evolved three complex and coordinated adaptations—carnivory, light, and webbing—that distinguish them from the simpler larval habits of ancestral fungus gnats: burrowing into mushrooms, munching all the way.

In a total life cycle (egg to egg) of ten to eleven months, *Arachnocampa luminosa* spends eight to nine months as a larval glowworm. Larvae molt four times and grow from three- to five-millimeter hatchlings to a final length of some thirty to forty millimeters. (By contrast, imagoes are twelve to sixteen millimeters in length, males slightly smaller than females, and live but one to four days, males usually longer than females.)

Carnivory is the focus of larval existence, the coordinating theme behind a life style so different from the normal course of larval herbivory in fungus gnats. Consider its three principal ingredients:

Luminescence: The light organ of *A. luminosa* forms at the rear end of the larva from enlarged tips of four excretory tubes. These tubes carry a waste product that glows in the presence of luciferase, an enzyme also produced by the larva. This reaction requires a good supply of oxygen, and the four excretory tubes lie embedded in a dense network of respiratory tubules that both supply oxygen to fuel the reaction and then reflect and direct the light downward. This complex and specially evolved system functions to attract insects (mostly small midges) to the nest. Pupae and imagoes retain the ability to luminesce. The light of female pupae and adults attracts males, but the glow of adult males has no known function.

The Nest and Feeding Threads: From glands in its mouth, the glowworm exudes silk and mucus to construct a marvel of organic architecture. The young larva first builds the so-called nest—really more of a hollow tube or runway—some two to three times the length of its body. A network of fine silk threads suspends this nest from the cave's ceiling. The larva drops a curtain of closely spaced feeding threads from its nest. These "fishing lines" may number up to seventy per nest and may extend almost a foot in length (or ten times the span of the larva itself). Each line is studded along its entire length with evenly spaced, sticky droplets that catch intruding insects; the entire structure resembles, in miniature, a delicate curtain of glass beads. Since these lines can be tangled by the slightest current of air, caves, culverts, ditches, and calm spaces amidst vegetation provide the limited habitats for *A. luminosa* in New Zealand.

Carnivory: Using its lighted rear end as a beacon, *A. luminosa* attracts prey to its feeding threads. Two posterior papillae contain sense organs that detect vibrations of ensnared prey. The larva then crawls partway down the proper line, leaving half to two-thirds of its rear in the nest, and hauls up both line and meal at a rate of some two millimeters per second.

The rest of the life cycle pales by comparison with this complexity of larval anatomy and behavior. The pupal stage lasts a bit less than two weeks and already records a marked reduction in size (fifteen to eighteen millimeters for females, twelve to fourteen for males). I have already noted the imago's decrease in body size and duration of life. Imaginal behavior also presents little in the way of diversity or complexity. Adult flies have no mouth and do not feed at all. We commit no great exaggeration by stating that they behave as unipurpose mating and egg-laying machines during their brief existence. Up to three males may congregate at a female pupa, awaiting her emergence. They jockey for position and fight as the female fly begins to break through her encasement. As soon as the tip of her abdomen emerges, males (if present) begin to mate. Thus, females can be fertilized even before they break fully from the pupal case. Females may then live for less than a day (and no more than three), doing little more before they expire than finding an appropriate place for some 100 to 300 eggs, laid one at a time in clumps of 40 to 50. Males may live an additional day (up to four); with luck, they may find another female and do it again for posterity.

As a final and grisly irony, emphasizing larval dominance over the life cycle of *A. luminosa,* a rapacious glowworm will eat anything that touches its feeding threads. The much smaller imagoes often fly into the lines and end up as just another meal for their own children.

To throw in a tidbit for readers interested in the history of evolutionary theory, this tightly coordinated complex of larval adaptations so intrigued Richard Goldschmidt that he once wrote an entire article to argue that light, carnivory, and nest building could not have arisen by gradual piecemeal, since each makes no sense without the others—and that all, therefore, must have appeared at once as a fortuitous consequence of a large mutational change, a "hopeful monster," in his colorful terminology.

This proposal (published in English in *Revue Scientifique,* vol. 86, 1948, pp. 607–12) inspired a stern reaction from orthodox Darwinians. Although I have great sympathy for Goldschmidt's iconoclasm, he was, I think, clearly wrong in this case. As J.F. Jackson pointed out (*American Midland Naturalist,* vol. 92, 1974, pp. 240–45), Goldschmidt made an error in the taxonomic assignment of *A. luminosa* among the Mycetophilidae. He ranked this species in the subfamily Bolitophilinae. All larvae of this group burrow into soft mushrooms, and none show even incipient development of any among the three linked features that mark the unique form and behavior of *A. luminosa.* Hence, Goldschmidt argued for all or nothing.

But *A. luminosa* probably belongs in another subfamily, the Keroplatinae—and, unknown to Goldschmidt, several species within this group do display a series of plausible transitions. *Leptomorphus* catches and eats fungal spores trapped on a sheetlike nest slung below a mushroom. Some species of *Macrocera* and *Keroplatus* also build trap nets for fungal spores but will eat small arthropods that also become ensnared. Species of *Orfelia, Apemon,* and *Platyura* build webs of similar form but not associated with mushrooms—and they live exclusively on a diet of trapped insects. Finally, *Orfelia aeropiscator* (literally, air fisher) both builds a nest and hangs vertical feeding threads but does not possess a light.

These various "intermediates" are, of course, not ancestral to *A. luminosa.* Each represents a well-adapted species in its own right, not a transitional stage to the threefold association of New Zealand glowworms. But this array does show that each step in a plausible sequence of structurally intermediate stages can work as a successful organism. This style of argument follows Darwin's famous resolution for a potential evolutionary origin for the extraordinary complexity of the vertebrate eye. Darwin identified a series of structural intermediates, from simple light-sensitive dots to cameralike lens systems—not actual ancestors (for these are lost among nonpreservable eyes in a fossil record of hard parts) but plausible sequences disproving the "common sense" notion that nothing in between is possible in principle.

Please do not draw from this essay the conclusion that larvae are really more important than imagoes, either in *A. luminosa* or in general. I have tried to show that larvae must not be dismissed—as preparatory, undeveloped, or incomplete—by false analogy to a dubious (but socially favored) interpretation of human development. If any "higher reality" exists, it can only be the life cycle itself. Larva and imago are but two stages of a totality—and you really can't have one without the other. Eggs need hens as much as hens need eggs.

I do try to show that child-adult is the wrong metaphor for understanding larva-imago. I have proceeded by discussing a case where larvae attract all our attention—literally as a source of beauty; structurally in greater size, length of life, and complexity of anatomy and behavior; and evolutionarily as focus of a major transformation from a simpler and very different ancestral style—while imagoes have scarcely modified their inherited form and behavior at all. But our proper emphasis on the larva of *A. luminosa* does not mark any superiority.

We need another metaphor to break the common interpretation that degrades larvae to a penumbra of insignificance. (How many of you include maggot in your concept of fly? And how many have ever considered the mayfly's longer larval life?) The facts of nature are what they are, but we can only view them through spectacles of our mind. Our mind works largely by metaphor and comparison, not always (or often) by relentless logic. When we are caught in conceptual traps, the exit is often a change in metaphor—not because the new guideline will be truer to nature (for neither the old nor the new metaphor lies "out there" in the woods), but because we need a shift to more fruitful perspectives, and metaphor is often the best agent of conceptual transition.

If we wish to understand larvae as working items in their own right, we must replace the developmental metaphor of child-adult, with an economic simile that recognizes the basic distinction in function between larvae and imagoes—larvae as machines built for feeding and imagoes as devices for reproduction. Fortunately, an obvious candidate presents itself on the very first page of the founding document itself—Adam Smith's *Wealth of Nations*. We find our superior metaphor in the title of chapter 1, *On the Division of Labor*, and in Smith's opening sentence:

> The greatest improvement in the productive powers of labor, and the greater part of the skill, dexterity, and judgment with which it is anywhere directed, or applied, seem to have been the effects of the division of labor.

By separating the different, sometimes contradictory, functions of feeding and reproduction into different phases of the life cycle, insects with complete metamorphosis have achieved a division of labor that permits a finer adaptive honing of each separate activity.

If you can dredge up old memories of your first college course in economics, you will remember that Adam Smith purposely chose a humble example to illustrate the division of labor—pin making. He identifies eighteen separate actions in drawing the wire, cutting, pointing, manufacture of the head, fastening head to shaft, and mounting the finished products in paper for sale. One man, he argues, could make fewer than twenty pins a day if he performed all these operations himself. But ten men, sharing the work by rigid division of labor, can manufacture about 48,000 pins a day. A human life spent pointing pins or fashioning their heads or pushing them into paper may strike us as the height of tedium, but larvae of *A. luminosa* encounter no obvious psychic stress in a life fully devoted to gastronomy.

All hobbyists and professional entomologists will, no doubt, have recognized an unintended irony in Smith's selection of pin making to illustrate the division of labor. Pins are the primary stock-in-trade of any insect collector. They are used to fasten the dry and chitinous imagoes—but not the fat and juicy larvae—to collecting boards and boxes. Thus, the imagoes of *A. luminosa* may end their natural life caught in a larval web, but if they happen to fall into the clutches of a human collector, they will end up transfixed by the very object that symbolizes their fall from conceptual dominance to proper partnership.

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