

1 | The Flamingo's Smile

BUFFALO BILL played his designated role in reducing the American bison from an estimated population of 60 million to near extinction. In 1867, under a contract to provide food for railroad crews, he and his men killed 4,280 animals in just eight months. His slaughter may have been indiscriminate, but the resulting beef was not wasted. Other despoilers of our natural heritage killed bison with even greater abandon, removed the tongue only (considered a great delicacy in some quarters), and left the rest of the carcass to rot.

Tongues have figured before in the sad annals of human rapacity. The first examples date from those infamous episodes of gastronomical gluttony—the orgies of Roman emperors. Mr. Stanley, Gilbert's "modern major general," could "quote in elegiacs all the crimes of Heliogabalus" (before demonstrating his mathematical skills, in order to cadge a rhyme, by mastering "peculiarities parabolous" in the study of conic sections). Among his other crimes, the licentious teen-aged emperor presided at banquets featuring plates heaped with flamingo tongues. Suetonius tells us that the emperor Vitellius served a gigantic concoction called the Shield of Minerva and made of parrot-fish livers, peacock and pheasant brains, lamprey guts and flamingo tongues, all "fetched in large ships of war, as far as from the Carpathian sea and the Spanish straits."

Lampreys and parrot fishes (though not without beauty)

have rarely evoked great sympathy. But flamingos, those elegant birds of brilliant red (as their name proclaims), have inspired passionate support from the poets of ancient Rome to the efforts of modern conservationists. In one of his most poignant couplets, Martial castigated the gluttony of his emperors (circa 80 A.D.) by speculating about different scenarios, had the flamingo's tongue been gifted with song like the nightingale's, rather than simple good taste:

Dat mihi penna rubens nomen; sed lingua gulosis
Nostra sapit: quid, si garrula lingua foret?

(My red wing gives me my name, but epicures regard my tongue as tasty. But what if my tongue could sing?)

Most birds have skinny pointed tongues, scarcely fit for an emperor, even in large quantities. The flamingo, much to its later and unanticipated sorrow, evolved a large, soft, fleshy tongue. Why?

Flamingos have developed a surpassingly rare mode of feeding, unique among birds and evolved by very few other vertebrates. Their bills are lined with numerous, complex rows of horny lamellae—filters that work like the whalebone plates of giant baleen whales. Flamingos are commonly misportrayed as denizens of lush tropical islands—something amusing to watch while you sip your rum and coke on the casino veranda. In fact, they dwell in one of the world's harshest habitats—shallow hypersaline lakes. Few creatures can tolerate the unusual environments of these saline deserts. Those that thrive can, in the absence of competitors, build their populations to enormous numbers. Hypersaline lakes therefore provide predators with ideal conditions for evolving a strategy of filter feeding—few types of potential prey, available in large numbers and at essentially uniform size. *Phoenicopterus ruber*, the greater flamingo (and most familiar species of our zoos and conservation areas in the Bahamas and Bonaire), filters prey in the predominant range of an inch or so—small mollusks, crustacea, and insect larvae, for example. But *Phoeniconaias minor*, the lesser flamingo, has filters so dense and efficient that they segre-

gate cells of blue-green algae and diatoms with diameters of 0.02 to 0.1 mm.

Flamingos pass water through their bill filters in two ways (as documented by Penelope M. Jenkin in her classic article of 1957): either by swinging their heads back and forth, permitting the water to flow passively through, or by the usual and more efficient system that inspired the Roman gluttons—an active pump maintained by a large and powerful tongue. The tongue fills a large channel in the lower beak. It moves rapidly back and forth, up to four times a second, drawing water through the filters on the backwards pull and expelling it on the forward drive. The tongue's surface also sports numerous denticles that scrape the collected food from the filters (just as whales collect krill from their baleen plates).

The extensive literature on feeding in flamingos has highlighted the unique filters—and often neglected another, intimately related, feature equally remarkable and long appreciated by the great naturalists. Flamingos feed with their heads upside down. They stand in shallow water and swing their heads down to the level of their feet, subtly adjusting the head's position by lengthening or shortening the s-curve of the neck. This motion naturally turns the head upside down, and the bills therefore reverse their conventional roles in feeding. The anatomical upper bill of the flamingo lies beneath and serves, functionally, as a lower jaw. The anatomical lower bill stands uppermost, in the position assumed by upper bills in nearly all other birds.

With this curious reversal, we finally reach the theme of this essay: Has this unusual behavior led to any changes of form and, if so, what and how? Darwin's theory, as a statement about adaptation to immediate environments (not general progress or global direction), predicts that form should follow function to establish good fit for peculiar life styles. In short, we might suspect that the flamingo's upper bill, working functionally as a lower jaw, would evolve to approximate, or even mimic, the usual form of a bird's lower jaw (and vice versa for the anatomical lower, and functionally upper, beak). Has such a change occurred?



The enigmatic smile of a swan—or is it?

Nature harbors a large suite of oddities so special that we scarcely know what to predict. But, in this case, we encounter a precise reversal of anatomy and usual function—leading to a definite expectation: upside-down animals should reorient the form of their bodies to a new function when current behavior and conventional anatomy conflict.

We may begin by sparing the usual pontification (but only for a while) and looking at a picture. If this picture excites a vague feeling of familiarity slightly awry, your perceptions are acute, but ride with me for a while.

We seem to see a long-necked swan with a broad smile. But look carefully, for details betray this impossible beast. Its mouth opens *above* the eyes; its feathers run the wrong way; and where are its legs? I now show you the celebrated original in its proper orientation (and with the legs restored)—the flamingo from J.J. Audubon's *Birds of America*, and a sure entry on anyone's hit parade of most famous pictures in natural history.

This dramatic perceptual switch from happy swan to haughty flamingo recalls any standard item in the psychological arsenal of optical illusion—particularly the young well-dressed lady looking away who becomes the old hag in profile. In fact, any accurately executed picture of a flamingo produces the same jolting effect when viewed upside down (I have checked all historically important portraits)—and for an obvious reason. The jaws have evolved to fit their reversed function. The flamingo's upper jaw does look like a typical bird's lower bill, and we therefore see the upside-down flamingo not as an absurdity, but as an only slightly odd swan-like bird.

The morphological alterations extend far beyond the changes in external form that produce such a striking perceptual shift from upright flamingo to inverted "swan." But note first the peculiar curve of the beak itself. The flamingo's bill projects out from its face, but then makes a sharp angular turn, producing the pronounced hump that looks like a trough (and works like one) when inverted for feeding. Some Near Eastern peoples call flamingos "camels of the sea," not because the inclined bill recalls the hump on a camel's back, but because it mimics the bend of the nose that imparts an inappropriate (but unshakable) impression of haughtiness to both animals (see my essay on the history of Mickey Mouse and the messages accidentally conveyed by facial features of animals—essay 9 in *The Panda's Thumb*). Turned upside down, the hump becomes a grin as a smiling "swan" replaces the haughty flamingo.

The bills are elaborately adapted to their reversed roles, not simply bent in the middle for proper reorientation. First, relative sizes have been rearranged to complement



The famous flamingo, FROM J.J. AUDUBON'S *Birds of America*.

the shapes. The upper bill is small and shallow, the lower deep and massive. (In most birds, the smaller lower bill moves up and down against the larger upper beak.) Second, the flamingo's lower bill (functionally upper in feeding) has

evolved unusual rigidity. The bones of each half (or ramus, in technical parlance) are tightly fused, and the rami themselves are then bonded extensively to each other. The lower bill is massive and well braced. The tongue runs fore and aft in a deep trough cut into the lower jaw. (Remember that filter feeding serves as a coordinating theme for all these changes—the upside-down feeding posture, the attendant alteration in size and shape of the bills, and the fat tongue that once almost sealed the flamingo's fate.) Third, in most species of flamingo, the smaller upper jaw slots into a receiving space on the larger lower jaw, a reversal of the usual convention—lower jaw moving up and fitting into a larger upper bill.

These complex, coordinated changes make a persuasive case, but they leave a missing piece, recognized as the key to flamingo peculiarities ever since Menippus recorded the first preserved speculation nearly 300 years before Martial's plea: are movements also reversed to match the inversion of form?

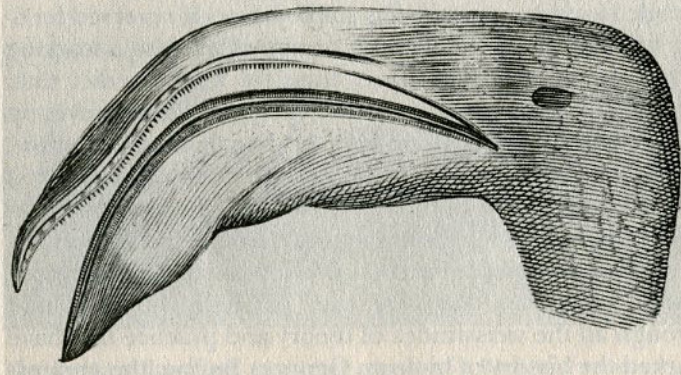
In most birds (and mammals, including us), the upper jaw fuses to the skull; chewing, biting, and shouting move the mobile lower jaw against this stable brace. If reversed feeding has converted the flamingo's upper jaw into a working lower jaw in size and shape, then we must predict that, contrary to all anatomical custom, this upper beak moves up and down against a rigid lower jaw. The flamingo, in short, should feed by raising and lowering its upper jaw.

With great credit to the clear thinking of our finest naturalists, I noted with pleasure in my readings that this central question has been continually posed as paramount for more than 2,000 years—by scientists of many cultures and through all the vicissitudes of theory and practice that have marked the history of biology. Georges Buffon, the greatest of all synoptic naturalists, began his mid-eighteenth-century essay on flamingos by admitting the fame of their red color, while maintaining that the odd form of their beak posed a problem of even greater interest: "This fiery color is not the only striking character displayed by this bird. Its beak has an extraordinary form, the upper bill flattened and

strongly bent at its midpoint, the lower thick and well set, like a large spoon." In short, and in his own lovely tongue, "une figure d'un beau bizarre et d'une forme distinguée." Then, tracing the question right back to Menippus, Buffon stated the *primum desideratum* of flamingo studies—"to know if, in this singular beak, it is (as many naturalists have said) the upper part that moves, while the lower remains fixed and motionless."

The first extensive and explicit commentary had been offered in 1681 by Nehemiah Grew, the great English naturalist (known primarily for his early microscopical studies of plants). Cataloguing the collections of the Royal Society—in his *Musaeum Regalis Societatis, or a catalogue and description of the natural and artificial rarities belonging to the Royal Society and preserved at Gresham Colledge, whereunto is subjoynd the comparative anatomy of stomachs and guts*—he encountered a lone flamingo (see figure) and stated: "that wherein he is most

Phoenicopter's Head



Nehemiah Grew's flamingo, 1681. The illustration accompanying the first important proposal that flamingos feed by moving their upper jaw up and down against their lower. Look at this figure upside down as well. FROM N. GREW, *MUSAEUM REGALIS SOCIETATIS*, 1681. REPRINTED FROM *NATURAL HISTORY*.



Flamingos in their characteristic feeding pose—upside down. PHOTO BY D. PURCELL.

remarkable, is his bill." Grew suspected that the oddities of the bill would all be resolved if the upper beak moved against a stationary lower jaw. He stated that the "shape and bigness of the upper beak (which here, contrary to what it is in all other birds that I have seen, is thinner and far less than the nether) speaks it to be more fit for motion and to make the appulse and the nether to receive it."

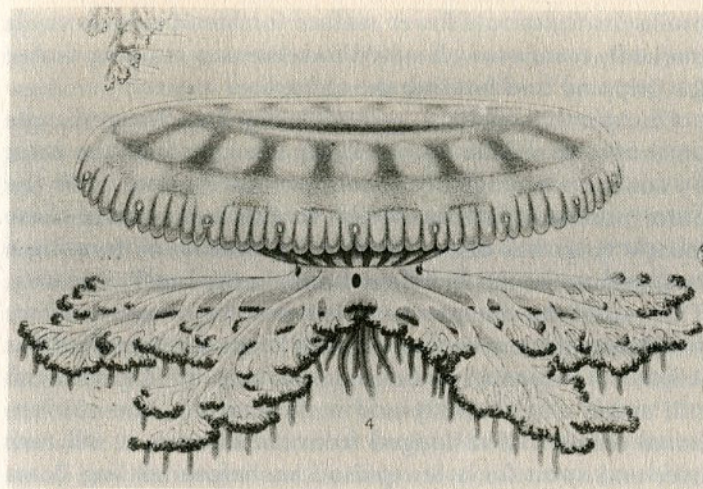
The question was not fully resolved until Jenkin published her comprehensive paper in 1957—affirming with hard data the suspicions and good judgment of Menippus, Grew, and Buffon. In fact, flamingos (along with many other birds) have developed a highly mobile ball and socket joint between upper and lower jaws. The beaks therefore have great mobility, and each can move independently. In preening, either the upper or lower jaw may be opened and operated against the other. But, in feeding, the upper jaw usually

drops and raises against a stationary lower jaw—just as the great naturalists had always expected.

The flamingo's flip-flop is complete and comprehensive—in form *and* motion. The shapes are overturned by bending, the sizes reversed, the slotting inverted, the buttressing transposed. The action, too, is topsy-turvy. A peculiar reversal in behavior has engendered a complex inversion of form. Evolution as adaptation to particular modes of life—Darwin's vision—gains strength from an extreme test imposed by life upside down.

But do flamingos just provide a funny example, or do they symbolize a generality? What about other creatures that live upside down? Consider another animal of shallow West Indian waters, the inverted jellyfish, *Cassiopea xamachana* (the unorthodox trivial name honors the Native American designation for the island of Jamaica).

Cassiopea is an unconventional jellyfish in many ways. It grows neither marginal tentacles nor central mouth. Instead, eight fleshy and complexly branched "oral arms" (so called because each contains a separate mouth) emerge from a short and stout central stalk, itself attached to a usual jellyfish umbrella with a difference (see figure—a reproduction of the classical lithograph from Mayer's 1910 monograph, *Medusae of the World*). The oral arms are crammed with symbiotic algal cells, a possible adaptive impetus for their elaborate branching (to provide light-capturing surfaces for the photosynthetic symbionts). Each oral arm harbors about forty oral vesicles—hollow sacs connected with the feeding canals and containing bags of nematocysts, or stinging cells, at their tips. The vesicles shoot their nematocysts at prey (mostly small crustaceans) in strings of mucus; the strings with their attached and paralyzed victims are then pulled into the oral mouths. (Yes, I was as amused as some of you by the redundant "oral mouth"—the zoological equivalent of pizza pie or AC current. This clumsy phrase arises as unfelicitous fallout from a prior decision to call the appendages "oral arms"—as a shortcut for "mouths of the oral arms.")



Cassiopea xamachana. Note concavity of bell's upper surface and the raised muscular ring. Figure reproduced as presented (in the ecologically wrong right-side-up position). FROM MAYER, 1910. REPRINTED FROM NATURAL HISTORY.

Cassiopea's unusual anatomy matches its unconventional orientation and style of life. Ordinary, self-respecting jellyfish swim actively with their umbrellas uppermost and their arms and tentacles below. *Cassiopea* lies stationary on the bottom of shallow ponds and coastal areas—upside down. The top of its umbrella hugs the sediment and the oral arms wave above, waiting for small crustacea to enter their orbit. Sailors at Fort Jefferson in the Tortugas, where *Cassiopea* lined the docks, called them "moss cakes." (Since *Cassiopea* can give a nasty sting, and since men in blue usually spice their language to match the stimulus, I wonder what the sailors really called them. But Mr. H.F. Perkins, writing in 1908 on the anatomy of *Cassiopea*, didn't choose to tell us.)

The umbrella of *Cassiopea* recalls the flamingo's jaw in its adaptation to reversed life. The umbrella's upper surface is smoothly convex in ordinary jellyfish, as hydrodynamic efficiency dictates. But the upper surface of *Cassiopea's* um-

rella (its functional lower surface for life upside down) is markedly *concave*—well suited to serve as a cupping device for gripping and holding the substrate.

Cassiopea has made a second intriguing change for its unusual reversed life. Most jellyfish move through the water by contracting rings of concentric muscles that circle the outer portion of the umbrella. In *Cassiopea*, one of these muscle rings has been raised and accentuated, forming a continuous circular band surrounding the inner concavity. This raised rim operates together with the concave surface to form an efficient suction cup that keeps the “head” of this jellyfish in its proper position on the bottom. (*Cassiopea* can still swim, albeit weakly and inefficiently, in the conventional manner. If dislodged from the bottom, it will turn over and swim for a few pulsations before settling down again on its head.) Some scientists have also suggested that the pulsating contractions of the concentric muscles, ordinarily used in swimming, serve other important functions in *Cassiopea*'s attached, upside-down position—maintaining connection with the substrate by pushing the animal down and moving water currents with potential prey towards the oral arms. But these reasonable proposals have not been properly tested.

Thus, flamingos and *Cassiopea*—two animals that could scarcely differ more in design and evolutionary history—share the common feature of feeding upside down. As a general message amidst the particulars, they have both redesigned conventional anatomy to match reversed life style. The flamingo's upper bill has changed radically—in size, shape, and motion—to look and work like the lower beak of most birds. The structural top of *Cassiopea*'s umbrella has inverted its shape, all the better to work properly as an ecological bottom.

Adaptation has a wonderful power to alter an anatomical design, widespread and stable among thousands of species, for the reversed requirements of an odd life style assumed by one or a few aberrant forms. Yet, we should not conclude that Darwinian adaptation to local environments has unconstrained power to design theoretically optimum shapes for

all situations. Natural selection, as a historical process, can only work with material available—in these cases, the conventional designs evolved for ordinary life. The resulting imperfections and odd solutions, cobbled together from parts on hand, record a process that unfolds in time from unsuited antecedents, not the work of a perfect architect creating *ab nihilo*. *Cassiopea* co-opts a band of muscles ordinarily used in swimming and forms a raised rim to grasp the substrate. Flamingos bend their bill in a curious hump as the only topological solution to a new orientation.

These adaptations to life upside down are not just funny facts. They help us to comprehend the solution to a major, and classical, dilemma in evolutionary theory (hence my decision to unite them in this essay). We can easily understand how flamingos and *Cassiopea* work; their unusual features do fit them for their unconventional lives. But how do these odd structures arise if evolution must proceed through intermediate steps (no one will seriously suggest that the first proto-flamingo turned its head upside down and then produced offspring with a complete set of complex adaptations to reversed life).

In pre-Darwinian years of the early nineteenth century, when evolution was new, and when early exponents of such a radical idea were trying to work out its ramifying implications, two schools emerged and carried out an interesting (and largely forgotten) struggle until Darwin resolved their debate. Both sides admitted the good fit that usually exists between form and function—adaptation in its static, non-historical meaning. Structuralists, like Etienne Geoffroy Saint-Hilaire argued that form must change first and then find a function. Functionalists, like Jean Baptiste Lamarck, held that organisms must first adopt a different mode of life to trigger some sort of pressure for a subsequently altered form.

The nature of this “pressure” inspired another famous (and better remembered, but no more important) debate. Lamarck held that organisms respond creatively to the needs imposed by their environments and then pass the resulting changes directly to offspring—“inheritance of ac-

quired characters" in the usual jargon. Darwin argued that environments do not impose their adaptive requirements directly. Rather, those organisms that vary, by good fortune, in directions better suited to local environments leave more surviving offspring by a process of natural selection.

Since Darwin won this argument about the nature of signals that pass from environment to organism, Lamarck has been eclipsed and still, despite many efforts by historians to set the record straight, suffers from an imposed reputation as a loser not to be taken seriously for any of his ideas.

But Lamarck had the right answer (the same as Darwin's) to the larger dispute between structuralists and functionalists. (He only proposed the wrong mechanism for how environment gets its message to organisms.) Geoffroy's structuralist solution poses an obvious dilemma. If structure changes first, according to unknown "laws of form," and then finds the environment best suited to its altered state, how can precise adaptation arise? We might allow that some very basic and general changes could precede any functional meaning or advantage—an animal might, for example, get larger and then exploit the inherent advantages of increased size. But can we seriously believe that something so complex, so multifarious, and so intimately suited for an unusual ecology as the flamingo's bill might arise before the fact and without relationship to its usefulness—permitting the flamingo to discover only later how nicely such a beak worked upside down?

Lamarck's functionalist solution has an elegant simplicity accepted by nearly all evolutionists today (but usually attributed to Darwin, who also supported it. However much I revere Darwin, I want to advance a plea for recognizing this basic principle as Lamarck's primary contribution. It does not appear as an incidental footnote in Lamarck's *Philosophie zoologique* of 1809, but as a central theme of his book. Lamarck knew exactly what he was arguing and why.). Lamarck simply recognized that change of behavior must precede alteration of form. An organism enters a new environment with its old form suited to other styles of life. The behavioral innovation establishes a discordance between

new function and inherited form—an impetus to change (by creative response and direct inheritance for Lamarck, by natural selection for Darwin). The protoflamingo first inverts its normal bill—and it doesn't work very well. The proto-*Cassiopea* turns over, but its convex umbrella doesn't clutch the substrate. Lamarck wrote:

It is not the shape either of the body or its parts, which gives rise to the habits of animals and their mode of life; but it is, on the contrary, the habits, mode of life, and all the other influences of the environment, which have in course of time built up the shape of the body and of the parts of animals.

The direct evidence for Lamarck's solution cannot emerge from such "completed" adaptations as the flamingo's beak or *Cassiopea*'s umbrella—though the inference even here becomes quite compelling (for why should flamingos, uniquely among birds, develop such a peculiar beak if not to exploit their chosen, odd environment). We must catch the process at its beginning stages—by finding upside down animals that have already altered their behavior, but not their form.

African catfishes of the family Mochokidae include several species that characteristically swim upside down (see G. Sterba, in bibliography). Behavior has already changed radically, and we even have good hints about the triggers in some cases. (*Synodontis nigriventris*, for example, eats algae by grazing the undersides of leaves on water-dwelling plants.) But form has altered scarcely, if at all. A few species have reversed the usual pattern of cryptic coloration for fish swimming near the surface. The light bellies of most fish render them invisible to predators looking up through the water into sunlight above. But *S. nigriventris*, as its name (black belly) implies, is dark on its anatomical underside, and light on its structural top. Since this fish swims upside down, the light side lies below, as usual. Yet, beyond this switch in color, most upside-down mochokids look just like their upright relatives. Size, shape, and position of fins have

not changed. The trigger (presumably recent) is behavioral. We shall wait to see what changes in form might still ensue.

As a final point, readers might acknowledge my argument, but dismiss the examples as trivial or peripheral. We all love flamingos, and *Cassiopea* might prick our interest (our bodies too, if we get in the way). Mochokids are amusing in aquaria. But can we view life upside down as any more than a funny little corner of natural history? All my examples are the dead-end adaptations of a few species; can turning upside down lead to anything fundamental and expansive?

As an important illustration from history (though almost surely an incorrect idea), life upside down once compelled attention as a leading speculation for the origin of vertebrates—the “worm that turned” theory, so to speak. Annelids and arthropods, the most complex of segmented invertebrates, develop ventral (bottom) nerve cords; the esophagus pierces the nerve cords and connects an even more ventral mouth to a central alimentary (gut) canal lying above the nerve cords. In vertebrates, the major nerve cord runs fore and aft in a dorsal (top) position, and the alimentary canal, including mouth and esophagus, lies entirely below.

These two designs seem quite incompatible and unrelated. But, and ironically in the context of my contrast between structural and functional views, the greatest of all structuralists, Geoffroy Saint-Hilaire himself, noted that an annelid turned on its back would look more than a bit like a vertebrate—for the ventral nerve cord would then become dorsal and lie above the alimentary canal. In solving one problem, others emerge: the mouth now opens atop the inverted worm. Geoffroy suggested, as an *ad hoc* solution straining credulity, that the old mouth and nerve-piercing esophagus simply disappeared, and that an entirely new opening (the vertebrate mouth) developed below the dorsal nerve cord, connecting directly with the gut canal, and no longer piercing the nervous system. (So many other differences plague the comparison—lack of any annelid structure resembling the notocord or gill slits of vertebrates, funda-

mental disparities in embryological development between the two groups, for example—that the worm theory never commanded general assent, though it remained a leading contender for nearly a century.)

Geoffroy never intended his comparison of vertebrate to inverted worm as an evolutionary speculation, but only as a structural comparison to buttress his remarkable theory that all animals shared a common architectural plan. (He also argued that the segments of an insect's external skeleton matched our internal vertebrae—and that insects literally lived within their own vertebrae. This comparison compelled the additional and astonishing conclusion, forthrightly maintained by Geoffroy, that insect legs are vertebrate ribs.)

Geoffroy also did not advance his comparison as a functional hypothesis about adaptation—he did not argue (as Lamarck might have done) that a worm's innovative behavior (in turning over) triggered an adaptive pressure for redesign. Quite the contrary. As a structuralist, he contended that belly and back are meaningless terms of human invention to describe a superficial orientation utterly without significance to what really matters—abstract structural laws of form and permitted pathways of change.

Today, we reject Geoffroy's speculation along with his approach to form and function. Life upside down affirms Lamarck's claim that substantial change in morphology usually arises as a consequence of behavioral triggers. The famous fourteenth-century motto of that upstart institution, New College, Oxford, seems to embody an essential truth about history as well as conduct: *manners makyth man*.