

18 | Return of the Hopeful Monster

BIG BROTHER, THE tyrant of George Orwell's *1984*, directed his daily Two Minutes Hate against Emmanuel Goldstein, enemy of the people. When I studied evolutionary biology in graduate school during the mid-1960s, official rebuke and derision focused upon Richard Goldschmidt, a famous geneticist who, we were told, had gone astray. Although *1984* creeps up on us, I trust that the world will not be in Big Brother's grip by then. I do, however, predict that during this decade Goldschmidt will be largely vindicated in the world of evolutionary biology.

Goldschmidt, a Jewish refugee from Hitler's decimation of German science, spent the remainder of his career at Berkeley, where he died in 1958. His views on evolution ran afoul of the great neo-Darwinian synthesis forged during the 1930s and 1940s and continuing today as a reigning, if insecure, orthodoxy. Contemporary neo-Darwinism is often called the "synthetic theory of evolution" because it united the theories of population genetics with the classical observations of morphology, systematics, embryology, biogeography, and paleontology.

The core of this synthetic theory restates the two most characteristic assertions of Darwin himself: first, that evolution is a two-stage process (random variation as raw material, natural selection as a directing force); secondly, that evolutionary change is generally slow, steady, gradual, and continuous.

Geneticists can study the gradual increase of favored genes within populations of fruit flies in laboratory bottles. Naturalists can record the steady replacement of light moths by dark moths as industrial soot blackens the trees of Britain. Orthodox neo-Darwinians extrapolate these even and continuous changes to the most profound structural transitions in the history of life: by a long series of insensibly graded intermediate steps, birds are linked to reptiles, fish with jaws to their jawless ancestors. Macroevolution (major structural transition) is nothing more than microevolution (flies in bottles) extended. If black moths can displace white moths in a century, then reptiles can become birds in a few million years by the smooth and sequential summation of countless changes. The shift of gene frequencies in local populations is an adequate model for all evolutionary processes—or so the current orthodoxy states.

The most sophisticated of modern American textbooks for introductory biology expresses its allegiance to the conventional view in this way:

[Can] more extensive evolutionary change, macroevolution, be explained as an outcome of these microevolutionary shifts? Did birds really arise from reptiles by an accumulation of gene substitutions of the kind illustrated by the raspberry eye-color gene?

The answer is that it is entirely plausible, and no one has come up with a better explanation. . . . The fossil record suggests that macroevolution is indeed gradual, paced at a rate that leads to the conclusion that it is based upon hundreds or thousands of gene substitutions no different in kind from the ones examined in our case histories.

Many evolutionists view strict continuity between micro- and macroevolution as an essential ingredient of Darwinism and a necessary corollary of natural selection. Yet, as I argue in essay 17, Thomas Henry Huxley divided the two issues of natural selection and gradualism and warned Dar-

win that his strict and unwarranted adherence to gradualism might undermine his entire system. The fossil record with its abrupt transitions offers no support for gradual change, and the principle of natural selection does not require it—selection can operate rapidly. Yet the unnecessary link that Darwin forged became a central tenet of the synthetic theory.

Goldschmidt raised no objection to the standard accounts of microevolution; he devoted the first half of his major work, *The Material Basis of Evolution* (Yale University Press, 1940), to gradual and continuous change within species. He broke sharply with the synthetic theory, however, in arguing that new species arise abruptly by discontinuous variation, or macromutation. He admitted that the vast majority of macromutations could only be viewed as disastrous—these he called “monsters.” But, Goldschmidt continued, every once in a while a macromutation might, by sheer good fortune, adapt an organism to a new mode of life, a “hopeful monster” in his terminology. Macroevolution proceeds by the rare success of these hopeful monsters, not by an accumulation of small changes within populations.

I want to argue that defenders of the synthetic theory made a caricature of Goldschmidt's ideas in establishing their whipping boy. I shall not defend everything Goldschmidt said; indeed, I disagree fundamentally with his claim that abrupt macroevolution discredits Darwinism. For Goldschmidt also failed to heed Huxley's warning that the essence of Darwinism—the control of evolution by natural selection—does not require a belief in gradual change.

As a Darwinian, I wish to defend Goldschmidt's postulate that macroevolution is not simply microevolution extrapolated, and that major structural transitions can occur rapidly without a smooth series of intermediate stages. I shall proceed by discussing three questions: (1) can a reasonable story of continuous change be constructed for all macroevolutionary events? (my answer shall be no); (2) are theories of abrupt change inherently anti-Darwinian? (I shall argue that some are and some aren't); (3) do Goldschmidt's hopeful monsters represent the archetype of

apostasy from Darwinism, as his critics have long maintained? (my answer, again, shall be no).

All paleontologists know that the fossil record contains precious little in the way of intermediate forms; transitions between major groups are characteristically abrupt. Gradualists usually extract themselves from this dilemma by invoking the extreme imperfection of the fossil record—if only one step in a thousand survives as a fossil, geology will not record continuous change. Although I reject this argument (for reasons discussed in essay 17), let us grant the traditional escape and ask a different question. Even though we have no direct evidence for smooth transitions, can we invent a reasonable sequence of intermediate forms—that is, viable, functioning organisms—between ancestors and descendants in major structural transitions? Of what possible use are the imperfect incipient stages of useful structures? What good is half a jaw or half a wing? The concept of *preadaptation* provides the conventional answer by permitting us to argue that incipient stages performed ~~different~~ functions. The half jaw worked perfectly well as a series of gill-supporting bones; the half wing may have trapped prey or controlled body temperature. I regard preadaptation as an important, even an indispensable, concept. But a plausible story is not necessarily true. I do not doubt that preadaptation can save gradualism in some cases, but does it permit us to invent a tale of continuity in most or all cases? I submit, although it may only reflect my lack of imagination, that the answer is no, and I invoke two recently supported cases of discontinuous change in my defense.

On the isolated island of Mauritius, former home of the dodo, two genera of boid snakes (a large group that includes pythons and boa constrictors) share a feature present in no other terrestrial vertebrate: the maxillary bone of the upper jaw is split into front and rear halves, connected by a movable joint. In 1970, my friend Tom Frazzetta published a paper entitled “From Hopeful Monsters to Bolyerine Snakes?” He considered every preadaptive possibility he could imagine and rejected them in favor of discontinuous transition. How can a jawbone be half broken?

Many rodents have cheek pouches for storing food. These internal pouches connect to the pharynx and may have evolved gradually under selective pressure for holding more and more food in the mouth. But the Geomyidae (pocket gophers) and Heteromyidae (kangaroo rats and pocket mice) have invaginated their cheeks to form external fur-lined pouches with no connection to the mouth or pharynx. What good is an incipient groove or furrow on the outside? Did such hypothetical ancestors run about three-legged while holding a few scraps of food in an imperfect crease with their fourth leg? Charles A. Long has recently considered a suite of preadaptive possibilities (external grooves in burrowing animals to transport soil, for example) and rejected them all in favor of discontinuous transition. These tales, in the "just-so story" tradition of evolutionary natural history, do not prove anything. But the weight of these, and many similar cases, wore down my faith in gradualism long ago. More inventive minds may yet save it, but concepts salvaged only by facile speculation do not appeal much to me.

If we must accept many cases of discontinuous transition in macroevolution, does Darwinism collapse to survive only as a theory of minor adaptive change within species? The essence of Darwinism lies in a single phrase: natural selection is the major creative force of evolutionary change. No one denies that natural selection will play a negative role in eliminating the unfit. Darwinian theories require that it create the fit as well. Selection must do this by building adaptations in a series of steps, preserving at each stage the advantageous part in a random spectrum of genetic variability. Selection must superintend the process of creation, not just toss out the misfits after some other force suddenly produces a new species, fully formed in pristine perfection.

We can well imagine such a non-Darwinian theory of discontinuous change—profound and abrupt genetic alteration luckily (now and then) making a new species all at once. Hugo de Vries, the famous Dutch botanist, supported such a theory early in this century. But these notions seem to present insuperable difficulties. With whom shall Athena

born from Zeus's brow mate? All her relatives are members of another species. What is the chance, of producing Athena in the first place, rather than a deformed monster? Major disruptions of entire genetic systems do not produce favored—or even viable—creatures.

But all theories of discontinuous change are not anti-Darwinian, as Huxley pointed out nearly 120 years ago. Suppose that a discontinuous change in adult form arises from a small genetic alteration. Problems of discordance with other members of the species do not arise, and the large, favorable variant can spread through a population in Darwinian fashion. Suppose also that this large change does not produce a perfected form all at once, but rather serves as a "key" adaptation to shift its possessor toward a new mode of life. Continued success in this new mode may require a large set of collateral alterations, morphological and behavioral; these may arise by a more traditional, gradual route once the key adaptation forces a profound shift in selective pressures.

Defenders of the modern synthesis have cast Goldschmidt as Goldstein by linking his catchy phrase—hopeful monster—to non-Darwinian notions of immediate perfection by profound genetic change. But this is not entirely what Goldschmidt maintained. In fact, one of his mechanisms for discontinuity in adult forms relied upon a notion of small underlying genetic change. Goldschmidt was a student of embryonic development. He spent most of his early career studying geographic variation in the gypsy moth, *Lymantria dispar*. He found that large differences in the color patterns of caterpillars resulted from small changes in the timing of development: the effects of a slight delay or enhancement of pigmentation early in growth increased through ontogeny and led to profound differences among fully grown caterpillars.

Goldschmidt identified the genes responsible for these small changes in timing, and demonstrated that large final differences reflected the action of one or a few "rate genes" acting early in growth. He codified the notion of a rate gene in 1918 and wrote twenty years later:

The mutant gene produces its effect . . . by changing the rates of partial processes of development. These might be rates of growth or differentiation, rates of production of stuffs necessary for differentiation, rates of reactions leading to definite physical or chemical situations at definite times of development, rates of those processes which are responsible for segregating the embryonic potencies at definite times.

In his infamous book of 1940, Goldschmidt specifically invokes rate genes as a potential maker of hopeful monsters: "This basis is furnished by the existence of mutants producing monstrosities of the required type and the knowledge of embryonic determination, which permits a small rate change in early embryonic processes to produce a large effect embodying considerable parts of the organism."

In my own, strongly biased opinion, the problem of reconciling evident discontinuity in macroevolution with Darwinism is largely solved by the observation that small changes early in embryology accumulate through growth to yield profound differences among adults. Prolong the high prenatal rate of brain growth into early childhood and a monkey's brain moves toward human size. Delay the onset of metamorphosis and the axolotl of Lake Xochimilco reproduces as a tadpole with gills and never transforms into a salamander. (See my book *Ontogeny and Phylogeny* [Harvard University Press, 1977] for a compendium of examples, and pardon me for the unabashed plug.) As Long argues for the external cheek pouch: "A genetically controlled developmental inversion of the cheek pouch may have occurred, recurred, and persisted in some populations. Such a morphological change would have been drastic in effect, turning the pockets 'wrong side out' (furry side in), but nevertheless it would be a rather simple embryonic change."

Indeed, if we do not invoke discontinuous change by small alteration in rates of development, I do not see how most major evolutionary transitions can be accomplished at all. Few systems are more resistant to basic change than the

strongly differentiated, highly specified, complex adults of "higher" animal groups. How could we ever convert an adult rhinoceros or a mosquito into something fundamentally different. Yet transitions between major groups have occurred in the history of life.

D'Arcy Wentworth Thompson, classical scholar, Victorian prose stylist, and glorious anachronism of twentieth-century biology, dealt with this dilemma in his classic treatise *On Growth and Form*.

An algebraic curve has its fundamental formula, which defines the family to which it belongs. . . . We never think of "transforming" a helicoid into an ellipsoid, or a circle into a frequency curve. So it is with the forms of animals. We cannot transform an invertebrate into a vertebrate, nor a coelenterate into a worm, by any simple and legitimate deformation. . . . Nature proceeds from one type to another. . . . To seek for steppingstones across the gaps between is to seek in vain, forever.

D'Arcy Thompson's solution was the same as Goldschmidt's: the transition may occur in simpler and more similar embryos of these highly divergent adults. No one would think of transforming a starfish into a mouse, but the embryos of some echinoderms and protovertebrates are nearly identical.

1984 will mark the 125th anniversary of Darwin's *Origin*, the first major excuse for a celebration since the centenary of 1959. I hope that our "new speaking" these few years hence will be neither dogma nor vacuous nonsense. If our entrenched, a priori preferences for gradualism begin to fade by then, we may finally be able to welcome the plurality of results that nature's complexity provides.