e18 So-called laws of evolutionary biology < generalizations >

Oft expectation fails and most oft there / Where most it promises ... —William Shakespeare.[5]

Wherever the word *law* has been used to label a finding of geology, it should be mentally crossed out and be replaced by *principle*, *generalization*, or *rule*. The so-called laws formulated by evolutionary paleontologists are statements of general trends in the evolution of (animal) species.

The Law of Differentiation formulated by Karl Ernst von Baer (1792-1876) is that related vertebrates, while differentiated when adult (as in the pairs: human-pig, turtle-birds, fish-newt), are very similar at the embryo stage.[6] Johann Friedrich Meckel(1781-1833)-Étienne Serres (1786-1868) Law of Parallelism in 1811 notes parallels between the individual's developmental stages from fertilized egg to maturity (ontogeny) and the phylogenetic series (the major taxa ranked from simple to complex). With these pre-Darwinian observations, Darwin, in *Origin*, 1859, had no quarrel ("community in embryonic structure reveals community in descent" and in *Autobiography* recalls "my theory" predicts the found decreasing resemblances of embryos of different species as they mature) but Lyell had earlier (in *Principles*, 1830) eschewed evolutionary implications when referring to the same. By contrast, Ernst Haeckel (1834-1919) was enthused to propose in *Riddle of the Universe at the Close of the Nineteenth Century*, 1899, "... that this history of the embryo [ontogeny] must be completed by a second, equally valuable, and closely connected branch of thought—the history of race [phylogeny]. Both of these branches of evolutionary science, are, in my opinion, in the closest causal connection; this arises from the reciprocal action of the laws of heredity and adaptation ... 'ontogenesis is a brief and rapid recapitulation of phylogenesis, determined by the physiological functions of heredity [generation] and adaptation [maintenance].'"[7] Gavin Rylands de Beer's (1899-1972) "neoteny" is embryonic development that evolves to stop short of later stages.[8] (Adult humans more closely resemble young, rather than fully-adult chimpanzees.)

Comment: Haeckel's "biogenetic law" that ontogeny recapitulates phylogeny (in their development, organisms retrace in an abridged way their evolutionary history, which is also expressed by the catch phrase: "climb their own evolutionary tree"), rests on no better evidence, accused his rival Wilhelm His, than his artful tailoring of it. (His stylized, beautiful, illustrations of organisms in *Kunstformen der Natur*, 1998, were influenced by William Morris art nouveau prints and in turn influenced that Art movement.)[9] Indeed, evolutionary theory, as Stephen Jay Gould pointed out, is neutral on the subject, and is equally unperturbed by the empirical observation that the embryos of sea urchins can be greatly different in appearance and lifestyle whereas the adults of the same are near identical. So much for Baer's Law of Differentiation as a general rule.

Samuel Wendell Williston's (1851-1918) in 1914 wrote, "it is [also] a law in evolution that the parts [especially similar serially-reiterated parts] in an organism tend toward reduction in number, with the fewer parts greatly specialized in function."[10] Examples are in the reduction in fish to mammal lineages of the number of cranial bones and in mammal lineages of the number teeth in their jaws. The vertebrae count in snakes (to 500)[11] and in long-necked plesiosaurs is a counter example.

Louis Antoine Marie Joseph Dollo's (1857-1931) Law in 1893: "An organism is unable to return, even partially, to a previous stage already realized in the ranks of its ancestors."[12] In short, evolution is irreversible. A narrower claim, often referenced as Abel's Law or Merrick's law, is that lost structures as wings, fingers, and so forth, cannot be regained. But one must distinguish between phenotypic reversibility and molecular genetic reversibility. As to the former, Darwin himself recognized that when domesticated organisms "seed wild" or "go feral" they often regain ancestral features. In a controlled experiment, caged populations of *Drosophila* were maintained for 25 years under standard rearing conditions. Subsets of these flies were used to start another populations that were separately selected for late-life fecundity, intermediate generation time, resistance to starvation, and rapid development to adults. In 2000, H. Teotónio and M. R. Rose, reported that after some three years of being returned to the original standard conditions, eight different phenotypic traits monitored in each reversed, at various rates, in 20 to 50 generations. Most did completely, but partial reversals were different and not merely slower versions of complete reversals, as their initial rate of reversal was rapid but then reached a plateau. This Dollo's Law obedience has its easiest explanation if found mutational biases and epistasis precluded reversals back down original pathways. (Epistasis is an interaction of effects of different mutations, such that the consequence of a mutation depends on whether another mutation is present or absent.)[13]

Dudley Peter Allen's (1852-1915) Law (a scaling "law" in its original formulation by Carl Bergmann in 1847) is that warm-blooded animals in a given lineage tend to become larger and more compact as the average temperature of their environment falls.[14] That trend is exemplified by the comparison of mountain lions in Canada with pumas of Central America, and of human populations in the subarctic and tropical zones. An additional observation by Allen was that the extremities in mammals tend to shorten. But Allen's Law is a principle and no more. As such, its usefulness is not compromised by, for example, the existence of "pygmy" polar Cretaceous dinosaurs of southeastern Australia described by Thomas Rich and Patricia (Pat) Vickers-Rich in 1989. In a restricted area, dwarfism may be a response to selective pressure to increase the number of individuals so as to ensure a gene pool diverse enough for the species to survive. Additional examples are: dwarf elephants lived on Mediterranean islands in ancient times, and pygmy mammoths were recently found in 4,000-year-old sediments on islands off the north coast of Siberia.[15] Thus we could propose a Rich's Rule that individuals found on islands will tend to be smaller than their mainland cousins. However, the converse has sometimes been true (***Figure e18.1***).

Constantin W. Lambert Gloger's Camouflage Adaptation Rule in 1883[16] (much misapplied and to which are many exceptions) is that individuals of many species of insects, birds, and furred mammals are darkly pigmented in well-vegetated (shady) humid climates and lightly colored in arid (well lit) ones. (Florida's Gulf Coast beach mice, *Peromyscus polionotus*, living on coastal dunes and prey for owls and hawks with a change in one amino acid in their melanocortin-1 receptor have light colored coats.)[17] Ludwig Gumplowicz's Rule in 1893 [18] inverts this for UV-light related skin pigmentation.[19]

Eduardo H. Rapoport's Rule in 1982 is that species adapted to cooler climates are distributed along a wider range of latitudes than species adapted to warmer climates.[20]

Edward Drinker Cope's Law of evolutionary biology is that organisms tend to develop larger bodies over geologic time. This rule is seemingly descriptive of many lines of descent and it has been uncritically accepted since Cope promulgated it in 1871.[21] However, statistically objective tests of Cope's Law have found it wanting:

> David Jablonski in 1997 provided the first statistically objective test of Cope's Law. He analyzed fossil mollusk (clams and snails) species from the Atlantic and Gulf Coasts of North America and tracked how for over 65 to 81 million years time, species' sizes in 191 separate lineages changed. The largest known fossil specimens of 1,086 mollusk species studied did not all occur at the end of a lineage—27 to 30 percent of them did, 26 to 27 percent evolved to smaller body sizes, and 25 to 28 percent had moved toward wider variation with smaller species getting smaller and larger species getting larger. According to Cope's Law, large and small species in each lineage should have gotten bigger with time. That rule, eminently sensible to explain such things as the increase in size for defense against predators and for an advantage in the struggle for food and territory, is not generalizable to clams. Jablonski summarizes: "Large size is not universally advantageous."[22]

> Ann F. Budd and Anthony G. Coates in 1992 reported on "non-progressive evolution" of a genus of massive colonial reef-building corals *Monsastraea*.[23] Corallites of *Monsastraea* range from 2.0 to 8.0 millimeters in diameter. Living *Monsastraea* in regions of turbid water (where efficient removal of smothering sediment can be a factor) typically have large corallites (diameters >3.5 millimeters) and mostly feed on small planktonic animals while those in regions of clearer waters near the reef crest have small corallites (diameters <3.5 millimeters) and are nutritionally more dependent on zooxanthellae (photosynthetic algae) that live

encysted symbiotically within their tissues. Variation of *Monsastraea* species' corallite diameters during 80 million years of Cretaceous time, is not of directional evolutionary change but is of oscillation within a range set by minimal and maximal size of the corallites of the *Monsastraea* bush (***Figure e18.2***). Budd and Coates conjecture that ecological or developmental constraints limit the range of corallite diameters. Conceivably, corallites smaller than 2.0 millimeters could either not develop or not function adequately and a limit to the number of septa could prevent corallites from being greater than 8.0. Within these limits, ranges of corallite diameters are selected for fitness in different environments that are always available in some parts of the habitat. And so evolution oscillates back and forth, with no persistent directional component.

In fairness, Cope's Law was formulated from his study of fossil vertebrate mammals and reptiles. The value of his (or any such) generalization is how well it points up exceptions for further study.

Trivers-Willard hypothesis in 1973 [24] is that for species in which big males successfully maintain harems (as do red deer on Rum Isle, Scotland), females in glowing health will tend to bear robust sons whereas frailer stressed-females will tend (possibly because an uterine hormonal state selects whether a male or a female zygote implants) to give birth to daughters.[25] An alternative hypothesis to what is found, is that bad times kill sons more than daughters. As to which, the court is so long out that Andrew Cockburn in 1999 forecast: "people will see the two hypotheses can be married."[26]

Phylogenetic principles often invoked and which Ernst Mayr has labeled as *FALSE*, are: [27]

Simple is always ancestral to complex.

Ontogeny (larval or embryonic stages) recapitulates phylogeny

The "type" evolves harmoniously, and so all structures and organ systems evolve at equal rates.

There are goal-directed, teleological, evolutionary trends (orthogenesis).

New types of organisms originate by saltation (But in an uncommon case: primroses did—described in 1905 by Dutch plant breeder Hugo de Vries (1848-1935) who also originated the term "mutation" while experimenting on them.[28] Also, an undeniable saltation is single-gene speciation reported by G. Freeman and J. Wilhelm in 1982, of snail chirality (right- and left-handed coiling) determined by the maternal nuclear genotype at a single locus.[29] And in 2003, Rei Ueshima and Takahiro Asami reported on the genital mismatch (a condition unique to snails) that isolates lineages of the Japanese land snail *Euhadra* of which 4 of 20 species are sinistral (left) coiling. "Reversal to a dextral [right] coiling species," they find "has occurred multiple times after only sinistral coiling evolution." [30]

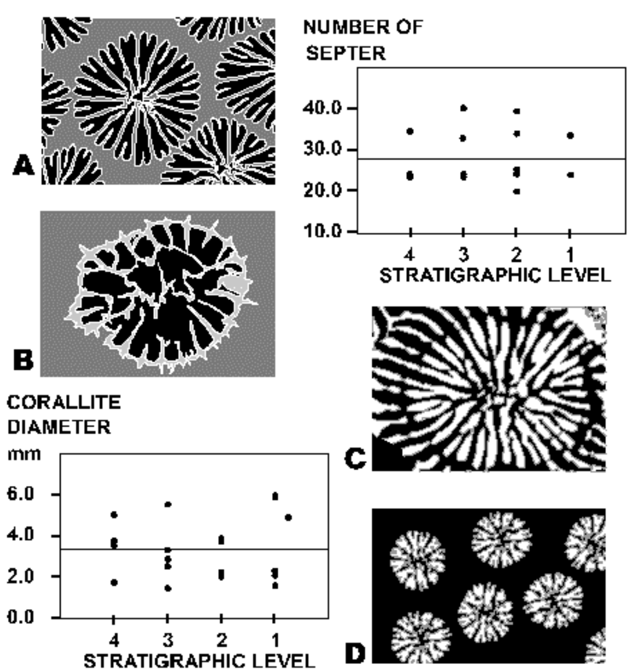

Figure e18.2 Four selected species (sketches of thin sections) and plots showing regression of morphology (vertical axis) on time (horizontal axis). Stratigraphic level 4 is 75 million years younger than level 1. Each point represents a species mean.[22]

Species A and B are from level 4 and show the number of septa plotted.

Species C and D are from level 1 and show the size morphology plotted.

Note: The regression lines in these plots of the size and the number of septa, are almost horizontal (showing a statistical trend that is essentially zero for both of these morphologies).