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## Evolution by Epigenesis: Farewell to Darwinism, Neo- and Otherwise

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Abstract. In the last 25 years, criticism of most theories advanced by Darwin and the neo-Darwinians has increased considerably, and so did their defense. Darwinism has become an ideology, while the most significant theories of Darwin were proven unsupportable. The critics advanced other theories instead of 'natural selection' and the 'survival of the fittest'. 'Saltatory ontogeny' and 'epigenesis' are such new theories proposed to explain how variations in ontogeny and novelties in evolution are created. They are reviewed again in the present essay that also tries to explain how Darwinians, artificially kept dominant in academia and in granting agencies, are preventing their acceptance. Epigenesis, the mechanism of ontogenies, creates in every generation alternative variations in a saltatory way that enable the organisms to survive in the changing environments as either altricial or precocial forms. The constant production of two such forms and their survival in different environments makes it possible, over a sequence of generations, to introduce changes and establish novelties – the true phenomena of evolution. The saltatory units of evolution remain far-from-stable structures capable of self-organization and self-maintenance (autopoiesis).

### 1. A SHORT HISTORICAL PRELUDE

Animals and plants evolve generation by generation, and within any one generation the development of each individual is itself an evolution.

Peter Medawar ([1983], p. 212)

This is the third and last, highly amended version of a review on ontogeny resulting in evolution (Balon [2002], [2004]). As Gottlieb ([1992], p. 46) already found out: "Mivart (1871) believed that evolution was brought about by the united action of internal and external forces that serve to change individual ontogenetic development, sometimes resulting in abortions and monstrosities, and, at other times in harmonious [...] new organisms". Even earlier, "seven years before the publication of the Origin of Species" Herbert Spencer "asks why people find it so very difficult to suppose 'that by any series of changes a protozoon should ever become a mammal' while an equally wonderful process of evolution, the development of an adult organism from a mere egg, stares them in the face. We can tell from the tone of his article that evolution was already an idea widely discussed by people of philosophic tastes" (Medawar [1983], p. 211). And some of them were already closer to the truth than Charles Darwin. For little is known that later in The Cambridge Guide to Literature in English (Ousby [1988], pp. 252-253) the passage on Charles Darwin concludes in these words: "In the 20th century his ideas have become part of the apparatus of assumptions to a degree where it is difficult to track them independently, though their power is still manifest, particularly among writers of science fiction such as Isaac Asimov and Stanislaw Lem" (bold in the Guide).

# 1.1. A Search for New Harmony

A number of articles and volumes appeared in which the prevailing orthodoxy of Darwinism, or neo-Darwinism was seriously questioned (e.g., Imanishi<sup>1</sup> [1952], [1984]; Løvtrup [1974], [1982],

<sup>&</sup>lt;sup>1</sup> Incidentally, "Imanishiism may have never represented a true alternative to Darwinism, but in the eyes of many Japanese it contained valuable, unique elements thus far ignored in the West" (concluded de Waal [2001], p. 125). In my view, reinforced by the

[1984a, b]; Riedl [1975]; Hitching [1982]; Ho and Saunders [1984]; Reid [1985], [2004]; Denton [1985]; Laszlo [1987]; Augros and Stanciu [1987], [1988]; Lima-de-Faria [1988]; Bruton [1989a]; Milton [1997]; Spetner [1998]; Ho [1999]; Wells [2002]; Müller and Newman [2003]; Hall *et al.* [2004]). In the light of our developmental data (see p. 276 and Balon [1986a, b], [1988a, b]), these criticisms reinforced my conviction that the so-called "mainstream" Darwinism is wrong.

It eventually led to ideas expressed, for example, by Robert ([2002], p. 605) who supported the Weiss and Fullerton [2000] suggestion "that it is not the genome that is especially conserved by evolution. Suppose the ephemeral phenotype really is what we need to understand and what persists over time. Genes would then be 'only' the meandering spoor left by the process of evolution by phenotype. Perhaps we have hidden behind the Modern Synthesis, and the idea that all the action is in gene frequencies, for too long (p. 192). Since 'evolution works by phenotypes, whole organisms, not genotypes', the Neo-Darwinian account of what evolution is would require a substantial conceptual overhaul (p. 193)". And so Conway Morris ([2003], p. 27) concludes that perhaps genes "importance is better pursued if we view them as a necessary tool kit, to be used as and when required, than as some sort of master template upon which evolution is meant both to act and unfold". Mae-Wan Ho ([1999], p. 65) said it all in her thorough and elegant refutation of the genetic determinism by the "fluid and adaptable genome". And she is right that consequently "our fate is written neither in the stars nor in our genes, for we are active participants in the evolutionary drama" (Ho [1988]).

In contrast to Løvtrup ([1974], [1982], [1984a], [1987]), whose ideas Hall ([1992], p. 171; [1999], p. 214) considered "not mainstream", Hall tried to remain in the "mainstream" by reconciling epigenetics with "neo-Darwinism". He nevertheless admits that "it is this domination of evolutionary theory by population genetics that is being questioned today" (Hall [1992], p. 9).

Gottlieb ([1992], p. 134) writes that "Matsuda has [...] recog-

frenzy of Beverly Halstead ([1984], [1988]), Imanishiism (Ikeda and Sibatani [1995]) is a valuable part of an alternative.

nized the essential similarity among the Baldwin Effect, genetic assimilation, and the second meaning of Schmalhausen's stabilizing selection (Matsuda [1987], pp. 43-46). He comments on it favorably, labels it a neo-Lamarckian scenario [...], and takes it as an accurate description of the way animals evolve in changing environments". A page earlier, Gottlieb (op. cit., p. 133) concludes that "phenotypes produced by the environment are erroneously seen as non genetic and thus have no place in modern synthesis". Moreover, as he states later (pp. 174-175) "evolution can occur without changing the genetic constitution of a population. Such changes may eventually lead to a change in genes (or gene frequencies) but evolution will have already occurred at the phenotypic level before the genetic change, ..." (see also Balon [1983]; Jablonka and Lamb [1995]). It clearly echoes the idea expressed by Bateson ([1979], p. 160) "that somatic change may, in fact, precede the genetic, so that it would be more appropriate to regard the genetic change as the copy. In other words, the somatic changes may partly determine the pathways of evolution".

The best way to replace "Darwinism" is expressed by Ho and Saunders ([1982], p. 93): "If evolution is emergent, the basis for this is to be found, not in the natural selection of random mutations but in the creative potential of epigenesis". If we agree that natural selection (random gene mutations and survival of the fittest; e.g., http://www.alternativescience.com/darwinism.htm) is not the true process of evolution causing the formation of novelties over time, then exactly what do we think are the epigenetic processes and "experiments of nature" that are at work instead? (e.g., Reid [1985], [2003]; Lima-de-Faria [1988]; Margulis and Sagan [1997]; Newman and Müller [2000]). The short answer can be found in Müller ([1990], pp. 99-100): "Development and its mechanisms are unquestionably central to the problem of novelty, since phylogenetic changes of morphology necessarily require modifications of ontogeny. [...] For this reason it is desirable to analyze novelty from a developmental point of view in contrast to earlier discussions that centered on selectionist genomic scenario ...". Like Robert Reid [2004], I consider epigenesis to be the mechanisms and processes of development. In Løvtrup's ([1987], p. 376) words, "... ontogenesis and epigenesis are parallel phenomena. In fact, ontogenesis may be said to comprise the observable and describable events taking place during individual development, whereas epigenesis represents the mechanisms responsible for their occurrence". As Ho ([1999], p. 71) stated "The epigenetic approach is one that takes the organism's experience of the environment during development as central to the evolution of the organism. It is potentially always subversive of the status quo, which is why it is invariably vehemently denied by the present orthodoxy".

# 1.2. Out of Tune

Diamond ([2001], p. xi) in his "Foreword" to one of Ernst Mayr's latest books stressed that "Darwinism has become so fascinating in recent years that now every year at least one new book is published with the word 'Darwin' in the title". Some books, ironically, remain ignored by Mayr and his disciples, even though they carry Darwin's name in the title, like Leith's [1982] The descent of Darwin: a handbook of doubts about Darwinism, Hitching's [1982] The neck of the giraffe or where Darwin went wrong, Løvtrup's [1987] Darwinism: the refutation of a myth, Behe's [1996] Darwin's black box, the biochemical challenge to evolution, and Milton's [1997] Shattering the myths of Darwinism. While Wells' [2002] book does not have "Darwin" in the title, it clarifies the reasons why Darwinism belongs in the history of science only.

Sadly, the so called hardened Darwinians often fake inconsequential wars I came to recognize as such after reading the true contestants cited above and earlier. For, instead of answering their serious objections these contestants are entirely ignored, and attention is artificially diverted, for example, by Ruse [2000] in *The evolution wars, a guide to the debates*, or by Sterelny [2001] in *Dawkins vs. Gould, survival of the fittest,* or even by McShea [2004] to contemptibly unimportant deviations in interpretation – leaving the issues that matter, like the beliefs in natural selection (e.g., http://www.alternativescience.com/natural-selection.htm) and gene-centric evolution (i.e. "genetic determinism", Ho [1999]), entirely intact. On rare occasions the serious opponents are subjected to "a campaign of vilification. I had expected (writes Milton [1997], p. 268) controversy and heated debate [...] But it was

deeply disappointing to find myself being described by a prominent academic, Oxford zoologist Richard Dawkins, as 'loony', 'stupid', and 'in need of psychiatric help' [...]". As if the Darwinians were "blessed with potent faith, and because of this their beliefs can weather any storm, including documents that contradict everything they hold dear. But what about the rest of the world?" (Brown [2003], p. 266).<sup>2</sup> For already Bateson ([1979], p. 26) knew that "those who lack all idea that it is possible to be wrong can learn nothing except know-how".

Ignoring contrary literature became a frequent strategy of hardened neo-Darwinians (e.g., Bynum [1985]) already unmasked by Riedl [1983], Reid [1985] and, of course, Løvtrup [1987]. "This intellectual degeneracy is the outward expression of the fact (concludes Milton [1997], p. 240) that neo-Darwinism has ceased to be a scientific theory and has been transformed into an ideology ...". In his 1433-page opus, Gould ([2002], p. 585) covers the emptiness of the selectionists' program by a verbose sophistry, admitting himself that "cynics may be excused for suspecting the academic equivalent of glitz and grandstanding". A few pages later (p. 590) he adds with typical obscurity: "Much that has been enormously comfortable must be sacrificed to accept this enlarged theory with a retained Darwinism core – particularly the neat and clean, the simple and unifocal, notion that natural selection on organisms represents the cause of evolutionary change, and (by

<sup>&</sup>lt;sup>2</sup> It is embarrassing to react to the piece by Kamler [2002, p. 81] who in a most unscholarly manner used citation counts to claim that "after a quarter of a century, Balon's terminology remains poorly accepted", and without any new facts or data then stated "I consider the embryonic period to be from egg activation to hatching, and the larval period to begin thereafter". Foremost, it is not a matter of terminology but of grammar - grossly misused adjective larval - and especially of understanding a full range of ontogenies often not present in local faunas (see Balon [1999]). Voluminous factual arguments that she chose to ignore have already proven her wrong (see p. 276 and my earlier developmental papers on European fishes, Balon ([1956a, b], [1958], [1959a, b, c], [1960a, b], [1961]) little improved in later papers she cites, for example, by Peňáz). And again without any new evidence she then declares: "I consider that ontogeny is a continuous process with temporary accelerations". In the same year Urho's [2002] paper cited as unpublished by Kamler appeared in print. To conclude in their vein, neither she nor Urho had any experience in working on comparative ontogenies of fishes, especially of a wide range of reproductive styles, and so both are defending at best a mere "terminology" based on comfortable beliefs in lay tradition rather than on factual knowledge.

extrapolation) the *only* important agent of macroevolutionary pattern". In this context I cannot resist quoting a novelist acquaintance: "From time to time, the little, long-tongued animal with the independently moveable eyes appeared in the montage, each time in a different colour. It must have been apparent, even to people not as well trained in the interpretation of symbols as college professors, that the little creature was conveying a message, and that message obviously was: someone is lying" (Skvorecky [1999], p. 164). For more of this kind see Wells ([2002], e.g., pp. 108-109).

## 1.3. Should Socially Motivated Disharmony be Tolerated?

Why have the Darwinian ideas, in spite of most of them being wrong, persisted for so long (e.g., Pauly [2004])? Gregory Bateson ([1979], p. 206) explained it to his daughter: "... what Darwin called 'natural selection' is the surfacing of the tautology or presupposition that what stays true longer does indeed stay true longer than what stays true not so long". Denton ([1985], pp. 58-59) elaborated further on Darwin's motivation to insist on gradualism:

"For Darwin the term evolution, which literally means 'a rolling out', always implied a very slow gradual process of cumulative change [...]. In his book *Darwin on Man*, Howard Gruber (1981) remarks: *Natura non facit saltum* – nature makes no jumps – was a guiding motto for generations of evolutionists and proto-evolutionists. But Darwin encountered it in a sharp and interesting form, posed as an alternative of terrible import: nature makes no jumps, but God does. [...] ... therefore if something is found in the world that appears suddenly, its origins must be supernatural".

Furthermore, as Robert Reid [2003] explains in his forthcoming book: "... Darwin offered belief in natural selection as a replacement for belief in Special Creation. And stable belief systems characteristically tailor facts and definitions to suit their acolytes and thus ensure their survival".

Why it all was not replaced long ago by better theories and paradigms ceased to be a mystery some time ago. Expanding on Gregory Bateson's famous sarcasm cited earlier, "we are learning from our masters that there is no better proof of the truth", Baudolino concluded, "than the continuity of the tradition" (Eco

[2002], p. 96). As emphasized by Ho ([1999], p. 67) "Genetic determinism has a strong hold over the public imagination. Its ideological roots reach back, deep within the collective unconscious of our culture, to Darwin's theory of evolution by natural selection, which is itself a product of the socio-economic and political climate of nineteenth-century England".

### 2. GRADUAL OR SALTATORY ONTOGENIES?

Thus it is with many biologists: They realize that Darwinian evolution cannot adequately explain what they know in their own field, but assume that it explains what they don't know in others.

Jonathan Wells ([2002], p. 231)

At any given time, a population of phenotypes of the same recognizable evolutionary unit (e.g., species, subspecies, morph), consists of various individuals (Figure 1) in different intervals of their ontogeny (stages in the lives of these phenotypes). A single cell the egg - cannot be in the same stabilized state as a more differentiated multicellular larva, chrysalis or a reproducing adult. Therefore, the entire ontogeny must consist of a sequence of stabilized states. A developing individual cannot remain stabilized all the time during the constant additions and subtractions of structures and functions, and during the constantly changing multitude of environmental, cellular, structural and endocrine interrelations. Precisely these sequences of stabilities are what the theory of saltatory ontogeny predicts, and what facts in comparative studies of ontogeny failed to falsify (e.g., Balon [1959d], [1977a], [1980], [1981a], [1984b], [1985<sup>3</sup>]; Cunningham and Balon [1985], [1986a, b]; Haigh [1990]; Kováč [1992], [1993a, b], [2000]; Holden and Bruton [1992], [1994]; Crawford and Balon [1994a, b, c], and most of the references given in Smirnov et al. [1995]).

"Darwin's emphasis on gradualism was a struggle to preserve for natural selection the creative role in evolution ..." (Ho and Saunders [1982], p. 88). As most people view changes in struc-

<sup>&</sup>lt;sup>3</sup> And studies reprinted within.

tures and functions during ontogeny as gradual processes, many admit that these proceed at various rates at different times. Yet in their minds, development proceeds via continuous, inconspicuous accumulations of small changes, in spite of numerous claims and proofs to the contrary (e.g., Wells [1904]; Steinbeck [1960]; Hedgpeth [1978]; Balon [1979a], [1986b]; Lampl *et al.* [1992]; Wray [1995]; Depew and Weber [1996]).



Figure 1 – Stages within the four main saltatory intervals of the painted lady butterfly: The egg differs entirely from the externally feeding caterpillar (= larva) as does the metamorphosing chrysalis from the definitive phenotype of butterfly. From Augros and Stanciu [1988] by permission.

Each individual metazoan organism starts from a single cell and ends with the "death" of a multicellular, complex individual, often long after its ability to reproduce has ended, but after a lifetime of experience for the longer surviving ones. Ontogeny (of vertebrates, for example) never creates immortal phenotypes, but each act of reproduction reduces a multicellular organism – an autopoietic

entity (sensu Varela et al. [1974]; Maturana and Varela [1988]; Margulis and Sagan [1997]) – to a number of less-specialized single cells. From "activation" (sensu Balon [1985]) of the single cell until death, again and again, a phenotype is created and allowed to perish. Can so much ado be about nothing, as most hardened neo-Darwinians would like us to believe (e.g., Dawkins [1982])?

"The genotype is the starting point and the phenotype the endpoint of epigenetic control [...] (writes Hall [1992], p. 215). It is because there is no one-to-one correspondence between genotype and phenotype that epigenetic mechanisms are of much importance in ontogeny and phylogeny" (italics removed by me; for more explanations see Müller [1990]; Newman and Müller [2000]). "A life-history (states Ho [1987], p. 184) is simultaneously a transformation sequence from a given structure in the context of existing contingencies, and a process of enstructuring the present, as well as future generations by the assimilation of novelties". Consequently, a phenotype is also an information gathering and transmitting device, for nothing less important can justify all the elaborate and expensive construction activity. Epigenesis creates new phenotypes according to "instructions" given not only by the genome (e.g., Sapp [1987]). The genome works from programmatic information recorded as the "memory" of past environments, developments and their genetic assimilations, but the phenotype is formed by an interaction with the present environment, with the building activity adding developmental information to the instructions based on programmatic information (Riedl [1975], [1988]; Balon [1983], [1989c]). Novelties appear only during epigenesis.

## 2.1. Homeostasis and Homeorhesis

In contrast to homeostasis (e.g., Cannon [1939]) as a process keeping something at a stable or stationary state, Waddington (1968, in [1975], p. 221) proposed for living systems the term homeorhesis, meaning stabilized flow; "the thing that is being held constant is not a single parameter but is a time-extended course of change that is to say, a trajectory". Later Waddington ([1977], p. 105) elaborated by saying that "the stabilization of a progressive system acts to ensure that the system goes on altering in the same sort of way that it has been altering in the past". Therefore we

may define, for our purposes, any steady state as homeostasis and any stabilized state as homeorhesis. The current perception "that life involves far-from-equilibrium conditions beyond the stability of the threshold of the thermodynamic branch" (Prigogine [1980], p. 123) fits well the Waddingtonian concept of homeorhesis, i.e., that phenotypes constantly try, alas unsuccessfully, to reach homeostasis by maintaining stabilized states and change from one to another such stabilized state in ontogeny as much as in phylogeny. "Homeorhesis is a necessary property of an epigenetic system. But a system which possesses this property will also have the capacity for heterorhesis, i.e., for large, organized change" (Saunders [1984], p. 255).

During a stabilized state, cells and tissues differentiate, and structures grow at various rates, as if accumulated and canalized in preparation for the next, more specialized, stabilized state. The homeorhetic processes of the system 'resist' de-stabilization (e.g., Alberch [1980]) for as long as possible, enabling structures to be completed and functions to progress without interfering with stabilized life activities. When ready for new or additional integrative actions (sensu Adolph [1982]), a switch is rapidly made via a far-from-stable threshold into the next stabilized state of ontogeny.

While the usage of "threshold" in developmental biology was often only vaguely linked to the thresholds of saltatory ontogeny, they are basically the same phenomenon. "The system will assume a new steady state upon the crossing of the threshold (writes Müller [1990], p. 104) and the resulting phenotypic transformations will then depend on the reaction norms of the system at this point, as well as on the secondary reactions of associated systems". Further to the idea of developing or introducing novelties at thresholds, Müller (op. cit., p. 109) "emphasize[s] that thresholds are an inherent property of developing systems, able to trigger discontinuities in morphogenesis which can automatically result in the generation of a new structure. Novelty can thus arise as a side effect of evolutionary changes ..." between two self-organized and maintained states.

# 2.2. Epiphenotypes

Gradual development is a comfortable hypothesis, allowing one

to believe that a sequence of arbitrarily selected "stages" is a realistic representation of ontogeny. In spite of bold claims that "Placing embryos and postnatal organisms into morphological stages is a reliable way of measuring the passage of time" (Hall [1999], p. 367), it never is, although, as a result of outdated and parochial methodology and belief in gradualism, it is often claimed to suffice (see, e.g., Townsend and Stewart [1985]; Shardo [1995]; Dünker et al. [2000]; Everly [2002]). Other ideas like "cell division" (Berrill [1935]), a "mitotic cycle" (Dettlaff and Dettlaff [1961]), or "somite pair formation" (Gorodilov [1996]) explained little in relation to the problem of measuring the "passage of time" in ontogeny, because the problem is not a gradual "conventional time" but irregular rates of saltatory homeorhesis (see Kováč [2002] for the complementary concept of synchrony and heterochrony)!

The theory of saltatory ontogeny forces us to be more careful in designing sampling schemes and interpreting results, for between any two intervals, unknown as well as different rates and dynamics of interactions may operate and make interpolation impossible. In most cases, many of the inconspicuous processes of epigenesis will be overlooked and the true life-history style of an organism misinterpreted if the saltatory character of ontogeny is not acknowledged. As genes alone cannot account for the organization of the whole and its increasing complexity (e.g., Løvtrup [1974]; Holm [1985]; Hall [1999]), so the definitive phenotype – e.g., after metamorphosis – cannot be in the same stabilized state as an embryo or a larva, which possess numerous specific but temporary organs and lack some definitive ones.

A metazoan organism is, therefore, a sequence of separate homeorhetic states which constantly spiral in a generation lineage (Ho [1988]) from a single cell to a multicellular mortal, from simple to complex, but within the increasing organization of the whole (cf. Prigogine [1980]; Maturana and Varela [1988]). During these generation lineages – both as a recreation of complexity and specialization – epigenesis enables variation to be maintained or increased and novelties to occur (e.g., Müller and Wagner

<sup>&</sup>lt;sup>4</sup> Moreover, the "reason for concentrating on continuous variation was that they were mathematically tractable using the linear, additive models that allowed equations to be solved" (Ho [1999], p. 85).

[1991]; Newman and Müller [2000]). Epiphenotypes (Løvtrup [1974]) are the products of a saltatory self-organizing system, which maintains a hierarchical sequence of stabilized states, expressed as intervals of ontogeny and separated by far-from-stabilized thresholds during the switch from one to the next stabilized state (Balon [1986b]). As told by Müller ([1990], p. 120) among many others: "In addition to its regulatory capacities, the epigenetic nature of development also accounts for the fact that relatively small initial changes in morphogenesis [...] can be magnified into a prominent phenotypic effect during the further course of development – a phenomenon we may call amplification". And since in our scheme of things evolution is merely a sequence of generations and associated epigenetic processes, there is little need to consider other mechanisms.

Vasnetsov [1953] and Kryzhanovsky et al. [1953] envisaged a sequence of "etaps" (sometimes translated from Russian as "stanzas") of quantitative morphogenesis and growth, linked by rapid leaps - the qualitative changes in the organism-to-environment relationships – as a pattern peculiar to ontogeny. The application of this pattern to fish ontogeny by these authors and some others (e.g., Peňáz [1983], [2001]) was almost certainly triggered by the earlier misapplication of dialectics to socio-economics (see Medvedev [1969]). "Etaps" in ontogeny remained practically unchanged from the Vasnetsov/Kryzhanovsky version, i.e., from the environmental, selectionist and adaptationist program (e.g., Soin [1969]), and they were never even remotely linked to anything like self-organization and self-maintenance (also called autopoiesis). Ultimately, the theory of saltatory ontogeny (Balon [1986b]) abandoned the dialectics of conflict for the harmonious interactions of the ancient dualism I named "Tao of life" (Balon [1988a, b], [1989a, b]; Sermonti [1988]).

# 2.3. The Life-history Variations

The saltatory ontogeny of organisms can be described with the hierarchical life-history model of embryo, larva, juvenile, adult and senescent periods, each period separated by natural boundaries and each consisting of a sequence of saltatory self-organizing intervals – homeorhetic states called steps – separated by far-from-stabilized

thresholds. In comparative studies, such a model provides the possibility of recognizing and interpreting shifts in thresholds (e.g., heterochrony), which often result in a new life-history style (e.g., Hall [1984], [1992]). It elucidates, for example, the ecological significance of not having an orally ingesting and intestine digesting larva (Balon [1977a], [1984b]; Matsuda [1987]; Flegler-Balon [1989]) as well as the importance of having a larva despite the "cost" of metamorphosis (Balon [1978], [1979b], [1984a], [1985]).

The first, the embryo period of ontogeny is primarily characterized by endogenous feeding, i.e., by the acquisition of nutrients from parental sources. Transition to taking exogenous nutrients by oral ingestion and intestine digestion, i.e., the acquisition of nutrients from sources in the external environment, marks the beginning of the next period of life history, be it a larva period in the case of indirect, or juvenile period in the case of direct ontogeny (Figure 2).

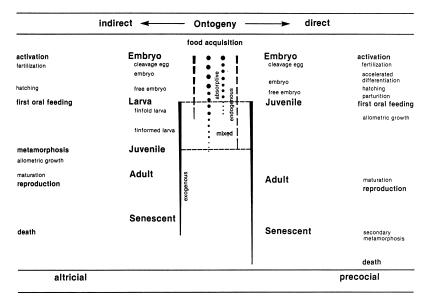


Figure 2 – Comparison of the types of food acquisition within the indirect (left) and direct (right) ontogenies according to the life-history model (intermediate and extreme ontogenies are ignored). The decisive and some accompanying events in either type of ontogeny are given in the marginal columns. At the center the solid vertical line = exogenous feeding, dashed line = endogenous, and dotted line = absorptive nutrient uptakes (note the time of mixed feeding).

Larvae are, in general, more vulnerable than any other life-history stages. Eggs with a small amount and low density of yolk (see Crawford et al. [1999]), however, can be produced in larger quantities to compensate for the high mortality of larvae. Being chiefly nutrient-gathering entities sometime also used for dispersal, larvae are designed to compensate for the insufficient yolk before a definitive phenotype can be formed. Besides high mortality there is another price to be paid for having a larva period. Numerous cenogenetic (temporary) structures of larvae, specialized for separate habitats and niches, need to be remodeled into permanent organs and shapes at some energy cost. This process of remodeling - metamorphosis - terminates the larva period (e.g., Fostner et al. [1983]; Matsuda [1987]). In some cases (e.g., nonparasitic lampreys, elopomorphs, stomatioids) much of the size gained during the larva period must be sacrificed in the remodeling process, thus losing the survival advantage of larger size. This, by the way, provides clear circumstantial evidence that the main purpose of a larva period is the acquisition of external nutrients when the endogenous supply is insufficient.

In contrast, when sufficient endogenous food is provided at the disadvantage of a lower number of eggs (e.g., O'Connor [1984]; Balon [1984b], [1986a]), elimination of the vulnerable larva period and costly metamorphosis facilitates direct development into a juvenile that is comparatively advanced at the time of its first oral feeding; this is a clear survival advantage. Moreover, fewer eggs, larger egg size or a greater density of yolk (negative buoyancy), prolonged developments inside the egg envelopes, and sessile stages of embryos even after hatching pave the way for further protection by parental care (Balon [1975], [1981a, b], [1984a]; Wake [1989]; Crawford and Balon [1996]). In birds and mammals, by contrast, mobility of precocial young further facilitates survival (e.g., Nice [1962]; O'Connor [1984]).

<sup>&</sup>lt;sup>5</sup> Direct development from eggs with more yolk (large eggs) is by some (e.g., Matsuda [1987]; Wake [2004]) considered as retention inside the egg envelopes – called embryonization – of the free embryo, larva, and often also metamorphosis. It is a mistake common when hatching is taken as a significant boundary. Cases, like the early development of *Cyphotilapia frontosa* or marsupials had proven this idea wrong (see pp. 285-286).

It is possible that the increase in vitellogenesis responsible for the larger amount of yolk is mediated by the environment (Gerbilsky [1956]) via endocrine mechanisms (e.g., Campbell and Idler [1976]; Matsuda [1987]). It is likely that the resulting specialization of some individuals on larger, more nutritious food items, may enhance vitellogenesis and produce more precocial progeny (e.g., Goto [1980], [1982]; Balon [1980], [1985]). Even changes in temperature may initiate the epigenetic formation of larger and more specialized individuals (Balon [1980], [1983], [1985]). Maybe it is unwise to interpret as a "response" what might be merely a lucky chance in successfully making do with what is available after structural modifications (Goldschmidt [1940]; Gould and Vrba [1982]; Goodwin and Trainor [1983]; Løvtrup [1987]).

In the evolution of reproductive styles (Balon [1975], [1985], [1990]), the survival of the offspring is enhanced by an increase in the endogenous food supply and parental care (Crawford and Balon [1996]), the evolutionary sequences ranging from scattering gametes to hiding them, from guarding a clutch on a selected or prepared substratum to bearing a clutch on or inside the parent body (Balon [1975], [1981a, b], [1985]). Bearing the offspring internally (i.e., live bearing) further decreases its exposure to predators and eliminates some of the adverse environmental perturbations (e.g., water level fluctuations) because the clutch is carried by the mobile parent. The released young are fully differentiated juveniles grown on mixed food supply. Elimination of the larva period from the life history is, therefore, an important ecological and evolutionary phenomenon, which deserves more of our recognition and attention (cf. Balon [1986a], [1999]; Flegler-Balon [1989]; Smith et al. [1995]).

Most of the final form of a phenotype and its life history are determined during early ontogeny at a time when types of feeding (endogenous, absorptive, mixed) other than the purely exogenous one operate. An organism should always be considered over its entire ontogeny, from the single cell at activation until death (Balon [1985]). Focusing on the later parts of ontogeny (juvenile, adult or senescent) restricts us to studies of the definitive phenotypes only, while the processes that create this bewildering diversity of forms and functions cannot be explained.

Metamorphosis, of course, is rarely only a threshold. More often it is a separate step or sometimes a lengthy and special interval (Balon [1999]) that ends the larva period and separates it from the juvenile period. As the larva is the vegetative form, required by organisms with eggs and embryos of low endogenous food supply in order for them to develop into adults capable of reproduction, the beginning of the larva period must be the beginning of exogenous (i.e., orally swallowed and an intestine digested) feeding. In fishes having larvae, this threshold rarely coincides with hatching. Justifications for calling a "freshly hatched" embryo a larva are clearly wrong (e.g., Makeyeva [1988]; Kamler [1992], [2002]; Urho [2002]). The presence of a large amount of yolk signifies endogenous feeding; a fish feeding endogenously is an embryo, whether it is inside or out of its egg envelopes.

Furthermore, hatching is never a natural threshold but a "process in which the embryo emerges from the egg envelope (or a fertilization envelope) which encloses it. This process is observed not only in the embryos of oviparous animals but also in those of viviparous animals such as mammals" (Yamagami [1981], p. 459). Thus, hatching should not be equated with parturition (birth); it is not an instantaneous event but a process that occurs at various times in different individuals and is influenced by stimuli of the internal and external environment (Cunningham and Balon [1985], [1986a, b]; Helvik [1991]; Helvik and Walther [1992], [1993a, b]; Crawford and Balon [1994a, b, c]).

All of us accept the date of birth as an important point in our lives (as emphasized by the importance of birth certificates); rarely do we realize that this date marks an event erroneous for the biological life history. Individuals born prematurely are older on paper than those born at the normal time; yet they are born in a less developed state than those born at the normal time. A similar paradox also applies to the time of hatching. Both hatching time and time of parturition (birth) are impossible to define in terms of "normality" because both are largely influenced by the environment and do not necessarily occur at a particular state and time of development (Balon [1981a]). Moreover, we often believe that hatching and birth (parturition) are equivalent events in oviparous and viviparous animals, respectively. They are not (Hensel [1999]).

Therefore, it is erroneous to time ontogeny from parturition in one instance and from hatching in the other. In every ontogeny, the processes of hatching precede parturition.

The life-history model was constructed to reflect the natural intervals of different types of ontogenies and to serve as a sort of standard (Figure 2). Comparing actual ontogenies to this model helps in recognizing food acquisitions and heterochronies specific for various types of indirect and direct developments and in determining the deviations from the standard of intermediate life histories.

## 3. SOURCES OF ALTERNATIVE ONTOGENIES

... the difficulty is less in discovering than in having discoveries understood and adopted.

Irving Wallace ([1968], p. 334)

According to Scudo ([1997], p. 500), both Lamarck and Darwin were aware of the omnipresent dichotomies: "The typical divergence of 'high' animals through two sharp morphs or behaviours, at first coexisting in the same 'race' if not in the same individual, was for long the central problem in these theories". [...] "in *Philosophie Zoologique* Lamarck characterised this process in animals as a law –, i.e., only if either morph is maintained for long in a race it will become transmitted by generation ...". Ho and Saunders ([1982], p. 94) reasoned that "This problem is resolved if we take into account the ability of the epigenetic system to 'make sense' of a mutation or a large environmental disturbance by diverting development into an alternative pathway".

Essentially, to be prepared to answer "yes" or alternatively "no" is the most efficient way to be prepared for an as yet unpredictable question (Balon [1988a, b]). The ability to create a quasi generalist or a quasi specialist at any one time is the only solution that can prepare the organism for future demands from an unknown coevolving system (e.g., Bruton [1989b]). Saltatory ontogeny, as already explained, is an indispensable prerequisite for the introduction of changes or novelties during a threshold between two stabi-

lized states; the earlier in ontogeny the change, the more effective and extensive it is (Oster and Alberch [1982], p. 451, see figure 3.3).

The idea that natural selection acts on populations – one of the theories of Darwinism - is not correct either. Changes occur in an individual but may be synchronized to occur similarly to an entire clutch or a part of it. I envisage a group change to occur as follows: Developmental events triggered by environmental cues such as hatching, for example, will occur earlier in lower oxygen conditions and later in higher oxygen conditions (Balon [1980]). Not only will the same cue initiate the event in a group of individual embryos, but, if eggs are deposited in clusters, the hatching enzymes of the first embryo which has broken free will induce hatching of the adjacent embryos. Hence, both the environmental cue and the 'message' (hatching enzymes, pheromones) from the first individual will make the group develop in a synchronized manner, with ultimate consequences for the entire ontogeny. Other environmental cues, such as cellular interactions and positional activations, will have similar effects on various developmental events, as experiments on a temperature and skeletal calcification have shown (Balon [1980]). In no instance that I am aware of, did such synchrony encompass the entire population, even if it was restricted to a single nesting colony. The synchrony of developmental changes requires close proximity in the case of both exogenous cues and endogenous messages.

Even in close proximity, usually within a single clutch from one parental pair, the differences between centrally and peripherally located zygotes, or first and last deposited ova, or differences in placental plexuses, will suffice for bifurcations to occur in the various epigenetic interactions. Ultimately, such bifurcations will result in the formation of two distinct trajectories of stabilized states, as the resultant variation usually clusters in no more than two stability states (Alberch [1980]). Depending on the 'strength' of the cue or the 'size' of the activated field, the twin forms can be very close or quite different in their life-history attributes. Often only one form will survive to maturity, but it will again produce off-spring of both forms (Balon [1984a], [1988a, b]).

Following the long accepted terminology for birds (e.g., Nice [1962]; Ricklefs [1979]), I have used the term 'altricial' to describe

the quasi generalists and 'precocial' to describe the quasi specialists. The main attributes of the two forms are: relatively smaller or incompletely developed young in the altricial form, and relatively larger or completely developed young in the precocial form (Table 1). In the extreme cases, the definitive phenotype of the altricial form is arrived at via a slow differentiation and remodeling (metamorphosis) of temporary nutrient-gathering caterpillars, larvae and tadpoles, whereas the definitive phenotype of the precocial form differentiates directly because of sufficient endogenous food supply (yolk, trophodermy, placentotrophy) into a definitive phenotype.

As the ontogeny of each taxon is created in every generation lineage in a sequence of alternative "altricial ≠ precocial homeorhetic states", so different taxa are formed by a similar mechanism given many generation lineages, appropriate environment and isolation (e.g., Imamura and Yabe [2002]). "The possible paths of evolution resemble a decision tree with branching at each instability threshold" (Jantsch [1980], p. 48), and this simply reflects the underlying epigenetic mechanisms, in which each information "pulse" initiates bifurcation in structural or functional traits. After all, as Hennig [1960] has shown, "phylogenetic classifications usually take the form of dichotomous dendrograms" (Løvtrup [1987], p. 8). "Thus a possibility of punctuated equilibria [reasons Vrba ([1984], p. 119) forces us to consider not only the potential causes of origin and sorting of variation at the level of organismal phenotypes, but also those at the among-species level". This, however, has yet to be proven.

Let me briefly return to the consequences of the above mechanisms responsible for the creation of alternative states and, by summation through many generations, of evolution. Every successive reproductive lineage, as a consequence of ever-changing epigenetic variations and relationships, will produce both altricial and precocial forms with more specialized characters compared to the previous generations. For example, the larva period will become shorter and shorter, and the egg number per reproductive lineage will become lower and lower, but the yolk volume and density will be increasingly higher until a specialized form has developed with, for example, semelparous reproduction or one single large off-spring (Figure 3). By then a very vulnerable existence, on the verge

Table 1

The suites of characters typically associated with altricial or precocial life-history styles (after Bruton [1989b], modified).

	Altricial	Precocial
Epigenetic		
<ol> <li>egg size</li> <li>egg yolk</li> <li>egg number</li> <li>larvae</li> <li>juvenile mortality</li> <li>size at first exogenous feeding</li> <li>parental investment per young</li> <li>developmental state of young</li> <li>frequency of reproduction</li> <li>chromosome number</li> </ol>	small low density large usually present high small low early high high	large dense small usually absent low large high advanced low low
Ecological  1. trophic niche 2. species diversity 3. specialized 4. species interdependence 5. adaptability 6. adaptedness 7. typical environment 8. environmental changes 9. surplus production of eggs 10. life style 11. community	wide low less lower high low unstable unpredictable high generalist pioneer	narrow high more higher low high stable predictable low specialist equilibrium
Associated		
<ol> <li>Tao (e.g., Balon [1988a])</li> <li>Geist [1971]</li> <li>Vrba [1980]</li> <li>MacArthur and Wilson [1967]</li> <li>Løvtrup [1984b]</li> <li>this essay</li> <li>this essay</li> <li>this essay</li> </ol>	yin maintenance generalized r-selected progressive Cro-Magnons !Kung San Mongoloids	yang dispersal specialized K-selected divergent Neanderthals Bantu Caucasoids

of extinction, is reached. This trend can, under special circumstances, be reversed by juvenilization and thus extinction postponed (Balon [1985]). Beyond the time scale of generations, similar mechanisms are probably responsible for taxonomic divergence and paedomorphosis, i.e., the processes which cause change in ontogeny may be canalized into the creation of a new taxon. This allows a totally new interpretation of the origin and relationships of species pairs, for example, an interpretation not considered in conventional approaches (e.g., Poynton [1982]; Taylor [1999]).

The intraspecific differences between altricial and precocial forms in ontogeny are usually very small. The quasi generalists will be a little more inclined toward the attributes of altriciality in comparison to the quasi specialists which will be a little more in-

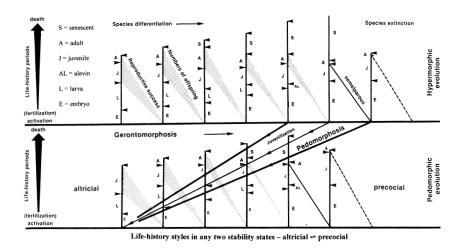


Figure 3 – Scheme to illustrate possible ontogenies (vertical lines) in a sequence of increased specialization (left to right) and, under certain conditions, despecialization by juvenilization/paedomorphosis (from upper right to lower left). The relative duration of ontogenetic periods (arrowheads) changes from more altricial toward more precocial, and the number of offspring (dotted areas) is reduced and paralleled by the truncation of adult period, elimination of larva period and prolongation of senescence period. Any two of the ontogenies can represent, at the same time or at different times relative to each other, the dichotomous steady conditions named 'altricial ≠ precocial homeorhetic states' (nicknamed alprehost). In both trajectories, the hypermorphic (upper) and the paedomorphic (lower) one, specialization equals gerontomorphosis (from Balon [1985] and [2004]).

clined toward the attributes of precociality. Fitting examples among fishes are the sympatric "dwarf" and "normal" forms of charr, Salvelinus spp. (e.g., Balon [1980], [1984a]; Klemetsen et al. [1985]), the dwarf Oreochromis mossambicus of Lake Sibaya (e.g., Bruton [1979], [1980], [1986]), the altricial Oreochromis shiranus chilwae and precocial O. shiranus shiranus (Lowe-McConnell [1982]), and the appearance of Cichlasoma minckleyi as an altricial papilliform morph and a precocial molariform morph (Liem and Kaufman [1984]).

Some such intraspecific twin forms have been identified independently as dwarf and large perch *Perca fluviatilis* (Alm [1946]; Svetovidov and Dorofeyeva [1963]; Oliva *et al.* [1989]), normal and giant tigerfish *Hydrocynus vittatus*, lake charr and siscowet, *Salvelinus namaycush*, and sea trout *Salmo trutta* and brown trout *Salmo trutta* morpha *fario* (e.g., Balon [1977b], [1980]). Recognition of such twin forms in a taxon depends to a large extent on the acceptance of the idea and on improved resolution in studies devoted to the life history of a species. "Genetic" evidence then may support the existence of twin taxa like in the case of African elephants, the precocial *Loxodonta africana* and the altricial *Loxodonta cyclotis* (see Roca *et al.* [2001]; Canby [2002]), or the precocial chimpanzees *Pan troglodytes* and altricial bonobos *Pan paniscus* (de Waal [2001]).

Larger differences are evident only when the same concept is applied at species or higher taxon level, like considering substratenesting cichlids as more altricial than mouth brooders (Balon [1993]), or marsupial mammals as altricial and placentals as precocial. It should always be made clear whether altricial and precocial are being referred to in terms of intraspecific life-history dichotomy or whether they are being applied in the much more obvious interspecific comparison. As both these dichotomies are probably created by the same epigenetic mechanisms, their universal usage is justified.

In most instances, even the simplest variables of early ontogeny are not known, comparative ontogenies are not available for most species, although the dwarf and normal pairs of charrs are part of the much broader known occurrence of "sibling species" or sympatric "species pairs" recently reviewed by Taylor [1999]. Inci-

dentally, the issue that Taylor [op. cit.] addresses concerns not "species pairs" but two forms of one species – what we have been calling altricial and precocial forms. Nearly always these "species pairs" are being interpreted narrowly according to the central neo-Darwinian dogma or population genetics (from Svärdson [1958], [1961], [1970] to Schluter [1996] and Taylor [1999] or Rundle et al. [2000]), although clearly the epigenetic interpretation begs to be applied. The case of four forms of Arctic charr in Thingvallavatn, Iceland, is a good example of the problem. Unfortunately, ontogenetic comparisons and an epigenetic interpretation were never seriously attempted because of strong neo-Darwinian beliefs. Instead, studies of "quantitative genetic differences in morphology and behaviour" (Taylor [1999], p. 314) led to a "mainstream" interpretation (e.g., Skúlason and Smith [1995]; Skúlason et al. [1989], [1993]) little different from Svärdson's [1961].

Consequently Taylor [1999], in his attempt to explain the origin of sympatric twin forms, is limited again to the "empty niche" in the post glacial temperate areas open to multiple invasions. The alternative epigenetic explanation would be that in spite of the ubiquitous occurrence of the twin forms in many species, often only one form survives, unless environmental conditions are suitable for both (Balon [1989b]). The altricial forms can also be effective invaders (into empty habitats, for example, formed by the retreating glaciation), but their dispersal becomes impossible when the system turns saturated; precocial quasi specialists are better at avoiding competition (Bruton [1989b]).

# 3.1. Altricial and Precocial Forms or Species Pairs

Alternative states of life histories have been noted many times before and I am sure that a more conscientious review of the literature would increase the number of examples given and interpretations available. And as I stated (Balon [1989b], p. 21) "Geist (1971) recognized and documented in a creative way the existence of two phenotypes in the mountain sheep (bighorn), *Ovis canadensis*. He named them 'maintenance' and 'dispersal' phenotypes, and later elegantly applied these concepts in a comparison of Neanderthal with other Upper Paleolithic people (Geist, 1981). In contrast to the latter, 'advanced Neanderthals enjoyed neither the luxury of

time nor the plasticity of a generalized economic exploitation strategy. They were specialists, and opportunities to practice their skill ran out quickly with rapid postglacial environmental changes (Geist, 1978, p. 300)". Consequently, the "dispersal phenotype" (= precocial) out of Africa (e.g., Wong [2003]) that led to the altricial Cro-Magnons and precocial Neanderthals (e.g., Stringer and Davies [2001]; Klein [2003]), and ultimately the altricial Mongoloids and precocial Caucasoids, left behind in its ancestral homeland – Africa – the altricial sympathetic but not competitive !Kung San (commonly called the bushmen) of the Van der Post (e.g. [1975]) or Lee [1979] and pygmies of the Canby's [2002] lore, and the precocial dominant Negroids (or Bantu, Table 1). A few of the above data are similar to the values used by Rushton (e.g. [2000]) who, however, applied the outdated Darwinian r-K selection concept (e.g., MacArthur and Wilson [1967]; Bruton [1989b]), tied via rather superfluous social consequences (e.g., Lieberman [2001]), to extant human diversity.

Our comparative studies of the early ontogenies in charrs of the genus *Salvelinus* (Balon [1980]) clearly indicated that some females produced smaller eggs than other females, or eggs with denser yolk than others (see Crawford *et al.* [1999]). Incubated separately but under identical conditions the smaller eggs resulted in more altricial progeny in comparison with more precocial progeny from larger eggs. When smaller eggs were incubated under two different temperature regimes (4.4°C vs. 9.5°C), the warm incubated progeny was more precocial in comparison to the cold incubated. The same results were obtained with larger eggs.

Alerted to the constantly-appearing dichotomies, I followed a large number of eggs from larger females in detail, only to find that again two separate ontogenies occurred, akin to the previous ones from large and small eggs or two different temperatures (some in Balon [1980], [1984a]; some unpublished experiments). Upon closer examination, I found that the eggs from each female can be separated into two size groups; those incubated under identical conditions again resulted in separate altricial and precocial progeny. While the differences were very small, all were indicative of the larger differences found in the early ontogeny of several species of charr from various habitats and even continents.

How does epigenesis of early ontogeny explain the existence of true species pairs? Crawford and Balon ([1994c], p. 371) "compared the morphological development of two closely-related North American killifishes, *Lucania parva* and *Lucania goodei*. These species inhabit very different environments, and represent an exceptional 'natural experiment' with which to explore the life-history model described above". At Newport Spring, the site where *L. goodei* was collected, the conditions were stable; the water flowing from an artesian spring showed little diel or seasonal fluctuations. Only 10 km away, the collecting site for *L. parva* at Tower Pond presented highly unpredictable conditions: it was exposed to sea and fresh water and large diel and seasonal temperature fluctuations. In addition, summer algal blooms caused severe dissolved-oxygen deficits and the influence of tides and precipitation caused large changes in salinity and water volume.

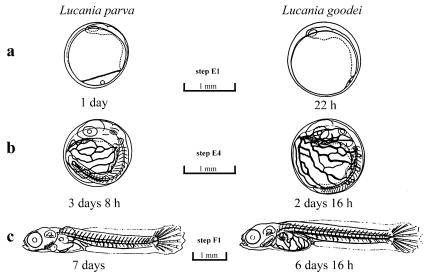


Figure 4 – Drawings of selected stages of *Lucania parva* and *L. goodei* during the embryo period from a lateral perspective (a – embryo body formation in step E1, b – segmental blood circulation in step E4, c – free embryo after hatching in step F1) (from Crawford and Balon [1994c]).

Crawford and Balon ([1994c], p. 395) concluded that "the lifehistory characteristics exhibited by *L. goodei* can be considered to be more precocial than those of *L. parva*" (Table 2, Figure 4). "Adult female *L. goodei* produced significantly fewer eggs, with significantly more yolk. The offspring of *L. goodei* developed at more rapid rates than those of *L. parva*, reaching the definitive (juvenile) phenotype at an earlier age, with lower mortality and with a different body shape". All these differences clearly agreed with the expected differences caused by epigenetic processes ultimately responsible for the true species-pair divergence.

Table 2 A comparison of characters between 25 cleavage eggs (step C2) each of *Lucania parva* (LP) and *L. goodei* (LG). Significant (p < 0.05) differences between means (t-test) and between variances (F-test) are indicated with directional signs (< or >).

	Mean		Variance	
Character	LP	LG	LP	LG
Clutch size	12.0	> 6.8	99.0	> 33.9
Activation rate (%)	79.4	> 61.1	602.9	1027.2
Yolk diameter (in mm)	1.060	< 1.201	2.6	2.7
Yolk volume (in mm³)	0.628	< 0.911	7.7	1.4
Yolk shrinkage (%)	6.96	6.95	13.460	10.445
Blastodisc height (in mm) Blastodisc width (in mm) Blastodisc volume (in mm³) Blastodisc:yolk ratio (%)	0.153	0.146	1.0	1.0
	0.614	0.645	6.0	8.0
	0.029	0.031	2.2	2.0
	4.8	> 3.5	6.6	3.5

## 4. ABANDONING DARWINISM

Let us reject the bad science that has served to exploit, to oppress, to obfuscate, and to destroy the earth and its inhabitants. Let us opt for a joyful and sustainable future – beyond genetic engineering.

Mae-Wan Ho [1999, p. 270]

The so-called mainstream scientists, the majority conforming to the "political" correctness (Sermonti [2002]), still refuse to admit (e.g., Pauly [2004]) that "there is evidence that the most sweeping

claims of Darwinism are wrong" (Jonathan Wells [2002], p. 329 in Research Notes). The evidence Wells compiled is overwhelming and confirms what many others were saying in the last twenty years, and some even earlier. Sadly, such criticisms and compilations of evidence did not trigger an open honest debate but instead caused more and more fundamentalist defenders of Darwinism and neo-Darwinism to react in ways that seriously hampered or even destroyed careers (see Margulis [1991a, b]; Margulis & Sagan [1997]; Milton [1997]; Wells [2002]). How else can we interpret losses of jobs in academia, refusals of grants from respective agencies, and censorship by most mainstream journals and publishers directed at anyone who dares to criticize Darwinism? It is amusing for the uninvolved to read that a Chinese scientist recently visiting the United States concluded "In China we can criticize Darwin, but not the government; in America, you can criticize the government, but not Darwin" (Wells [2002], p. 58). It is not so amusing for those who face this modern inquisition every day. "I was so little aware (mused Ho [1999], p. 10) of how science may be used, without conscious intention, to intimidate and control, to obscure, to exploit and oppress".

Milton ([1997], pp. 240-241) convincingly explained the early acceptance and continued attractiveness of the Darwinian and neo-Darwinian theories not only to most biologists but also to others: "The replacement of Darwinism-the-scientific-theory by Darwinism-the-ideology has been an important part of twentiethcentury political thinking just as it was important to the politics of the nineteenth century. In Darwin's day the theory was accepted partly because it supported the racism and European chauvinism on which the mercantile empire of Britain's ruling class was built and maintained. Today, Darwinism the ideology is one of the principal bulwarks of free-market economic theories and rightwing political thinking. It represents perhaps the most complete absorption of Darwinian thinking outside of the realms of biology. [...] Darwinists, and supporters of free-market economic policies, say that those who succeed are those who are best fitted or best adapted to the economic environment - in other words the best and the brightest. [...] It is merely an extension into human society of the great Darwinian principles of natural selection and the

survival of the fittest". Besides the socioeconomic reasons given by Milton [1997] and Ho [1999] for the lasting "success" of Darwinism – its icons are used by the least originative scientists to claim legitimacy and to secure their own survival (Balon [2002b]), while none of the "icons" has been proven valid (Wells [2002]).

Additionally, the "genetic determinism" of neo-Darwinism lends itself to the development of genetic-engineering biotechnology that "has produced a veritable industry for many third-rate scientists with limited imagination who can think of nothing better to do than dream up selective advantages for putative characteristics controlled by putative genes, thereby becoming an instant success [...] as well as the darlings of the equally simple-minded science journalists writing for the popular media" (Ho [1999], p. 106). And "genetic-engineering technology is really bad science working hand in glove with big business for quick profit ..." (*ibid.*, p. 13).

According to current knowledge, evolution by descent or replacement is a reality but the mechanisms by which it has happened are less known. Most of the suggestions made by Darwin and the neo-Darwinians clearly are wrong. Therefore, insisting on Darwinian explanations creates an obstacle in the free search for the real process, be it, as I believe, epigenesis (e.g., Løvtrup [1974], [1982], [1984a,b]; Balon [1983], [1990], [2002a]; Bruton [1989b]) or any other as yet unknown mechanism (e.g., Gutmann [1989], [1991]; Williamson [1992]; Ho [1998]). This search for truth should not be terminated by Mayr and his disciples (Mayr [2001]), nor delayed by artificial selection of demonstrative Darwinists for any new post in academia and support from granting agencies. Educators and the taxpayers should be told of this reality and be warned about the consequences of such deceptions (Wells [2002]); the defenders of Darwinism should be unmasked, and the innocent followers educated.

As was mentioned before, already Mivart [1871] and later Løvtrup [1974] and Reid [1985] among many others were closer to the truth than Darwin. In each generation of organisms, epigenesis creates new variations in ontogenies resulting in different alternatives. Depending on whether and how the environment has changed, one or the other alternative will survive and result in new forms.

Jantsch ([1980], p. 41) had concluded, "The dynamic existence of non-equilibrium structures is not only characterized by continuous oscillation and self-renewal, but also by the impossibility of ever achieving absolute stability". The maintenance of variation is, therefore, an essential prerequisite for the bifurcations of developmental events to create a new set of epiphenotypes each time within the changing environment. This variation can be further increased by novelties, introduced at various thresholds through the effects of external and internal environments, which enhance the flexibility of the system and provide a new set of binary answers on each occasion. "By extrapolation, the homeostatic mechanisms must have reserve capacity to deal with fluctuations in essential variables rather than to be in all-out activity all the time, which might preserve the desired equilibrium of the whole but would leave it vulnerable to further change" (Reid [1985], p. 305). "... what evolution seems to maximize is not efficiency or productivity, but flexibility to persist" writes Jantsch ([1976], p. 4) and later concludes: "A 'healthy' system at the same time effectively resists and copes with qualitative change; its flexibility in dealing with the unexpected makes life possible on both sides of the boundary, separating two stable regimes" (p. 7).

There exists an "almost unquestioned belief among the scientific community in the Darwinian and today the neo-Darwinian thesis, according to which evolution proceeds by natural selection from random variations (or genetic mutations for the neo-Darwinists)", writes Goldsmith ([2001], p. 386, and continues on p. 387). "As already intimated, the main reasons why Darwinism was so attractive to scientists is that it served to rationalise the socio-economic trends brought about by the industrial revolution. [...] Ludwig von Bertalanffy felt the same way. 'That a theory so vague, so insufficiently verifiable and so far from the criteria otherwise applied in 'hard science' has become a dogma [...] can only be explained on sociological grounds'".

Explaining evolution by epigenesis of alternative forms in each ontogeny and in a sequence of generations – a very logical thesis known by some already at the time the idea of natural selection emerged, was less socially attractive. As stated, for example by Kitcher ([2004], p. 12] "the breeder, interested in a particular

property of the flower or the pigeon, does select for a particular trait. Nature doesn't". If therefore natural selection exists, it plays no role in evolution (Wells [2002]) and survival of the fittest or even survival by differential reproduction is a myth. An altricial form may be less "fit" than the precocial, as proven valid for the "maintenance" phenotype of the mountain sheep (Geist [1971]), but given a particular environment it survives while the "fitter" precocial phenotype ("dispersal" of Geist) perishes. After all, the more "fit" imperial forces, created by the privileged class Darwin belonged to, failed to survive. Even in social context, therefore, it is not natural selection but artificial selection that is employed to maintain or create preferred relationships by the temporarily dominant group. Their dominant status is a consequence of epigenetic processes that sometimes result in "abortions and monstrosities" (e.g., due to inbreeding) instead of harmonious new beings (e.g., brought about by offering new options to the constantly changing environment).

As the demands of the industrial revolution are long gone, and a new revolution in communication is taking place, twenty-first-century demands on science will also change, hopefully deleting the former dogmas of Darwinism *sensu lato* into the trash file, much like, for example, the fittest executives of the "Enrons" and their likes. In the meantime, however, many innocent victims may still suffer as in any revolution before.

Let me close using the words of my favorite author Romain Gary ([1958], p. 7): "So don't ask me for any deep thoughts on this great adventure. All I can do is to place some fragments before you, myself among them, and accustomed as you are to digging things up and piecing them together, I trust you do the rest".

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## Eugene K. Balon

## EVOLUZIONE PER EPIGENESI: ADDIO AL DARWINISMO, NEO- E NON

### Riassunto

Negli ultimi 25 anni le critiche mosse alle teorie darwiniste sono aumentate considerevolmente. L'Autore passa in rassegna alcuni dei concetti proposti in alternativa alla "selezione naturale" e alla "sopravvivenza del più adatto". In particolare l'epigenesi è, per l'Autore, in grado di spiegare come vengano generate le variazioni nell'ontogenesi e le novità nell'evoluzione. L'epigenesi crea, in modo "saltatorio", variazioni che permettono agli organismi di sopravvivere in ambienti mutevoli come forme altricial o precocial. La costante produzione di queste due forme e la loro sopravvivenza in ambienti differenti rende possibile, in una serie di generazioni, l'introduzione di cambiamenti e la creazione di novità, i veri fenomeni dell'evoluzione.

L'Autore ritiene che il darwinismo sia diventato un'ideologia e che l'accettazione di teorie alternative sia ostacolata dai darwinisti, i quali sarebbero artificialmente mantenuti in posizione dominante nell'ambiente accademico.