

The theory of saltation and its application in the ontogeny of fishes: steps and thresholds*

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It seems that nature is fond of blowing smoke-rings.

Arthur Koestler (1974)
in *The heel of Achilles*

The view that development proceeds gradually is so engraved in our minds that any other possibility is not only treated with disbelief but viewed with distaste. Gould (1977, p. 409) put it admirably: 'The reconciliation of our gradualistic bias with the appearance of discontinuity is a classical problem of intellectual history. We have sought to reduce the external phenomena of saltation to an underlying continuity of process – to reduce the qualitative to the quantitative. Philosophies of change and progress have wrestled with this dilemma and have tried to resolve it by formulating such laws as the 'transformation of quantity into quality' of the Hegelian dialectic: the addition of quantitative steps will lead eventually to a qualitative leap ...'. It seems it is more comfortable to believe that ontogeny and phylogeny are gradual. Gradual ontogeny can be 'proved' by arbitrarily and leisurely sampling a sequence of stages, gradual phylogeny by expectations of finding every 'missing link'.

First, to alleviate the bad taste, I propose to talk of saltation instead of discontinuity. Saltation (Liem 1974, Ruse 1977) seems to be a better term for this phenomenon because it means 'an advance by a leap or leaps rather than by continuous gradation'. Development is not interrupted, but merely 'advancing in spurts' (Webster's New International Dictionary of the English Language, 1960).

The theory was first applied to the ontogeny of fishes by Vasnetsov (1953)¹ and Kryzhanovsky et al. (1953). They invented a sequence of 'etapes' of quantitative morphogenesis and growth, separated by a combination of brief but distinct qualitative changes in a developmental process. Brody (1945) and Martin

(1949) actually hinted at such processes. The 'normal stages' are, therefore, to be considered only a series of arbitrarily selected, disjunct moments in development (e.g. Balinsky 1948, Witschi 1962, Vernier 1969, Ballard 1973, Yamamoto 1975), whereas steps (= Russian etapy) characterize natural intervals of quantitative morphogenesis and growth (Fry in Martin 1949), separated by a combination of brief but distinct leaps forming a threshold. At this threshold structural and functional adaptations to the environment rapidly switch their mode of action. Thresholds may well be the most important intervals of ontogeny, during which adaptations to the environment express themselves and the future course of ontogeny is determined (Balon 1959, 1971). Unfortunately, limited observations rarely allow for exact recognition and placement of all the existing thresholds, forcing investigators to make decisions from uncertain leaps, or to adopt a sequence of steps distinguished by others for the same or closely related taxon.

Incidentally, little if anything of the thresholds can be recorded from preserved samples. The study of early ontogeny should employ frequent *in vivo* sampling and focus, beyond the usual external form and melanophore patterns (e.g. Misitano 1978), also on circulatory systems, respiratory pigments, cartilage and bone formations, behavior, cellular and organ movements, and many other features impossible to observe on preserved stages. Only then can a sufficient number of features be monitored to reveal the thresholds.

The theory of saltatory ontogeny expressed by steps and thresholds forms part of a natural model

* Editorial

¹ Russian authors usually cite three of Vasnetsov's (1946, 1948, 1953) articles in which the theory of 'etapes' was developed. It was, however, only clearly formulated in the last paper.

and should not be replaced by speculative systems designed for the convenience of, for example, larval taxonomy (Gühr 1957, Mansueti 1964, Snyder 1976, Allan & Ritter 1977, Doyle 1977, Fuiman & Loos 1977, Snyder et al. 1977). Such mechanistic disregard for the scientific principles of ontogeny must be considered as only a temporary convenience for overcoming the lack of any theoretical basis (Novak et al. 1969, Gould 1977) and cannot be excused by the different goals of such studies (Balon 1976).

Thom's catastrophe theory is probably closest to a mathematical model of the steps and thresholds (Thom 1973, Stewart 1975), but its application remains doubtful for lack of detailed knowledge of ontogeny in most organisms, and possibly, because of faults in the theory itself (Bari 1977). After all, it seems to be in part nothing but a geometrical model of Hegelian dialectic.

A sequence of steps forms periods, which are the main intervals of ontogeny (Balon 1958a, 1960, 1971 and 1975a). Modifications and extensions are required mainly with regard to the apparent existence, for example, of the larval period² in salmonids (Disler 1957, Smirnov 1975, Peñáz 1975). Like hatching, the onset of exogenous feeding occurs over a wide range of developmental features. Sometimes feeding begins when the embryonic finfold is entirely undifferentiated and at other times not until all fins are fully developed. Fish with fully developed fins, however, look very much like small adults or at least like their juvenile siblings, and it is illogical to consider them as larvae simply because most other fishes have larvae. Larvae require metamorphic changes before they take on the appearance of juveniles or 'small adults' (Cohen 1977).

I demonstrated (Balon 1977) that oviparous fishes, with reproductive hiding strategies, eliminate in varying degrees the larval period. This enables emergence (in salmonids, and acheilognathids) or release (in cichlids) of large juveniles at the start of exogenous feeding. In an evolutionary context, salmonids are the youngest fishes to hide their earliest stages of ontogeny and they may at times display a vestigial larval period incorporating characters typical of both the larval and juvenile periods in other fishes.

Since the development of hiding reproductive strategies is associated with an increase in egg size and yolk density, then graylings and landlocked salmonids with relatively small eggs should exhibit the larval vestige to a greater extent than other salmonids. The evidence presented by Soin (1963) and Peñáz (1975) for grayling, and by Smirnov (1975) for landlocked

Pacific salmon supports this contention. This means that species with the least developed hiding strategies retain more of the vestigial larval period during and immediately after the transitory interval of mixed feeding which separates the embryonic period of endogenous nutrition and the juvenile period in which all final adult structures have appeared. In fishes with more advanced hiding strategies this transitory vestige of the larval period does not exist. In these all juvenile characters (Balon 1975b) develop initially while feeding is still endogenous, either from the yolk (Balon 1977) or ultimately, as in viviparous fishes, from the female via special absorptive organs. With the advancement of hiding strategies, the transition from endogenous to exogenous feeding is more sudden, and the interval of mixed feeding is very brief or nonexistent.

It is obvious from the foregoing that truncations or prolongations in ontogeny will not only eliminate or expand the periods but also the steps. Consequently, steps are specific to every guild, every taxon and even every intraspecific form (Balon 1979). The various life history traits are only possible thanks to early ontogeny's flexibility for adaptation to new requirements. These adaptations occur through heterochronous shifts of characters. The next editorial will be devoted entirely to this heterochrony in ontogeny.

Thresholds occur at the start and end of steps as distinct functional changes (Vasnetsov 1953, Balon 1958b, 1959, 1960). In this sense a threshold should be defined as *an abrupt functional change during ontogeny*. It is at present impossible to decide if a change in the mitotic cycle or cleavage, from multiplication to differentiation of cells, can be considered a threshold. The distinction between a change of structure and a change of function is not always clear. The theory of steps or, more correctly, the theory of saltation will require detailed elaboration of all aspects — biochemical, physiological, morphological, ethological³ and ecological (and not necessarily in that

² For the sake of clarity let me repeat here again (Balon 1975a) the often confused intervals of ontogeny — periods, phases, steps, and stages — whose relationship should be compared to the relationship existing between measurable units of time — days, hours, minutes and seconds. Stage refers only to a just observed, immediate moment of ontogeny, steps and periods are units of the saltatory development (Kryzhanovskiy 1956, p. 5) and phases artificial intervals inserted for the convenience of nomenclature (Balon 1960).

³ At present discontinuities in ontogeny of behavior excite considerable interest (e.g. Flavell 1971, Isaac & O'Connor 1976, Kagan 1978, Bateson 1978); limited to behavioral aspects only, such contributions to the theory of saltation are insignificant.