About processes which cause the evolution of guilds and species*

Eugene K. Balon

Department of Zoology, College of Biological Science, University of Guelph, Guelph, Ontario N1G 2W1, Canada

Why, other than for names, must there always be species?

Van Valen (1976)

... evolution, in the sense of transmutation of species, is a basically epigenetic phenomenon that leads to adaptive responses to the environment during ontogeny ...
Rosen & Buth (1980)

If we accept that evolution (or for that matter phylogeny in a gradualistic sense) is a succession of ontogenies, the mechanism of change can be explained by saltatory processes and by heterochrony. These mechanisms may also contribute to our understanding of how lineages of species and guilds exist as separate entities at any given time. For, contrary to popular belief, separate evolutionary units and trends could hardly exist in a continuous world.

When I first presented a classification of reproductive styles in fishes (Balon 1975a,b) it was my intention to synthesize specific evolutionary trends (trajectories). My classification has since been accepted, at least by some, for its heuristic or didactic value (Welcomme 1979, Love & Cailliet 1979, Bond 1979, Miller 1979a, Simpson 1979, Moyle & Cech 1981) and referred to in relation to evolutionary theory, ontogeny of behavior, system modelling and ecology (e.g. Lett 1975, Chadwick 1976, Regier & 14 others 1976, Balon et al. 1977, Regier 1978, Noakes

1978, 1980, Mahon 1979, Miller 1979b, Balon & Chadwick 1979, Crowder 1980, Orth 1980, Noakes & Balon 1981, and Baylis 1981). In the meantime, I have found that in the initial classification some guilds were omitted (Balon 1981a) and at least one species assigned to the wrong guild (McElman 1978, 1981). Additions and amendments appear separately (Balon 1981b).

Here I will develop my concepts about the processes of saltation and heterochrony which explain evolutionary trends, such as reproductive guilds, and evolutionary patterns, such as Linnean species (biological, evolutionary or most of all terminal taxon, Løvtrup 1979, Wiley 1980). These, although hinted at previously (Balon 1975b, 1978, Balon et al. 1977), were never elaborated beyond the basic sequence of essential parts (Balon 1975c, 1979a, b, 1980a, b). I believe that these processes explain how changes are introduced into organisms, and that they provide for the understanding of the mechanisms of change. That structural changes indeed occur in the course of

* Editorial

evolution has been repeatedly documented. The patterns of change have been studied in detail (e.g. Greenwood et al. 1973 and ASZ Symposium on Evolutionary Morphology of the Actinopterygian Fishes, December 1980), although the explanations of the patterns were mostly ignored.

It may be a truism to say but I will nevertheless again emphasize that many evolutionary patterns may be biased to most common structures which leave ubiquitous evidence – the fossil record. The form and function of early ontogenic structures and reproductive behaviors can be at least as critical for the formation of patterns and trends – although not fossilized (see also Lagios 1979).

Just when the referees returned the initial version of this editorial a paper by Vrba (1980) came to my attention. As with the parade of rectangular evolution and punctuated equilibria, shown earlier to equal saltation (Balon 1981a), the ideas developed by Vrba parallel or confirm my altricial (r-like, eurytopic generalists) and precocial (K-like, stenotopic specialists) principle (Balon 1979b). More importantly, the phenomena covered by this 'principle' – hypermorphic and paedomorphic evolution through the mechanisms of environmentally induced heterochrony in early ontogeny – may be the *cause* of her '*effect* hypothesis'. It appeared like a good idea to explore this bisociation further.

Evolution of guilds

Like the Linnean classification of organismal units the classification of reproductive styles can be organized according to evolutionary trends. As more information becomes available the relationships and lineages can be gradually refined. Some relationships and evolutionary lineages are more clear than others; for example '...mouth brooding evolved from the substrate guarders' practice of cleaning and taking eggs into the mouth during hatching, and of transferring the brood orally from an incubation substrate to nursery pits. Transfer brooders could also have contributed to the development of mouth brooding (Oppenheimer 1970) [as could the aphrophils (B.2.1, see Table 1), indicating a probable polyphyletic evolution of mouthbrooding (Breder 1933, Peters 1965)]. For example, the female of *Trachyrus argyropleurodon*

Table 1. Reproductive guilds of fishes.

Section	
Group	Guild
A. Nonguarders	
A.1 Open substratum spawners	A.1.1. Pelagophils
	A.1.2. Lithopelagophils
	A.1.3. Lithophils
	A.1.4 Phytolithophils
	A.1.5 Phytophils
	A.1.6 Psammophils
	A.1.7 Aerophils
A.2 Brood hiders	A.2.1 Aeropsammophils
	A.2.2 Xerophils
	A.2.3 Lithophils
	A.2.4 Speleophils
	A.2.5 Ostracophils
B. Guarders	
B.1 Substratum choosers	B.1.1 Pelagophils
	B.1.2 Aerophils
	B.1.3 Lithophils
	B.1.4 Phytophils
B.2 Nest spawners	B.2.1 Aphrophils
	B.2.2 Polyphils
	B.2.3 Lithophils
	B.2.4 Ariadnophils
	B.2.5 Phytophils
	B.2.6 Psammophils
	B.2.7 Speleophils
	B.2.8 Actiniariophils
C. Bearers	
C.1 External	C.1.1 Transfer brooders
	C.1.2 Auxiliary brooders
	C.1.3 Mouth brooders
	C.1.4 Gill-chamber brooders
	C.1.5 Pouch brooders
C.2 Internal	C.2.1 Ovoviviparous
	C.2.2 Viviparous oophags
	C.2.3 Viviparous trophoderms

deposits her eggs in a basket formed by the pelvic fins from which she transfers them directly to the mouth of the male' (Balon 1975b). Several other probable evolutionary lineages in reproductive styles are indicated in that study, also for percids by Balon et al. (1977) and other lineages by Baylis (1981, this issue) in an elegant review; for most lineages, however, there is insufficient information.

Notwithstanding our ignorance, some trends in

[1] If in doubt consult the arguments developed in the Journal of Herpetology (13: 119–121 and 14: 79–80, 80–81, 81–82) and my review (Balon 1981a) where, briefly, paedomorphosis = juvenilization or rejuvenation, altricial (generalist) = progenesis and precocial (specialist) = neoteny.

the evolution of reproductive styles can be established. To begin at the beginning, through paedomorphosis[1], a ciliated auricularia-like larva probably became a fish-like creature. The sessile lophophore-feeding adult interval was eliminated and the first pelagophilous fish appeared (Garstang 1928, 1962, Young 1978), its entire ontogeny adapted to planktonic life (Schmalhausen 1968). In the Silurian the planktonic fish-like chordates reinvaded benthic habitats (similarly to some sciaenids, for example – Powles & Burgess 1978) and most likely evolved some kinds of guarding and bearing reproductive styles (Moy-Thomas & Miles 1971). The intromittent organs of fossils from that time (Miles 1967), and the antiquity of some internal bearers (Lund 1980) support this contention. Nevertheless, pelagophilous reproduction and pelagophilous early ontogeny have predominated throughout the ages (Johannes 1978, Balon 1978, Barlow 1981, Baylis 1981) and prevail amongst extant fish-like chordates. This situation is obviously a reflection of habitat diversity, and competitive density so much higher in freshwater than in marine systems (see also Cohen 1970, Horn 1972), in spite of popular opinion to the contrary (Balon 1978, p. 150 and footnote).

In this light I can no longer ignore the evolution of reproductive styles and waiving any fear of ridicule, have risked a schematic presentation of my ideas in a form of Figure 1. Numerous caveats, however, ought to be born in mind: 1. the fossil record of reproductive behavior and of early stages of ontogeny is many times weaker than that of adult morphologies, and with increasing geological age, the scheme presumably reflects more this fact than the true reproductive diversity; 2. some reproductive styles may have evolved only since the last glacial episode, but for graphical reasons penetrate through the entire Anthropozoic; 3. whereas paired formation of reproductive styles is most frequent and consistent with the principle of altricial and precocial twin form, there are more polyphyletic lineages than could be shown in the figure; and finally, 4. the above biological principle allows not only the derivation of guilds from original ones but also, in principle, the reverse. There is strong evidence that some freshwater pelagophils evolved from phytophils or lithophils (Kryzhanovsky et al.

1951). Their buoyancy adaptations, for example a large perivitelline space, differ from those most common in marine pelagophils – oil globules, tendrils and other appendages.

As stated earlier (Balon 1975b), reproductive guilds have different properties than terminal (Linnean) species. Guilds may behave as saltatory units, in essence being adaptive peaks in the reproductive landscape (e.g. Vrba 1980, Fig. 1). In this sense guilds can be classified. But they are not evolutionary units equal Linnean, evolutionary or terminal species, they merely follow evolutionary trends of their own irrespective of the evolutionary units of which they are comprised. In some cases the same species will touch on characters of two or more guilds tempting to construct an infinite number of intermediate guilds. Furthermore, individuals may vary in prominence of one or the other features; in essence variability within a guild is similar to phenotypic variability (Balon 1980a, p. 710). I doubt, however, that reproductive guilds are therefore less valid entities than the more intensively studied species which are also often difficult to define (Van Valen 1976). The problem is that it is difficult to avoid the species bias in perceiving other entities of evolution.

Table 1 gives the latest revised classification of reproductive guilds (Balon 1981b) and a reorganization of guild sequence according to the evolutionary trend (Fig. 1).

Guild and species dichotomy: altricial and precocial forms

Hence, a reproductive guild is a saltatory (discontinuous, in a less correct sense) peak in the variability of reproductive and developmental styles, whereas a species (or other terminal taxon) is a saltatory unit which has punctuated the evolution of morphological, physiological and ethological variations. Both are dynamic states created by saltatory forces (Balon 1979a), but guilds reflect only evolutionary trends, whereas species are 'nature's real units', forming evolutionary patterns. The processes which cause the evolutionary sequence of guilds or species may however, be similar. Environmental changes initiate heterochronous shifts of

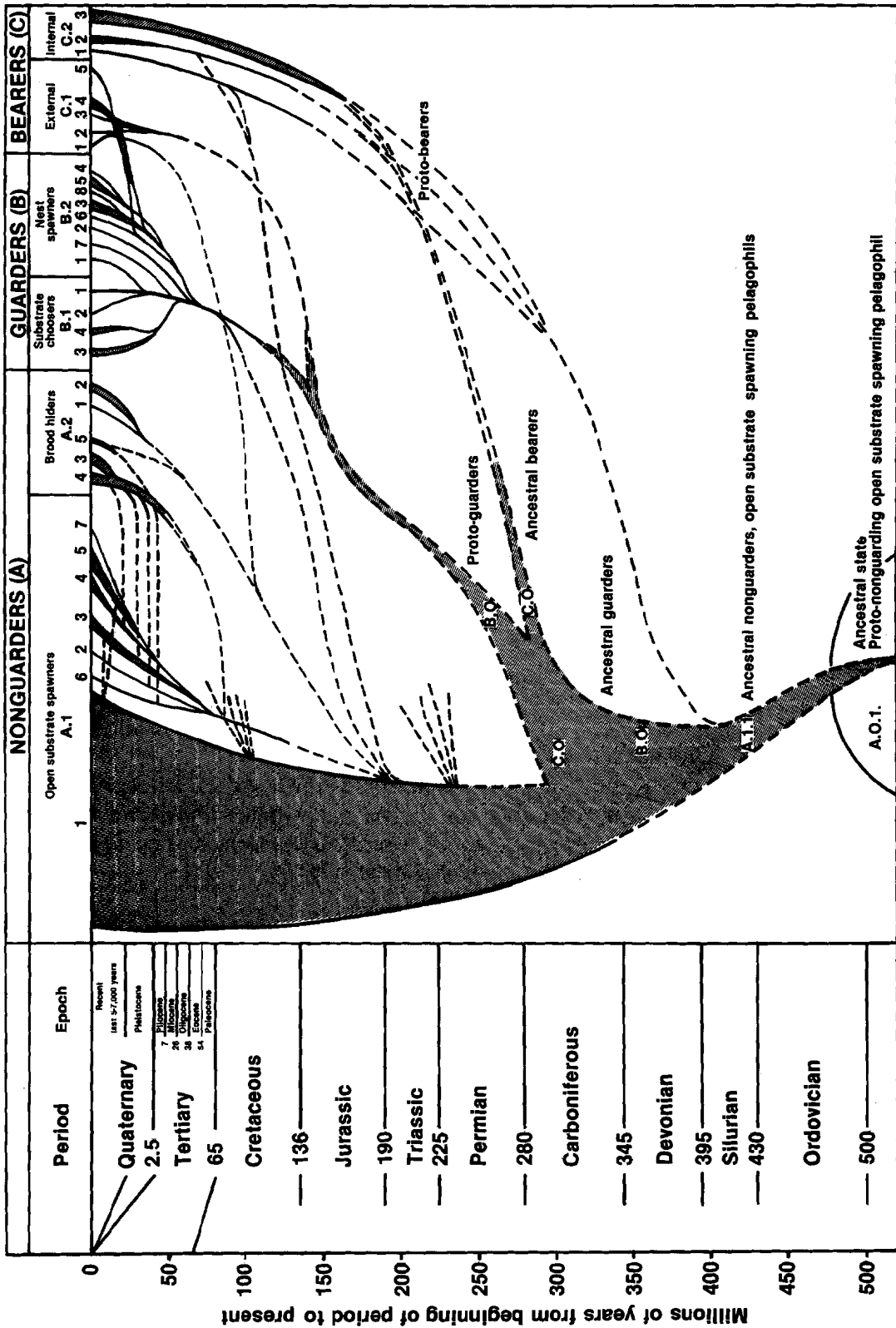*Fig. 1.* Very putative, schematic representation of the major trends in the evolution of reproductive styles (symbols and numerals of sections, subsections and guilds follow Table 1 except for ancestral groups A.0, B.0 and C.0; the absolute time of radiometric dating is after Eicher 1968). The specialized styles may have risen more than once as marked by the dashed branches to the right of A.1.1.

character anlagen in early ontogeny (see next section), creating an altricial or precocial[1] form, whichever is better suited for the ecosystem at the given time. These shifts are more significant (Løvtrup 1974) than the conventional 'natural selection' (but see footnote 5) affecting variation of adult characters only (Waddington 1975, p. 174)[2]. If the factors inducing the formation of the precocial style persist, a saltatory threshold may lead to a sudden switch into a new guild or species (and thus achieve a new equilibrium). An example is the case of *Fundulus heteroclitus;* some demes are open substrate spawning phytolithophils (A.1.4), whereas others have adopted air incubation linked with tidal cycles (Taylor et al. 1977). Consequently, the same species can switch from the purely aquatic altricial guild of phytolithophils to an intermediate style of semiaerophils. The saltatory change from altricial to precocial or from a less specialized to a more specialized form can occur in both directions along the evolutionary lineage. More specialized forms are created in circumstances of environmental stability, high species or guild diversity and strong competition, such as that which lead to a precocial form. Polyploidy may be an effective way to accomplish this (Schultz 1980). Less specialized guilds are created in opposite circumstances which lead to an altricial form (see Balon 1981a).

Ample evidence on the omnipresence of twin forms (altricial and precocial) can be found in the literature and may be interpreted as the initial consequence of Hennig's (1966, p. 235) paradigms that '... processes of species cleavage are the characteristic feature of evolution'. For example, *Alosa sapidissima* as characterized by Leggett & Carscadden (1978) appears to be altricial to the north

of its range and precocial to the south. Similarly, the life history pattern of *Poeciliopsis occidentalis* (Constantz 1979) clearly points to the existence of twin forms, as do data presented for other fishes (e.g.Fenderson 1964, Frost 1965, Rupp & Redmont 1966, Messieh 1976, Kobayasi 1976, Copeman & McAllister 1978, Bruce 1980, but see Stearns 1980). This concept is consistent with other aspects of ontogeny (e.g. Schultz 1980) and evolution (e.g. Williams 1977); most organisms may have followed the same dichotomy (Hennig 1966, Løvtrup 1977). So may man (Lovejoy 1981). Neanderthal man was most probably precocial and the Upper Paleolithic man altricial (Geist 1981), whereas, recently the bushman-like forms are the altricial people of the paedomorphic genus *Homo.* I have devoted ample space to this elsewhere (Balon 1981a).

Genetically programmed and environmentally induced heterochrony in early ontogeny may increase phenotypic variation in reproductive styles and in specific characters, and result in rapid selection of phenotypes (and subsequently genotypes) adapted to the local environment (Horn 1972, Balon 1978, Baylis 1981). This neatly resolves the time dilemma in organic evolution (Eicher 1968, Dobzhansky et al. 1977) and may explain explosive speciation (White 1978). As previously suggested (Balon et al. 1977) the evolutionary classification of reproductive styles may contribute to the palaeogeographical interpretation of organismal evolution and reveal evolutionary lineages otherwise hidden by or from Linnean classification.

The cause and effect hypothesis

Since evolution is nothing but a sequence of ontogenies, the theories explaining processes and especially changes of ontogenic development must also explain evolution. Therefore, attempts to separate microevolution from macroevolution[3] are probably

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[2] 'Darwin used as a central theme of his argument for natural selection that many more young are born than survive. The situation is especially extreme in fishes, where there are often many orders of magnitude more zygotes produced than will survive. It is obvious, given this situation, that selection operates most heavily on these pre-adult stages. The fuel of evolution is variation, and clearly there is a great deal more genetic and phenotypic variation in the zygotes than in the few adults that survive from those zygotes. Moreover, the adult phenotype must pass through a complex ontogenic sequence; it is not a static thing but rather a dynamic phenotype with continuous change and many stages, most of the changes occuring before adulthood. The fixation on adult characters is naive, to say the least' (J.R. Baylis in lit. 20.10.1980).

[3] Microevolution is used 'for evolutionary processes observable within the span of a human lifetime as opposed to macroevolution, on a geological scale' (Goldschmidt 1940, p. 8), modified to mean the evolutionary change within a form (microevolution) as opposed to the rise of a new form separated from the old by a saltatory threshold (macroevolution). I agree with the statement by Nachtsheim that 'the laws governing macroevolution are the same as those governing microevolution' (as cited by Hennig 1966, p. 225).

misleading (Heberer 1958). As I elaborated earlier (Balon 1981a) the entire difference may rest in the 'amplitude' (strength) of thresholds, which form as a consequence of essentially the *same* biological processes. The delayed or accelerated appearance of thresholds in early ontogeny modifies the formation of morphological, physiological and ethological characters with adaptive and/or evolutionary consequences. Selection favors genotypes with enough variation to permit phenotypic shifts back and forth between two alternative stable states.

In my opinion heterochrony in early ontogeny is the main source of variation. When the consequences of heterochronies combine, they are responsible for the strength and timing of thresholds – in short are an important cause of changes, which are intuitively equal to Waddington's *rewriting of the genetic programmes*. As to the question of how the mechanism of heterochrony works, we may just as well accept Waddington's (1975, p. 9) explanation: '... it had become apparent that the 'gene-concrescence' itself undergoes processes of change; at one embryonic period a given concrescence is in a phase of 'competence' and may be switched into one or other of a small number of alternative pathways of further change – but the competence later disappears and if you've missed the bus the switch won't work'[4].

Now then, the survival of the overabundant zygotes, the numerous stages of early ontogeny, depends on the (a) hard selection (Whyte 1965, Wallace 1970, Cohen 1977, p. 19) – defective expressions of the genome, and (b) soft selection[5] for a most suitable combination of phenotypic characters (hence, not in the sense of Wilson 1980). The phenotypic variation is probably increased or decreased in the convenient direction by environmentally induced heterochrony. Consequently, a highly heterogenous gene pool may produce individuals phenotypically almost identical (Waddington 1975) and, as a rule, of phenotypic variability far below the genotypic variability (Ferguson et al. 1981). A homogenous gene pool in contrast may, through heterochrony, produce high phenotypic variation and possibly, at least in part, recover some heterogeneity via the process of juvenilization (paedomorphosis).

The relative importance of the two epigenetic and evolutionary processes – juvenilization and saltation[6] – for the understanding of the following hypothesis cannot be overemphasized. I have given details quite recently elsewhere (Balon 1979a,b, 1980a, 1981a) and will therefore refrain from repetition. As a biologist, I lack sufficient mastery, I confess, of the sophisticated geometry which would be required to produce a convincing illustration. Probably therefore my earlier figure failed to excite a response even from collaborators. Realizing, however, that it may yield an additional perspective to the 'effect hypothesis' (Vrba 1980)[7] I feel that I am justified in combining the two as a possible cause and effect (Fig. 2).

The lower part of the figure represents my original presentation of the 'altricial ⇌ precocial principle', a theory of the continuous tendency of organisms to produce specialists (left to right), with the way back to generalists remaining open (paedomorphosis). The generalists with a highly heterogenous gene pool, and an ability to survive harsh, fluctuating environments, are as a rule organisms of early maturity and/or long reproductive interval associated with a high fecundity, low energy gametes and low parental investment. Early ontogenic features of highly general nature are retained through most of the life span in a large number of

[4] Whiteheadian term 'concrescence' equals Waddingtonian term 'chreod', and to a certain degree Thomian 'catastrophe' and my usage of 'threshold'. I feel justified to use consistently the last term as part of my desire to keep the excessive proliferation of terms in check as well as to identify, comparatively, the same or similar phenomena by the same name; retention of the term saltatory for evolution instead of rectangular (Stanley 1975) or punctuated equilibria (Eldredge & Gould 1972) evolution are parts of the same desire.

[5] Irrespective of the principles behind natural selection (e.g. Van Valen 1976a, and hypercycles of Eigen & Schuster 1979).

[6] It is naive and uninformed to accuse proponents of saltatory processes of Marxist sympathies (e.g. Halstead 1980). Hegelian dialectic is a philosophical concept innocent of Engels' (and consequently Marx's and Lenin's) application to social events (Patterson, Hughes-Games, Rothman 1980, Wade 1981, see detailed review in Balon 1981a).

[7] The 'effect hypothesis' is best summarized by Lewin (1980, p. 885): '... specialists both speciate and become extinct frequently whereas generalists speciate and become extinct infrequently. The upshot of this is that the evolutionary history of a group of related species (such as the antelopes) that display a spectrum of lifestyles from specialist to generalist can be sketched as a skewed branching bush leaning heavily toward the rapid speciators'.
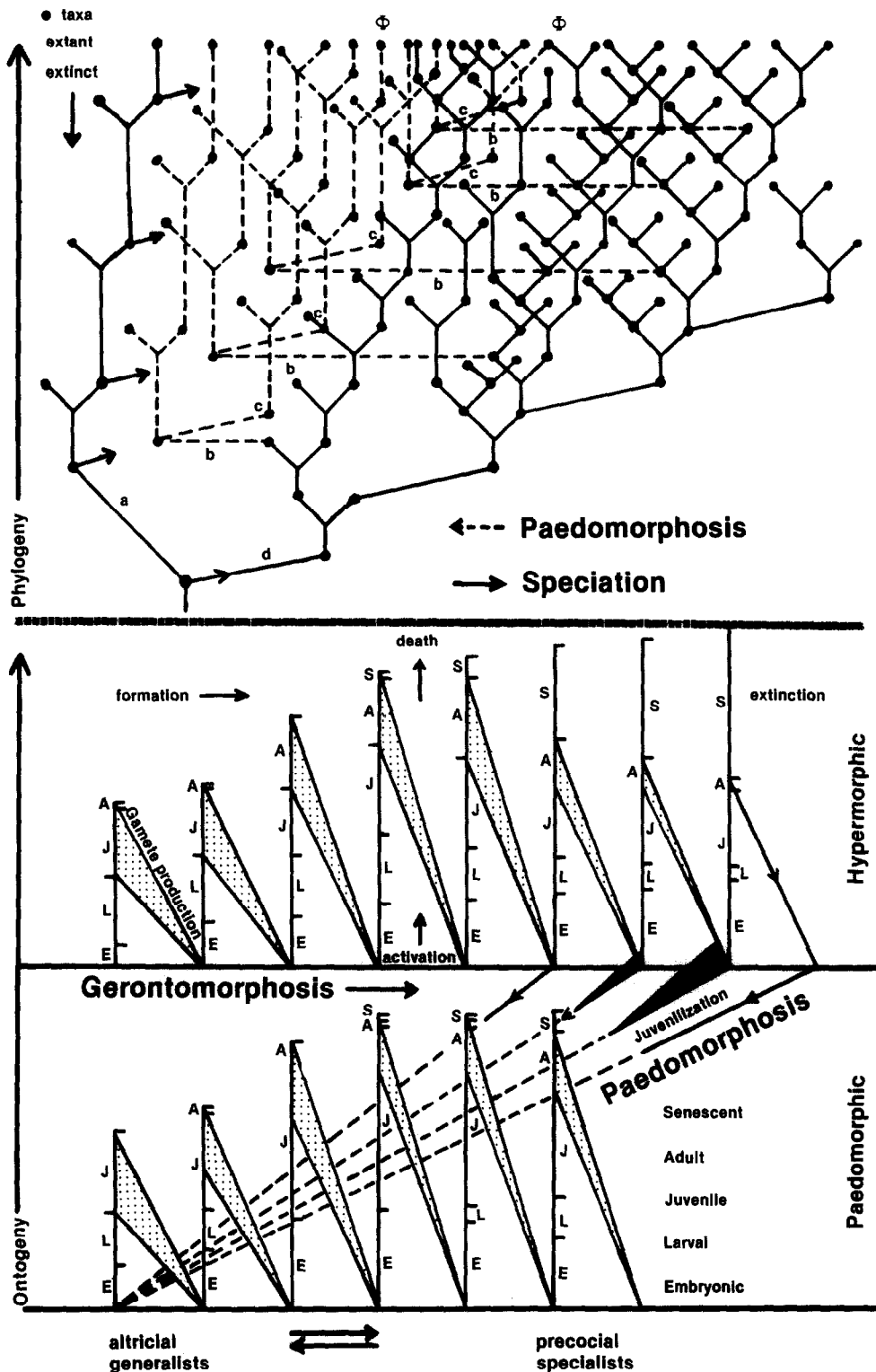
Fig. 2. Putative hypothetical scheme combining the 'altricial ⇄ precocial principle' with the 'effect hypothesis'. Speculative numbers of taxa formed in the depicted case are about 9 per hypermorphic altricial (a), 20 per paedomorphic altricial (b), 26 per paedomorphic precocial (c) and 99 per hypermorphic precocial (d), each to be multiplied by numbers resulting from repetitive sequences (not represented) noted by diagonal arrows. Smaller paedomorphic range and the narrowing range of hypermorphic sequences reflect the decrease of variability in evolution, the area of overlap in speciation through gerontomorphosis and paedomorphosis (Φ) the intuitive area of explosive speciation.

zygotes, enabling a constant presence of an extremely broad range of variability capable of satisfying a wide environmentally dictated selection. Given some degree of environmental stability and increasing competitive pressure, selection would favor specialization resulting in more energy efficient reproductive styles. After a certain number of ontogenies (= generations) along the trend of specialization (left to right in the figure), the phenotypic variation will be severely reduced, with the ultimate loss of some genetic heterogeneity[8]. The delayed reproduction became less 'wasteful', ultimately limited to a few precious zygotes, and the lifespan prolonged, most significantly by the senescent period which is of no reproductive value (Balon 1975c). A reduced number of specialized early ontogenetic stages result. This restricts variability so much that previously accommodated environmental changes become totally destructive. For this process I have used the term gerontomorphosis – the initial hypermorphic sequence of ontogenies and evolution.

Since the constant development of altricial and precocial forms or (if you like), generalists and specialists is temporal and saltatory, the development of a phenotype will follow the 'canalized pathway of change' (Waddington 1975) to a threshold and change into a new developmental quality of the homeostatic pathway, recognized at present as form (Balon 1981a), species (Van Valen 1976b), guild (Balon 1975b), or, as a result of much stronger thresholds (e.g. juvenilization), any higher taxon (Løvtrup 1979, Wiley 1980)[9]. This process is represented in the upper part of the Figure 2 as speciation and illustrates the trend of evolution modified according to the effect hypothesis.

Given that the only possible sequence of ontogenies (evolution) was hypermorphic, every species would sooner or later become extinct. However, each organismal unit or trend (i.e. form, species, guild), reacts to unpredictable environmental fluctuations by displaying in turn or at the same time altricial and precocial traits, a biological dichotomy made possible by saltation and heterochrony in early ontogeny. These traits may accumulate into an evolutionary event. Some time prior to hypermorphic extinction the process of juvenilization, in a strong threshold fashion, may change a specialist back into an altricial generalist, enabling the original sequence to be repeated along a new paedomorphic evolutionary trend. In the process, some of the genotypic variability may be lost and the resultant paedomorphic speciation less diverse (Fig. 2 dashed lines). When the hypermorphic and paedomorphic speciations overlap, the phenomenon of explosive speciation (but see Reid 1980) may occur. I must admit that this is an intuitive rather than a rational suggestion put down to stimulate ideas – after all the main purpose of this entire editorial.

Acknowledgements

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[8] Which I mean not literally in the sense of Fechner (1873) or Rosa's (1899) rule of 'progressive reduction of variability', but in the sense of Beurlen (1937): 'The breadth of evolution of successive groups shows a distinct narrowing, since the basic divergences of organization become progressively smaller' (as cited by Hennig 1966).

[9] For example, the presence of 'multispecies' (sensu Van Valen 1976b) in fishes is highly indicated not only in darters (Etheostomatini, Echelle et al. 1975) but in many salmonid (e.g. *Salvelinus*, Balon 1980) and cichlid genera (e.g. *Haplochromis*, Greenwood 1974, and others, Balon 1977, 1978).

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