ZIG-ZAG EVOLUTION

By

Gunnar Henningsmoen

(Paleontologisk Museum, Oslo 5)

Abstract. Evolution which takes place alternately in opposite directions (e.g. increase and decrease in size) is called zig-zag evolution. In zig-zag or fluctuating evolutionary trends, the course of the evolution is repeatedly reversed. The possibility of confusion with other types of trend is discussed.

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Introduction

As maintained by Romer (1949, p. 110) "evolution is definitely known to be reversible". Thus structures once gained can be lost again. Examples cited by him are the loss in typical tetrapods of the bony armour of their piscine ancestors, and the loss in snakes of the typical tetrapod limbs found in their lacertilian ancestors.

The doctrine of irreversibility is usually ascribed to the late Louis Dollo as "Dollo's Law". However, as pointed out by Romer (1949, p. 112) and others, Dollo's theory (Dollo, 1893, 1922) was more modest and of restricted application. The doctrine of irreversibility apparently applies only to complex structures and organs; when lost, they are not regained again. Since every complex structure is presumably produced by a considerable number of genes, the chance of a reversion of structures to far earlier and quite different stages is very small (MULLER, 1939).

ROMER (1949, p. 110) further points out that, apart from organs, trends in phyletic development are frequently reversed; thus an increase in size may be followed by a decrease in size. Other examples are given below.

It seems to be accepted that a feature may develop and then disappear again within what may be called an evolutionary cycle. Reversibility is thus accepted within this cycle. However, there seems to be a "doctrine of non-repetition" implying that such cycles may not be repeated along a single phylogenetic trend. This may be true of the cycle absence — presence — absence of complex structures, but it seems that other cycles (e.g. the cycle small — large — small size) may be repeated along a single trend. Apparently there are both reversible and irreversible, repetitive and non-repetitive evolutionary trends. Some different types of trend are discussed below.

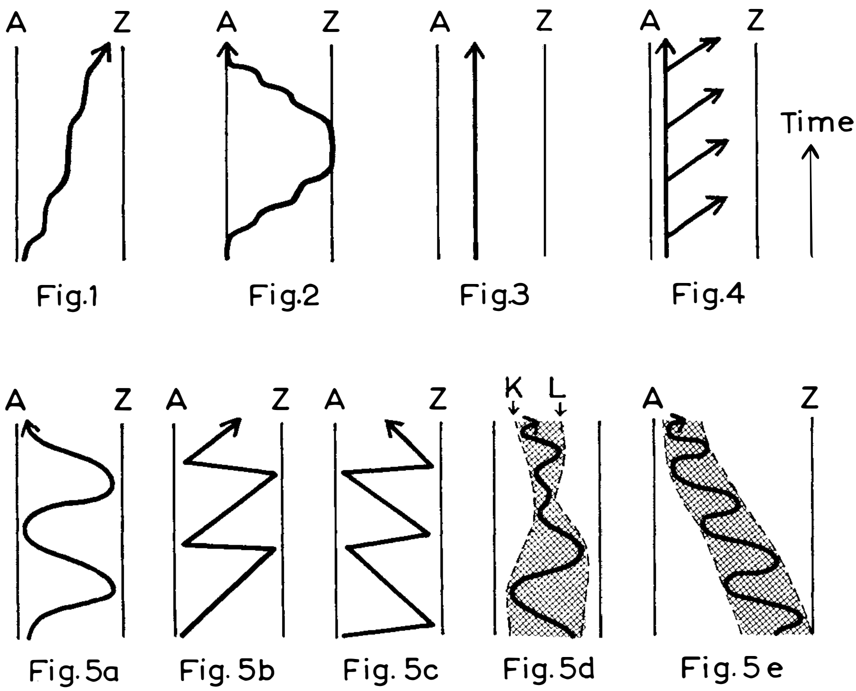
Types of evolutionary trend.

One-way trend (*orthogenesis*)

The trend is always the same, e.g. towards a greater size or towards an increasing adaptation of a certain feature to a certain environment. This is an example of orthogenesis. ROMER (1949, p. 108) believes that "it is perhaps better, as SIMPSON and others suggest, to use some such term as rectilinear evolution for this type of phenomenon and thus avoid the implication of teleology usually attached to the word orthogenesis". SYLVESTER–BRADLEY (1962, p, 123) uses the term orthogenesis in its original sense for steady adaptations along trend lines. Since the pace of evolution is not generally the same all the time, the trend is not, as a rule, represented by a straigt line in a diagram with time along the ordinate (fig. 1), and the term rectilinear might be somewhat confusing. This type of trend is here referred to as a one-way trend. It is a typical irreversible and non-repetitive trend.

Detour trend.

Another type of trend may be exemplified by the development and later complete loss of a structure. In fig. 2, A represents the ab-



Figs. 1—4, 5a—e. Diagrams showing various types of evolutionary trends: 1) one-way trend, 2) detour trend, 3) stillstand, 4) iterative trends, 5a—e) fluctuating trends (see text for explanations).

sence and Z the maximum development of a structure. The trend may be described as a roundabout or detour trend. There is only one cycle in the trend, with a phase of development (positive phase) succeeded by a phase of reduction (negative phase). The trend is non-repetitive.

Stillstand or no evolution.

The diagram (fig. 3) is added for the sake of comparison.

Iterative trends.

There are several kinds of branching trends. For the following discussion only repeated parallel trends (iterative trends) are of importance. In a diagram (fig. 4) they appear as a comb-like pattern, each "tooth" of the comb representing a side-branch. Such iteration has been accepted for many fossil groups (e.g. see SYLVESTER-BRADLEY, 1959, p. 193). An example in trilobites is suggested by KAUFMANN (1933, p. 9, fig. 2).

Zig-zag or fluctuating trend.

An increase in size may be followed by a decrease along a phylogenetic trend, and this cycle may be repeated several times, thus giving a picture as diagrammatically shown in fig. 5a. Such evolution, which takes place alternately in opposite directions, may be called zig-zag evolution. A zig-zag or fluctuating trend is exemplified by the absolute size of the horse (as indicated by the length of the cheek tooth series) from "*Eohippus*" to the Recent *Equus*, as illustrated by ROMER (1949, p. 112, text-fig. 2). Further examples are known in trilobite phylogeny (cf. HENNINGSMOEN, 1957, pp. 84—85). Thus a decrease in number of thoracic segments is succeeded by an increase in the rather well established lineage *Olenus* (15–13 segments) → *Parabolina* (12) → *Parabolinella* (16–21 segments). The size of the dorsal shield of adult olenids may decrease and later increase in a phylogenetic lineage[1], e.g. *Peltura* (medium-sized) → *Acerocarina* (small) → *Westergårdia* (small) → *Boeckapis* (medium-sized) (fig. 6). The same applies to restricted areas of the shield; the postocular areas of the fixed cheeks are wide in *Olenus*, rather narrow in the descendant *Protopeltura* and especially in *Peltura*, and rather wide again in later pelturines like *Boeckaspis* (fig. 6). Furthermore, axial and genal spines apparently disappear and reappear in some olenid lines. The presence or absence of glabellar furrows also seem to alternate along phyletic lineages; they are well developed in *Protopeltura*, effaced or even absent in *Peltura* species, and well developed again in later derivatives such as *Acerocare*. The position of the eyes also show examples of fluctuating trends in olenids. In *Olenus* they are rather far from the glabella in earlier species, closer to the glabella and more anteriorly located in later *Olenus* species, and this is even more the case in the succeeding *Protopeltura* and *Peltura* species, whereas the eyes in later, descendant, pelturine genera (*Westergårdia*, *Boeckaspis*) are again

[1] It might be argued that this represents only two phases, perhaps of a detour trend. However, somewhere along the line leading to *Peltura*, at least in the pre-trilobite part, the size must have been smaller, so that at least 3 phases are known, and thus a fluctuating trend.

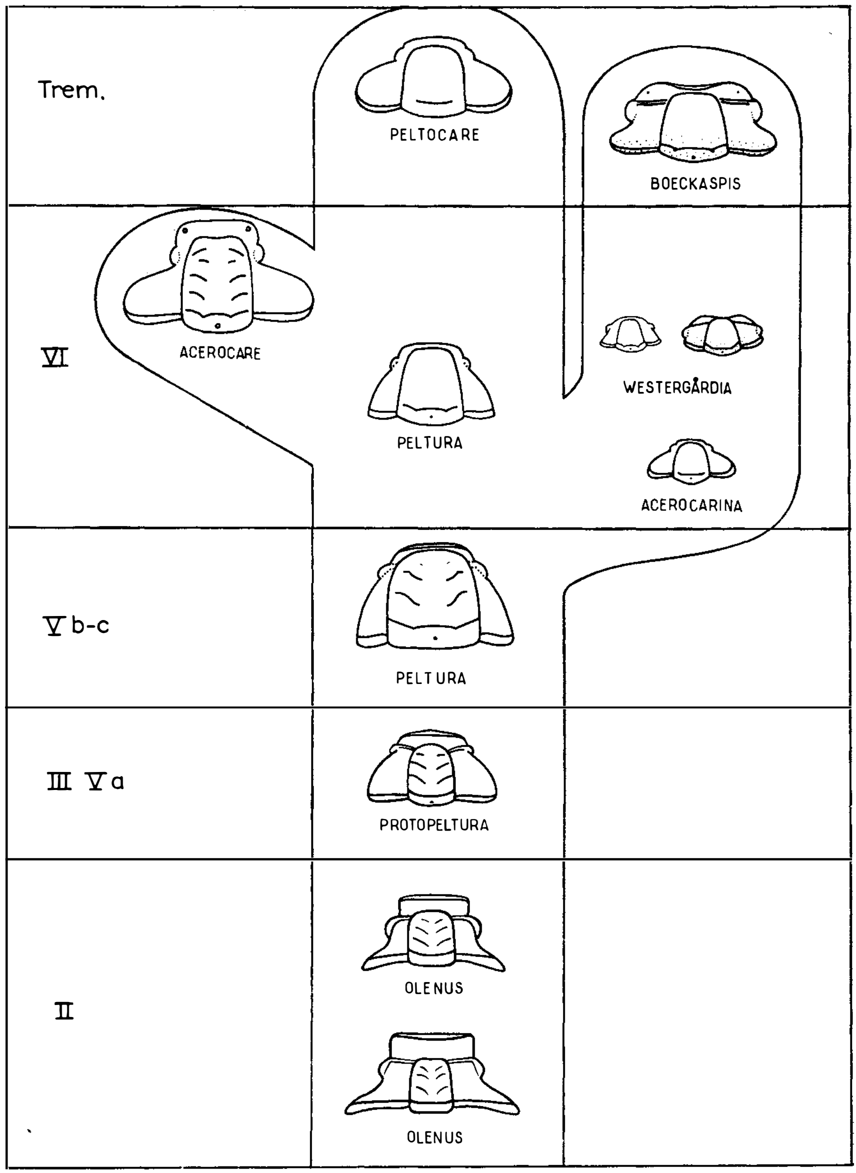


Fig. 6. Phylogeny of some Scandinavian olenid genera. II—VI, Upper Cambrian stages; Trem., Tremadocian.

situated further back and further away from the glabella, duplicating the position of the eyes in early *Olenus* species (fig. 6). Recently, ROBINSON (1964, p. 518) has likewise maintained that "... apparent evolutionary trends among trilobites often seem to have been reversed, espesially on the specific level".

Like the cycle of the monocyclic detour trend, each cycle of the in principle polycyclic fluctuating trend consists of a positive phase (of development) and a negative phase (of reduction). The two phases need not be symmetrical (as in fig. 5a), and asymmetrical undulations may be developed (e.g. as in figs. 5b and 5c). The type of undulation may change from cycle to cycle, and periods of stillstand may, of course, also occur. Features showing fluctuating trends display a certain range of variation and thus form morphological series. The range of variation is unlikely to be as constant as shown in fig. 5a, but generally changes from cycle to cycle. Thus the size dispersal is generally not the same in descendant units. The fluctuating trend may be said to have its course within boundaries (K, L in fig. 5d), delimiting an "evolutionary channel" (stipled). The width of the channel shows the range of variation at different stages, and the channel is thus rarely of even width. The channel may well show a trend of its own, as for example the trend shown in fig. 5e, or even a fluctuating trend.

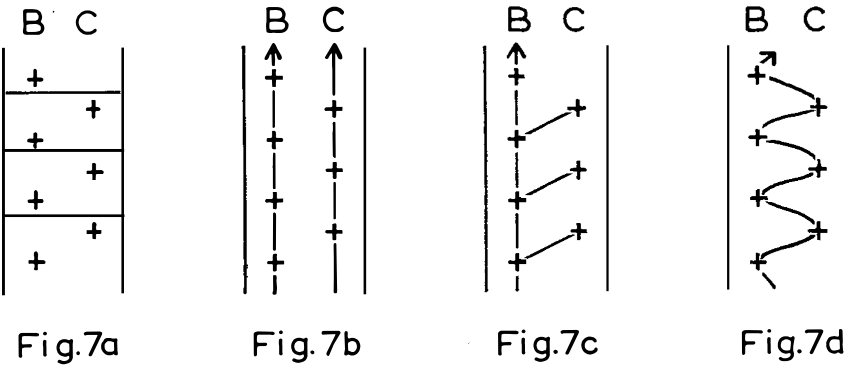
Fluctuating trends show examples of reversible and repetitive evolution.

Discussion

A one-way evolutionary trend may persist for, geologically, long periods of time, and then reverse, so that the general picture becomes that of a detour trend or even part of a fluctuating trend. Stillstands may also be followed by periods of evolution. It is debatable whether or not some apparently one-way evolutionary trends are truly irreversible, — and if so, why. One possible explanation, given by ROMER (1949, p. 107), is orthoselection, a process of increasingly improved adaptation to a relatively stable environment. As further stated by him, "under such conditions any deviation from the 'normal' line would be negative to survival value, and would tend to be eliminated; the potential branches of the 'tree' would tend to be pruned by selection before they became marked enough to become apparent in the fossil record". Thus a far-reaching adaptation to a certain environment would render it difficult to change the trend. If the environment changed, the chance of extinction would be greater the further the adaptation had gone, and the chances for a reversed trend correspondingly smaller. In case of extinction, the fossil record would show a pruned one-way trend, which might perhaps better be referred to as an *irreversed* trend rather than an *irreversible* trend. However, a one-way trend would generally be regarded as an irreversible trend.

A single cycle of a fluctuating trend might easily be mistaken for a detour type of trend. The crucial point is, of course, whether the ability to produce a certain feature or structure has really been lost. An apparent loss may be produced by a single masking mutation (or even an environmental change in developmental conditions), and the structure may readily reappear after a few generations with the removal of the "block" to its expression (ROMER, 1949, p. 113). An interesting case of the return of an apparently long lost structure (2nd. lower molar) in the evolution of the felid dentition has been discussed by KURTÉN (1963, p. 9). Another difficulty is that a feature of the hard parts of the animal may become completely obliterated, whereas the soft parts producing it are not lost, so that the hard part feature may reappear. This is probably the case with alternating presence and absence of glabellar furrows in trilobites, mentioned above. One may assume that the glabellar furrows were formed by the pull of cephalic muscles, and that these muscles no doubt were present also in trilobites with a smooth, unfurrowed glabella. The absence of glabellar furrows may have been due to a structurally more resistant form of the glabella (e.g. thicker shell or more convex surface). In other cases a structure which is lost in adults is developed in larval stages. If so, this structure might readily reappear in adults of descendant forms. This may be the explanation of the disappearance and reappearance of axial and genal spines in trilobites along phylogenetic trends. We palaeontologists should perhaps not think so much in terms of the evolution (transformation) of one adult form to another, but remember that the ontogenetic series also is a morphological series with quite a variation in features as well as in dimensions.

Apparently one should distinguish between the loss of a structure



Figs. 7a—d. Fossil record (7a) and possible explanations: 7b) two different genera, B and C, — 7c) iterative trends, and 7d) fluctuating trend.

and the loss of the *ability* to produce such a structure. In the latter case, the non-development of a structure may be due to environmental factors, for instance. Thus the ostracode *Cyprideis torosa* (JONES, 1850) generally has a smooth carapace. However, a decrease in salinity results in the development of nodes (cf. VAN MORKHOVEN, 1962, p. 45). The ability to develop nodes is not lost in this species, although the nodes are generally not developed. One should also bear in mind that a structure reduced to a minimum might be mistaken as lost, deceiving one to believe that it was a case of detour evolution. It might further be recalled that the shape of a certain structure may change with its size. A large-sized structure may be so different in shape from the corresponding small-sized one, that one might believe that they were genetically different structures.

A fossil record (as in fig. 7a) might be interpreted (fig. 7b) as showing the parallel evolution of two different genera (B and C). It might also be interpreted as showing iterative trends (fig. 7c), in which case the C's should rather be called grades (cf. HUXLEY, 1959). However, a third possibility is that it is an example of a fluctuating trend (fig. 7d). Especially if the fluctuating trend is asymmetrical and the negative phase took place in a relatively short time (fig. 5b), the fossil record could be rather similar to that of iterative trends.

If we regard two different features in a phyletic lineage, the one feature (Y) showing a one-way trend (e.g. the development from 1 to 4 spines), the other (Z) a fluctuating trend, this may be shown schema-

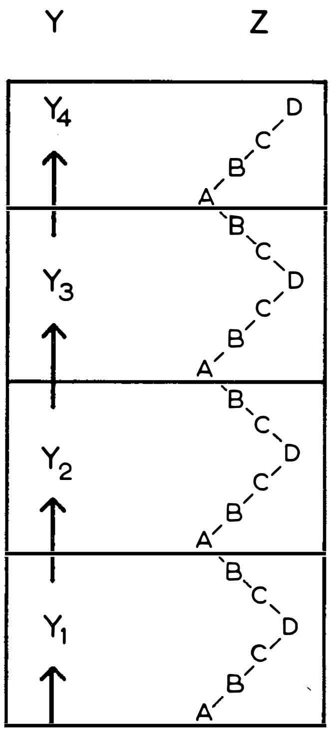


Fig. 8. Two features in a phyletic lineage, the one (Y) showing a one-way trend, the other (Z) a fluctuating trend with the morphological dispersion A to D.

tically as in fig. 8. There is a certain range of variation in feature Z, which may, for instance, refer to size (A small, B, C intermediate, D large size) or number of furrows (A, 1; B, 2; C, 3; and D, 4 furrows). The development from Y_1 to Y_4 may be regarded as evolutionary stages, which may well be supraspecific units such as genera. Each genus would then have a certain morphological dispersion (A to D) with respect to feature Z. Thus the genus with one spine would have a certain size distribution of its species (each of which would have its own size distribution), and the descendant species with two spines could likewise have a size distribution of its species, although rarely within the same limits as the ancestral genus. Generally any taxonomic unit has the capability to form a morphological series; the components of which may comprise smaller units (e.g. species of a genus).

Not all links (as A, B, C, D) of a morphological series may be realized at each evolutionary stage, and, going more into detail than in fig. 8, an evolutionary scheme might well appear as in fig. 9.

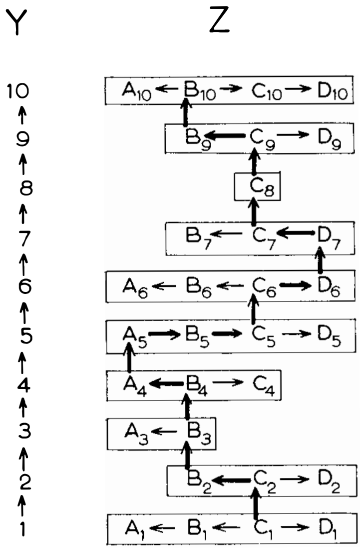


Fig. 9. Two features in a phyletic lineage, the one (Y) showing a one-way trend with stages 1 to 10, the other (Z) showing fluctuating and branching trends. Heavy arrows indicate a fluctuating trend. Feature Z has a morphological dispersion from A to D, but the whole series A to D has not been realized at each evolutionary stage (of feature Y). Evolutionary stages along the ordinate. If the ordinate had represented time, the horizontal arrows should have pointed more or less upwards.

If feature Y (like Z), was also subject to fluctuating evolution, the stratigraphically successive forms might easily show the dreaded specialization crossings, which are often taken as disproving a direct descent of one form from another. It would be an example of mosaic evolution. It thus seems important to consider whether or not a certain feature shows fluctuating evolution.

As to the reason for fluctuating trends, it seems that changing environmental conditions may be one, just as well as a stable environment may favour a one-way trend. Some environments may favour small size or spinose forms, others may favour large size or aspinose forms. Similarly, a change of habitat may result in a change of the evolutionary course. The terms positive and negative phase have been introduced as convenient, descriptive terms; they may, of course, both be progressive. Thus in the case of the cycle large — small, the (negative) phase towards a smaller size may represent an improved adaptation, just as well as the positive phase under other conditions. The change from the one extreme to the other may be more or less gradual, or more or less abrupt.

Concluding remarks

Whereas evolutionary trends were formerly depicted as phylogenetic trees, and later as phylogenetic "bushes", there is a tendency nowadays to construct phylogenetic "meadows", each line being traced equally far back. An example of such a phylogenetic "meadow" is the phylogeny of Proboscidea as interpreted by OSBORN (1925), where, as stated by ROMER (1949, p. 110), "every subordinate group is assumed to have sprung quite separately, and usually without any known intermediate stages, from hypothetical common ancestors in Early Eocene or Late Cretaceous. Despite the wealth of Tertiary mastodons, and the presence in the Pliocene of stegodonts which seem to bridge the gap, even the elephants of the Pleistocene are assumed to have emerged directly from these hypothetical ancestors, without any connection whatever with the other proboscideans!" Such assumptions may be due to the disbelief in reversible evolution and the non-acceptance of repetitive (zig-zag) evolution. Phylogenetic "meadows", on the other hand, may well be the result of explosive evolution, which apparently has occurred in various groups.

Finally, it should be stressed that zig-zag evolution is only one of several types of evolution. It may have taken place in some trends, just as well as one-way, parallel, detour, and iterative evolution have taken place in others. It still remains to find out whether zig-zag evolution is a rare or common type. It may especially be expected in features which readily respond to environmental changes.

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