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# THE ROLE OF THE BIOGENETIC CONVERGENCE RULE IN POLARIZING TRANSFORMATION SERIES – ARGUMENTS FROM NEMATOLOGY, CHAOS SCIENCE, AND PHYLOGENETIC SYSTEMATICS[1]

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**Abstract.**— The new term **biogenetic convergence rule** is suggested as a replacement for Haeckel's old term **biogenetic law**. It works as follows: by converging on identical adult structures, polarizations of phylogenetic transformation series are determined by those of corresponding ontogenetic transformation series. Examples from nematology are presented. Cases of paedomorphosis are subject to a second rule suggested as the **biogenetic suppression rule**. A third rule, suggested as the **adaptive convergence rule**, refers to well-known cases in which adaptions to particular environmental conditions result in the similarity of otherwise different structures. Essential findings of chaos science are outlined and illustrated by Waddington's epigenetic landscape in order to show that the biogenetic convergence rule fits to these new findings. Contrary to common belief, the popular outgroup algorithm reveals to be unsuitable for polarizing sequences of character states. For theoretical reasons, Hennig's unsupported demand is rejected to accept only holophyletic taxa as valid. Paraphyletic taxa must also be accepted as valid. Therefore, phylogenetic systematics sensu Hennig and evolutionary systematics sensu Mayr are suggested as synonyms.

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**Key words.**— Nematodes, biogenetic law, biogenetic convergence rule, chaos science, self-organization, epigenetic landscape, outgroup rule, phylogenetic systematics, cladistics.

## HAECKEL'S BIOGENETIC LAW REDEFINED AS THE BIOGENETIC CONVERGENCE RULE

According to general agreement, phylogeny deals with lineages not of adult stages but, instead, of ontogenies, each ranging from the very beginning of an organism's life to its death. Strikingly, there are many parallels between, or better, convergences of phylogenetic and ontogenetic lineages which led Ernst Haeckel to establish his **biogenetic law**. Because of many exceptions due to well documented cases of caenogenesis ("adaptions of juvenile stages to specific developmental conditions", Remane 1956: 156) and paedomorphosis ("retention of youthful ancestral features by adult descendants", Gould 1977: 179), the biogenetic law was reduced to the **biogenetic rule**. Remane (1956) and Gould (1977) reviewed the highly controversial debate on this rule and denuded it from Haeckel's unsupported belief that **adult** ancestral stages were recapitulated in the ontogeneses of organisms. Both authors concluded that the biogenetic rule – if understood correctly – is useful in a twofold manner: **1)** If adult structures of very different appearance may be bridged by intermediate ontogenetic stages, they belong to a common phylogenetic transformation series. To Remane, this is the most important aspect of the biogenetic rule, as it allows us to solve otherwise difficult problems of homology. **2)** Whenever both an ontogenetic and a phylogenetic sequence of character states converge on an identical adult character state (such as on character state $A^{**}$ in Fig. 1), the polarization of the ontogenetic sequence determines that of the phylogenetic one. Because of these typical convergences of ontogenetic and phylogenetic sequences, the term **biogenetic convergence rule** is suggested as a replacement for the less precise term **biogenetic rule**.

There is another well-known convergence rule which I suggest calling the **adaptive convergence rule**. According to it, phylogenetically different structures present in different species may become similar due to functional adaptions to particular environmental conditions.

The biogenetic convergence rule ranges among the most important tools for polarizing sequences of adult character states. In this sense, it is accepted even by Nelson (1978) and other cladists, recently by Fischer (1997), who strictly reject evolutionary reasoning in systematics and, hence, advocate the transformation of phylogenetic systematics sensu Hennig into a non-phylogenetic

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[1] Dedicated to Michael W. Brzeski, who suddenly died on 24th May 1999, and to my brother Henning Lorenzen, who suddenly died on 19th January 2000.

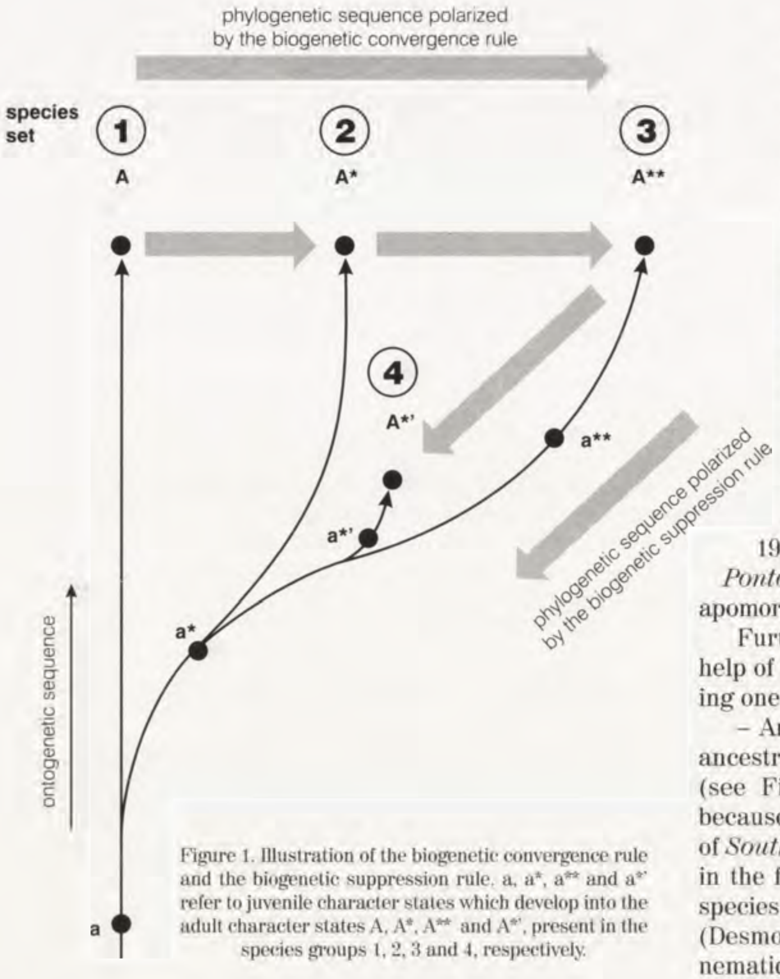

Figure 1. Illustration of the biogenetic convergence rule and the biogenetic suppression rule. a, a*, a** and a*' refer to juvenile character states which develop into the adult character states A, A*, A** and A*', present in the species groups 1, 2, 3 and 4, respectively.

cluster analysis called cladistics (for a discussion of this topic see Lorenzen 1996).

As mentioned above, cases of paedomorphosis do not fit the biogenetic convergence rule. The reason for this is that adult characters and character states present in ancestral species are suppressed in adults of descendant species. Therefore, the phylogenetic and ontogenetic transformation series no longer converge on stages farthest away from some original condition, but instead return back to stages similar to earlier ones (such as to A*' in Fig. 1, which resembles the earlier stage A* but is not identical with it). I suggest the term **biogenetic suppression rule** to cover such reversals of phylogenetic sequences leading to paedomorphic adults. Gould (1977) refers to various examples of paedomorphosis and stresses the importance of evolutionary reasoning to supporting such hypotheses.

## THE ROLE OF THE BIOGENETIC CONVERGENCE RULE IN NEMATOLOGY

According to Riemann (1977: 219), the most important device for polarizing sequences of adult character states of nematodes is the biogenetic convergence rule. Particularly, he pointed to the following examples:

– Although a rhabditoid stoma occurs in juveniles of many secernentean and some adenophorean species, it is retained by adults of only a smaller number of species, whereas in others, further ontogenetic development leads to other stoma types. Both the phylogenetic and ontogenetic transformation series converge on the latter which, therefore, are regarded as apomorphic (derived) with respect to the rhabditoid one.

– Typically, there are 6+6+4 cephalic sensillae arranged in three circles on the head of nematodes. The second and the third circles are separated from each other in all ontogenetic stages of many nematode species and only in the first juvenile stage of others, where they fuse together in the further course of ontogenetic development, for example in *Tobrilus*, *Pontonema* and other Oncholaimidae, *Enoplus* and *Lauratonema* (see Riemann 1966 and 1977, Wieser 1954, Lorenzen 1981; see Fig. 2 for *Pontonema vulgare*). Therefore, the fused position is apomorphic in comparison with the separated position.

Further nematological results corroborated with the help of the biogenetic convergence rule include the following ones:

– Amphids with round aperture are plesiomorphic (= ancestral) with respect to others with loop-shaped aperture (see Fig. 2 for *Synodontium* and *Pararaeolaimus*), because the former type is present in all ontogenetic stages of *Southerniella* (Diplopeltidae) and related taxa, but only in the first juvenile stage of many, if not all, axonolaimid species (see Lorenzen 1981), and of *Desmodora minuta* (Desmodoridae) and *Dracograllus chiloensis* (Draconematidae) (see Clasing 1980), in which it is replaced by amphids with loop-shaped or spiral aperture from the second juvenile stage onwards. In males of *Pararaeolaimus nudus* (Diplopeltidae), the replacement takes place during the last moult (see Lorenzen 1973 and Fig. 2).

– The occurrence of only three lips is plesiomorphic in comparison with six lips, because within the order Enoplida, three lips occur in both juvenile and adult nematodes of various families (e. g. Thoracostomopsidae), whereas in certain, if not all, oncholaimid species, the three lips of the first juvenile stage are replaced by six lips from the second juvenile stage onwards (see Fonseca et al. 1976, Voronov and Malakhov 1979; see Fig. 2 for *Pontonema vulgare*).

– Eight groups of subcephalic setae are present in adults of some *Steineria*-species and in all sphaerolaimid species, while they are absent in the first juvenile stage of most of these species (Lorenzen 1978a) as well as in both juveniles and adults of most other nematode species. Therefore, the occurrence of eight groups of subcephalic setae is apomorphic with respect to their absence.

– In females of heteroderid species (order Tylenchida), ontogenesis leads from a slender body shape in the first juvenile stage to a swollen body shape in the adults. As the latter is also approached by a phylogenetic sequence, it is apomorphic in comparison with the slender body shape.

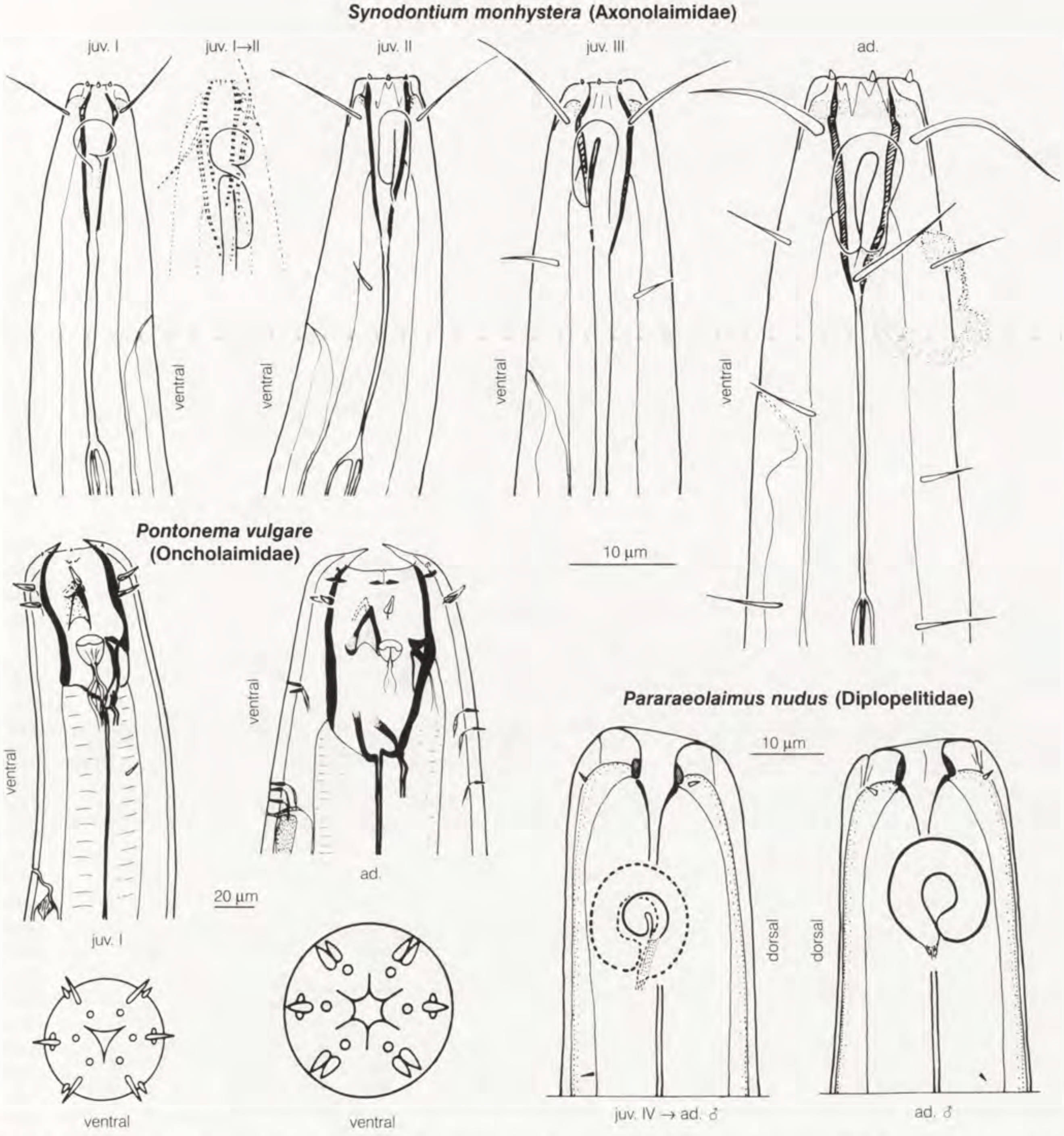

Figure 2. Postembryonic development of head structures in *Synodontium monhystera* (above, adapted from Lorenzen 1973), *Pontonema vulgare* (below left, adapted from Lorenzen 1981 [side views] and Voronov and Malakhov 1979 [en face views]) and *Pararaeolaimus nudus* (below right, adapted from Lorenzen 1973).

– Within the large taxon Rhabditia, the rhabditoid pharynx occurs in all postembryonic stages of many species, while in many parasitic species, it occurs only in the first juvenile stage and is then replaced by a slender pharynx, for example in Ancylostomatidae (order Strongylida). Therefore, the slender pharynx of rhabditian species is apomorphic in comparison with the rhabditoid one.

– In the family Monhysteridae, the *Diplolaimella*-like stoma type occurs in all stages of *Diplolaimella* and related genera, but only in the first juvenile stage of further monhysterid species, in which the continuation of ontogenesis leads to novel stoma types which, therefore, are apomorphic in comparison with the *Diplolaimella*-like one. The example of Fig. 3 refers to a branched phylogenetic

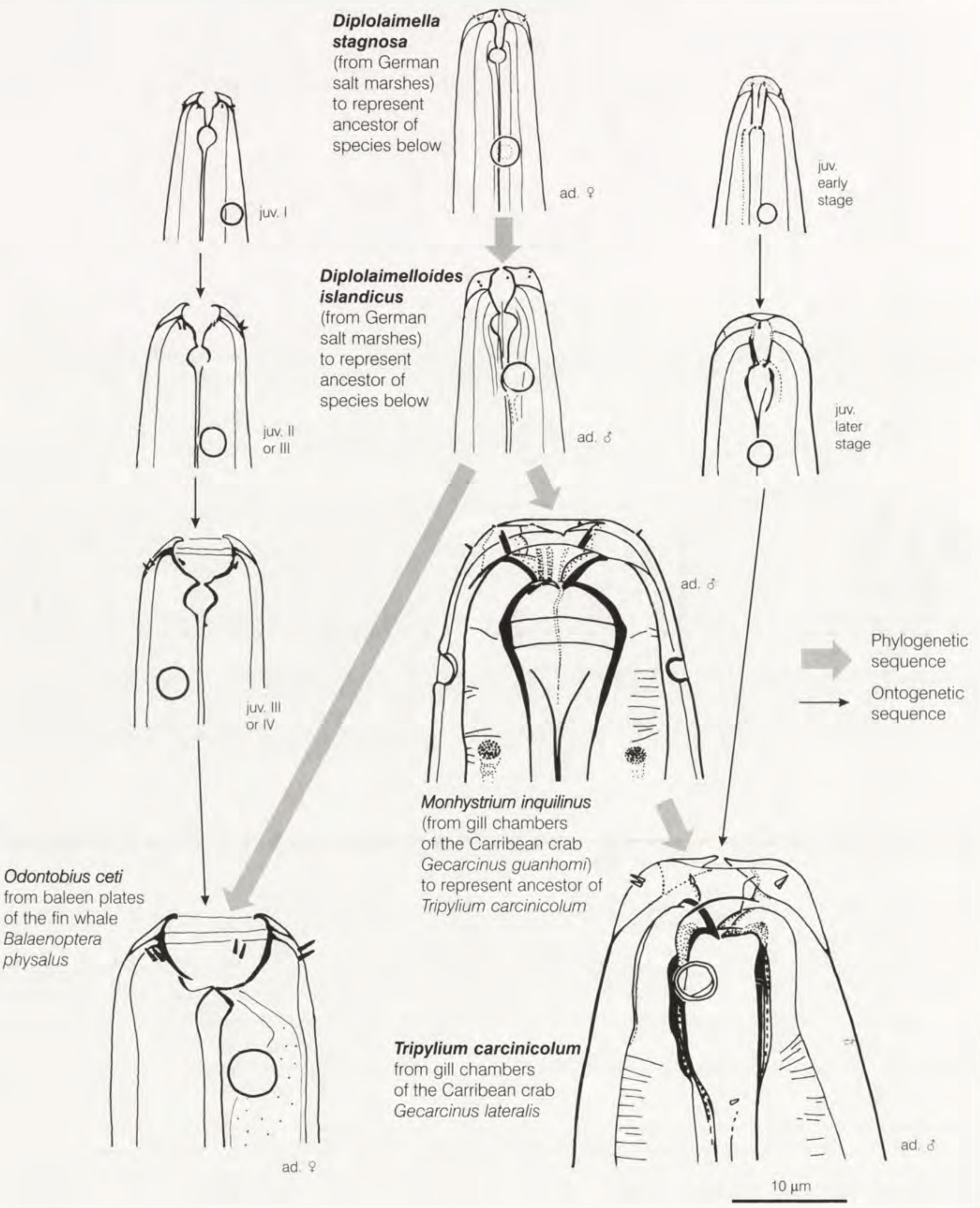

Figure 3. Convergence of ontogenetic and phylogenetic transformation series of the stoma in certain monhysterid species. Adapted from Lorenzen (1978 b: *Diplolaimella*, *Diplolaimelloides*), Lorenzen (1986: *Odontobius*), Riemann (1969: *Monhystrium*) and Riemann (1970: *Tripylium*).

series. In either branch, the final stage is converged by both an ontogenetic and a phylogenetic sequence.

– Last but not least, the biogenetic convergence rule applies even to cases of bicyclic life histories such as they occur in species of *Strongyloides* (order Rhabditida) and *Deladenus* (order Tylenchida, see Fig. 4, example from Bedding 1973). In either case, the body organization of the free-living phase strongly resembles that of the free-living relatives with monocyclic life history, whereas the body organization of the parasitic phase strongly resembles that of parasitic relatives with monocyclic life history. According to results from evolutionary biology, the free-living phase is plesiomorphic in comparison with the parasitic phase. Therefore, the free-living phases of *Strongyloides* and *Deladenus* represent phylogenetically ancestral conditions.

In all examples listed and further examples not listed, the results achieved with the help of the biogenetic convergence rule are stable, because no cases are known in which the ontogenetic development would take a route opposite to that described (e. g. Lorenzen 1981; separation of second and third circle of cephalic sensilla through all postembryonic stages of *Halalaimus*: see Coomans and Jacobs 1983). Unfortunately, the taxonomic standard of describing nematode species does not include the description of juvenile stages. Therefore, the postembryonic development of many nematode species remains unknown as yet.

## DISCUSSION

### Relations between chaos science, epigenetic landscape, and biogenetic convergence rule

Chaos science deals with processes governed by non-linear laws. Their non-linearity is caused by the combination of positive and negative feedback. Precisely such laws also govern any kind of self-organization of dynamic structures in both the biotic and the abiotic world. Essentially, the positive feedback is caused by the self-reproduction of reproductive units such as organisms, cells and autocatalytic cycles, whereas the negative feedback is ultimately caused by the limited availability of resources needed for self-reproduction. From a certain population density onwards, these limitations inhibit further population growth more strongly, the higher the actual density is. Negative feedback acting on population growth belongs to the strongest selective pressure acting on conspecifics of a population. The aspects just outlined circumscribe the essence of the principle of natural selection which governs any self-organization of dynamic structures and, hence, was expanded into the principle of self-organization (Lorenzen 1997).

Essential aspects of self-organization may well be illustrated by the **epigenetic landscape** of Waddington (1975). Its slope is inverse to that of a natural landscape, i. e. the system of valleys bifurcates in a downward rather than an upward direction. In chaos science and non-linear fractal geometry, the valley floors are called **attractors**. They correspond precisely to the **constraints** which – according to developmental biology – canalize all kinds of ontogenetic and phylogenetic self-organization (for a detailed discussion see Bonner 1982). The tops of the hills are called **repulsors** (Mandelbrot 1983) or **watersheds** (e. g. Waddington 1975), while the hillsides are called **basins of attraction** (Kauffman 1993). The course of the ball running down symbolizes the realization of one particular among various potential pathways of self-organization by a dynamic structure. In developmental biology, these dynamic structures include organs, organisms or species.

The following, essential aspects of self-organization are well illustrated by the epigenetic landscape:

– In any case of self-organization, the epigenetic landscape is determined by both intrinsic and extrinsic (= environmental) factors. In organisms, the intrinsic factors refer to genomes and their resulting products. How effective the epigenetic landscape may be in canalizing ontogenetic self-organization is well documented by the striking phenotypic uniformity of conspecifics. In genetics, this observation has led to the concept of the wild-type.

– The efficiency of developmental canalization includes the notion that self-organization of dynamic structures may be resistant to various kinds of perturbation, quite like the ball running down the epigenetic landscape will find its way back to its actual valley floor, after it was pushed upward to a hillside. However, if the running ball is pushed too strongly, it may surpass the watershed to then approach a novel valley floor. Equivalently, if the self-organization of a dynamic structure is perturbed too much, it may surpass a watershed to converge on a novel attractor.

– At critical points of self-organization, even the slightest perturbations may have dramatic effects on self-organization. In the epigenetic landscape, these critical points are illustrated by the cleavage points of valleys.

– Due to the many canalizing effects, dynamic structures resulting from similarly shaped epigenetic landscapes can differ only discontinuously from each other rather than being bridged by continua of intermediate stages. This effect refers to phylogenetic self-organization as well and is appreciated by systematicists, as it allows a clear distinctions of many supraspecific taxa.

– How effective even slight extrinsic factors may be in shaping an epigenetic landscape is strikingly documented by all kinds of bicyclic life cycles, particularly by all cases of metagenesis (alternation of sexual and asexual reproduction within a bicyclic life cycle). In all these cases, slight environmental factors may switch an epigenetic landscape into either of two different forms, each canalizing ontogenetic self-organization into its own phase which differs dramatically from the other (Fig. 4), even if they do not differ genetically such as in polyps and medusae of many cnidarian species. The two phases of the bicyclic life history of *Deladenus*-species are also strikingly different (Fig. 4; see Bedding 1973 for this highly interesting example). Prior to the knowledge of their bicyclic life history, both phases were regarded as independent species and were included in the very different families Neotylenchidae and Allantonematidae.

– In other cases, extrinsic factors may shape an epigenetic landscape to a lesser extent giving rise to only mod-

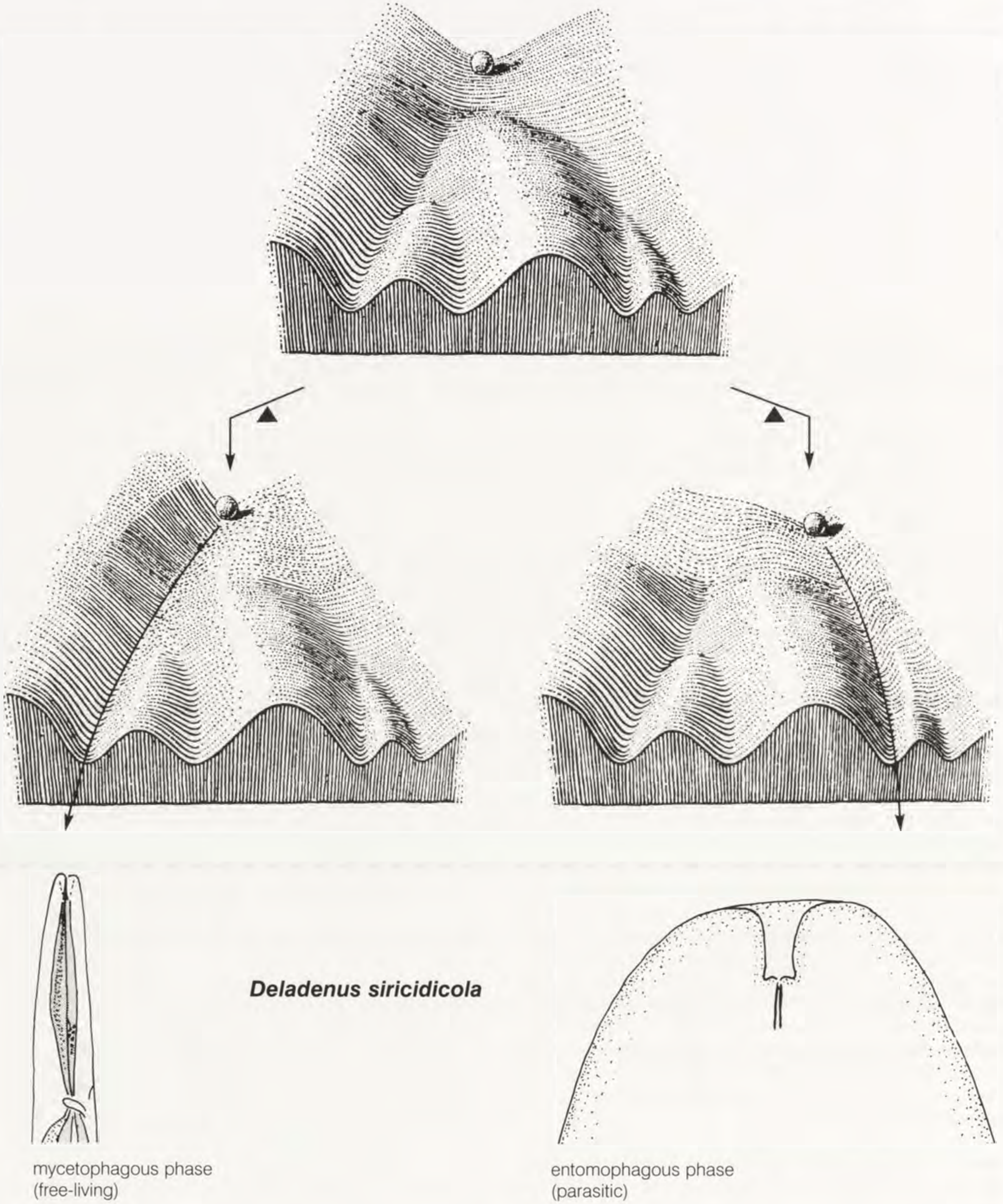

Figure 4. The epigenetic landscape of Waddington (above) and two alternative modifications of it, each caused by a specific environmental condition (illustrated by an arrow). In the bicyclic life history of *Deladenus siricidicola* (order Tylenchida), the resulting adult females are either mycetophagous or entomophagous. The nematode drawings are to the same scale (from Bedding 1973).

erate, but nevertheless characteristic, differences between conspecifics. Brzeski (1967) has provided evidence for such an example: if *Ditylenchus myceliophagus* (order Tylenchida) is reared on the less favourable fungus *Candida* sp., the pharynx lobe overlapping the intestine is significantly larger than in conspecifics reared on the more favourable fungus *Acrostalagmus albus* (see Fig. 5).

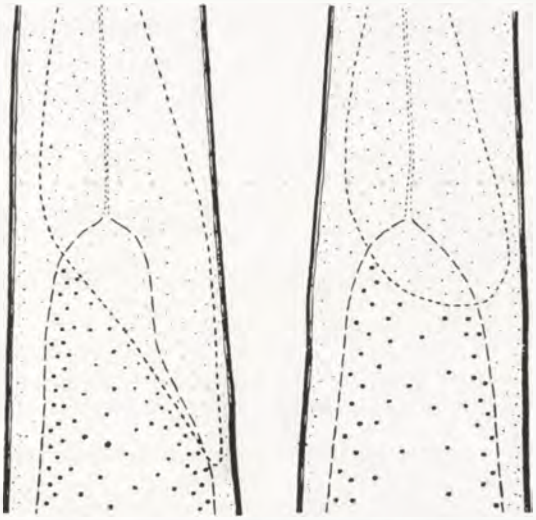

Figure 5. Pharynx lobe overlapping the intestine in *Ditylenchus myceliophagus* reared either on the fungus *Candida* sp. (left) or on the fungus *Acrostalagmus albus* (right) (adapted from Brzeski 1967).

How does the biogenetic convergence rule fit the epigenetic landscape? According to the rule, ontogenetic self-organization within related taxa is rather uniform, i. e. strongly canalized up to a certain, rather conservative stage reached at some intermediate level of the epigenetic landscape, from where a cluster of novel constraints may be opened, each leading to novel differentiations of originally similar structures. Additionally, the epigenetic landscape may illustrate findings of evolutionary biology, according to which canalizations of ontogenetic pathways may also canalize phylogenetic pathways, a process by which new species may arise.

## The two types of outgroup algorithm – both unsuitable for polarizing sequences of character states

Cladistics as performed contemporarily relies primarily on an unsuitable but nevertheless popular criterion for polarizing sequences of character states. This criterion is commonly referred to as the outgroup comparison method (e. g. Watrous and Wheeler 1981, Ax 1984), outgroup rule (e. g. Wiley 1981), outgroup criterion (e. g. Farris 1982), or outgroup algorithm (e. g. Maddison et al. 1984). It works as follows. If various character states have been shown to be components of a common sequence of character states, those observed exclusively in all or some species of an ingroup (commonly a taxon under study) must be synapomorphies of the ingroup or certain of its subgroups, while others observed in both the ingroup and at least one of its outgroups (species sets outside an ingroup but related to it) must be symplesiomorphies of the ingroup. Note that, in accordance with common but inappropriate usage, synapomorphy and symplesiomorphy are used as absolute rather than relative concepts. This usage does not permit calling the adult character state A* of species set 2 in Fig. 1 both a synapomorphy of 2 relative to state A in 1, and a symplesiomorphy of 2 relative to state A** in 3.

As has been shown earlier (Lorenzen 1993), there are two types of outgroup analysis called the **parsimony analysis based on test samples** and the **cladistic outgroup algorithm**. The former serves for examining the extent to which character states observed within an species group studied (called the ingroup) may also occur outside this group. This type of outgroup analysis has always been accepted as a must by all serious taxonomists and systematicists. Evidently, it does not serve for polarizing sequences of character states, even if a homologous character state shared exclusively by all species of a species group H (such as the occurrence of three ear ossicles in each middle ear of all mammalian species, an example referred to by Ax (1984: Fig. 43) is called both a synapomorphy of H and a symplesiomorphy of any subgroup of H. It was apparently this needless replacement of homology with synapmorphy and symplesiomorphy which has led Patterson (1982: 29) to regard the latter two as synonyms of homology.

Polarizations of sequences of character states have been claimed to be possible by using the cladistic type of outgroup algorithm. This claim is incorrect, simply because in- and outgroups needed in these instances cannot be chosen unambiguously (Lorenzen 1993). Even worse, the cladistic outgroup algorithm as advocated by Wiley (1981: 139), Ax (1984: 125), Maddison et al. (1984) and others may be a device for circular reasoning: some intuitive system – suppositions on the holophyly of certain species groups included – is taken as a basis for choosing in- and outgroups needed for carrying out the cladistic outgroup algorithm; subsequently, results achieved that way are used for **corroborating** the intuitive system.

The only way to overcome the cladistic error emerging from misunderstanding the outgroup algorithm is to rediscover classical methods for polarizing phylogenetic sequences of character states such as the biogenetic convergence rule. In phylogenetic systematics thus renewed, even synapomorphy and symplesiomorphy may be retained as useful concepts by using them in a relative rather than an absolute sense.

## Rejection of Hennig's unsupported demand to accept only holophyletic taxa as valid in a phylogenetic system

Most controversies surrounding Hennig's work arose from his rigid demand to accept only holophyletic taxa as valid within a phylogenetic system (see debate of Mayr 1974 and Hennig 1974). Holophyletic taxa are characterized by holapomorphies, which are homologous character states shown to be either present or secondarily absent in specified species sets which, therefore, are holophyletic (see Lorenzen 1996). Hennig's unsupported demand is rejected by arguments from the biogenetic convergence rule and for theoretical reasons:

The biogenetic convergence rule deals with cases in which a juvenile character state (such as state a in Fig. 1) is either similar to an adult character state (such as state A in Fig. 1) or is replaced by novel adult character states (such as states A*, A** and A*' in Fig. 1). In the example of Fig. 1, the juvenile character state a is common to the complete species group 1+2+3+4. Therefore, adult character state A may be justified as a holapomorphy corroborating the holophyly of 1+2+3+4. Correspondingly, by the adult character states A*, A**, A*', the holophyly of the species groups 2+3+4, 3+4, and 4 may be corroborated, respectively. In line with Hennig's demand, all these species groups may be included as valid taxa in a phylogenetic system. In such a case, the sister groups of the holophyletic taxa 2+3+4, 3+4, and 4 would be the paraphyletic (i. e. residual) species groups 1, 2, and 3, respectively, which could not be accepted as valid in a phylogenetic system sensu Hennig. However, they must be accepted as valid, if the underlying argumentation concerning their state is accepted to be correct. Herting (1993) has provided convincing support for the same view. Even Hennig seems to have felt the dilemma he himself posed by including paraphyletic taxa in his system of insects (Hennig 1969). As both Hennig and Mayr agree that any phylogenetic or evolutionary system should consist of a maximum amount of holophyletic taxa, virtually no difference is left between phylogenetic systematics sensu Hennig and evolutionary systematics sensu Mayr. Therefore, both terms become synonyms.

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