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A STRUCTURALIST APPROACH IN THE STUDY OF EVOLUTION AND CLASSIFICATION

by

L. VAN DER HAMMEN

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A survey is given of structuralism as a method that can be applied in the study of evolution and classification. The results of a structuralist approach are illustrated by examples from the laws underlying numerical changes, from the laws underlying changes in the chelicerate life-cycle, and from the laws underlying the evolution of the chelicerate appendages. Suggestions are given for the study of the laws underlying the transformation of form, and some notes are made on structuring forces and the early stages of organic evolution. Some concluding remarks are finally made on deep structure, phylogenetic classification and evolution.

L. van der Hammen, Rijksmuseum van Natuurlijke Historie, Postbus 9517, 2300 RA Leiden, The Netherlands.

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I. INTRODUCTION

In a recent paper on the natural philosophy of evolution (Van der Hammen, 1983: 191), I suggested that important data with reference to organic evolution could perhaps be disclosed by application of the structuralist method. A few years before (Van der Hammen, 1981a), I had already developed a type-concept (as model of the evolutionary potentialities of a taxon), in which special attention was paid to ontogenetic and phylogenetic data, and to evolutionary mechanisms. This type (or archetype) represents, in fact, the model of a system of transformation, i.e. a structure in the structuralist sense. After the appearance of my 1983 paper, Dr. R.C. Crow (Auckland, New Zealand) drew my attention to two papers by Webster & Goodwin (1981, 1982) in which the structuralist approach is discussed in the wider context of the history of morphology, morphogenesis and evolution; a short survey of both papers is given below.

Structuralism (see Piaget, 1968; Lane, 1970) is essentially a successful method currently applied to research in a wide variety of disciplines, among which mathematics, physical sciences, anthropology, mythology, linguistics and literary criticism. It is rather a method (in the sense of procedure adopted for investigation) than a theory, although it ultimately depends also on certain theoretical assumptions. Because of the great diversity of disciplines to which the structuralist method is applied, structuralism is not easy to define; in all disciplines, it employs the notion "structure" (in the sense of set of elements between which relations are defined), and its intention is to go beyond the description of the observational data, in the direction of the laws underlying the phenomena in which it is concerned. Relations at the level of observable reality are regarded as reflections of relations at the level of a structure below or behind reality; it is this "deep" structure (acting as a structuring force) which structuralism attempts to discover.

According to Piaget (1968) the notion of structure is comprised of three key ideas: the idea of wholeness, the idea of transformation, and the idea of self-regulation. The most distinct feature of structuralism is that it gives emphasis not to aggregates (or composites of independent elements) but to wholes. Structuralism attempts to study the relations between the elements, and it is in terms of these that the structure is defined. The relations between the elements are law-like regularities (the so-called laws of composition) and these include the so-called laws of transformation, by which one particular structured configuration changes into another. All structures are, in fact, systems of transformation (which makes the question of origin inevitable). Systems of transformation of this kind depend upon mechanisms of self-regulation (en-

tailing self-maintenance and a certain closure), and the basic mechanisms of self-regulation include regulations in the cybernetic sense of the word.

Structuralism does not look for causal explanations; one of its main purposes is to prepare a complete inventory of structural relations (among which binary oppositions). In addition to that, structuralism is mainly concerned with structural relations existing at the same time (because of the idea of wholeness); history is seen as a mode of development of a particular system, whose present nature must be fully known before any account can be given of its evolution. It may finally be remarked here that, in many cases, a hierarchy of structures can be imagined participating in the process of generation of a surface structure.

Webster & Goodwin (1981, 1982) criticized the current neo-Darwinistic view of biology, in which the organism as a real entity has virtually no place. They argued that a structuralist approach in the study of the organismic domain might favourably transform modern biology. They found the germs of this approach in the pre-Darwinian school of comparative anatomy and embryology (from Cuvier to Owen) and its concern with laws of form, as well as in some fringe figures outside the mainstream of twentieth-century biology (e.g., Driesch, 1908, and his analysis of morphogenesis; Thompson, 1917, and his studies of growth and form; Waddington, 1957, and his understanding of the organism in terms of a set of potentialities). Webster & Goodwin regarded organisms (structural wholes in which the parts are to be understood in terms of their relation to each other and to their place in the overall structure) as self-organizing totalities, and morphogenesis and evolution of these organisms as systems of transformation. According to these authors, it is in the course of history that nature's hitherto unexpressed designs are gradually disclosed. In this context they quoted Waddington's conception of living organisms as devices which use the contingent "noise" of history as a "motor" to explore the domain of structures which are possible for them. They believed that the diversity of living forms could ultimately be accounted for in terms of a relatively small number of generative rules or laws.

II. SURFACE STRUCTURE AND DEEP STRUCTURE, PHENETIC AND PHYLOGENETIC CLASSIFICATION

From a structuralist point of view, data supplied by the study of the comparative morphology and ontogeny, and the relationships of living (and, in a lesser degree, fossil) organisms constitute a surface structure which is a reflection of relations at the level of deeper structures. Whilst a phenetic classifica-

tion is evidently based on a surface structure, a phylogenetic classification should be based on the deep structure or, more precisely formulated, the hierarchy of deep structures (a hierarchy of synchronic systems). These deep structures are characterized by the presence of evolutionary potentialities which can manifest themselves at the level of the surface structure (partly as a result of the "contingent noise of history"). Parallel evolution (see Van der Hammen, in press 2) should be regarded as the separate manifestation, at the level of the surface structure, of identities at the level of the deep structure. (Atavisms are manifestations, at the surface level, of evolutionary potentialities which, now, usually no longer manifest themselves). The important difference between the evolutionary potentialities of the deep structure and their manifestation at the surface, is not always taken into account in current work in the field of phylogenetic systematics. The preparation of a model of the deep structure (the hierarchy of deep structures) is indeed difficult, and takes up long periods of wide research; it is, however, the only method to arrive at a classification which is really natural. In the following sections, a few examples are given of a structuralist approach in the study of evolution and classification, and suggestions are given for further research. The sections demonstrate that problems pertaining to deep structures should be studied simultaneously at the highest and lowest levels of taxonomic hierarchy.

III. LAWS UNDERLYING NUMERICAL CHANGES

Recently (Van der Hammen, 1981b), I have given a survey of the laws underlying numerical changes in Actinotrichid chaetotaxy. As a result of extensive studies in this group of mites (a chelicerate subclass) it has been possible to recognize a hierarchy of systems of transformation. In fig. 1, I have represented, in dorsal and ventral view, the body of a species of primitive Oribatid mite of which the setae are arranged in patterns that are regarded as basic for several groups of Actinotrichida. In these basic patterns, the setae are found in fixed numbers, and occupy recognizable positions with respect to each other. In the course of transformation of these patterns, each seta appears to have an individual evolution, although changes in number transform also the pattern as a whole. There is some evidence (see Van der Hammen, 1981b: 28) that the basic patterns represented in fig. 1 have been preceded, in the course of evolution, by more chaotic patterns in which setae occurred in irregular numbers and occupied more irregular positions. Whilst the setae represented in fig. 1 appear to be individually coded in the genotype (although the patterns are certainly also the result of the relations between the elements),

the irregularly distributed setae are apparently coded as fields. Further numerical transformations of the basic patterns are schematically represented in fig. 2; these transformations pertain either to regression or to multiplication. It appears that, in the case of regression in number (see Van der Hammen, 1981b: 25), the individual setae are suppressed (a non-manifestation; the

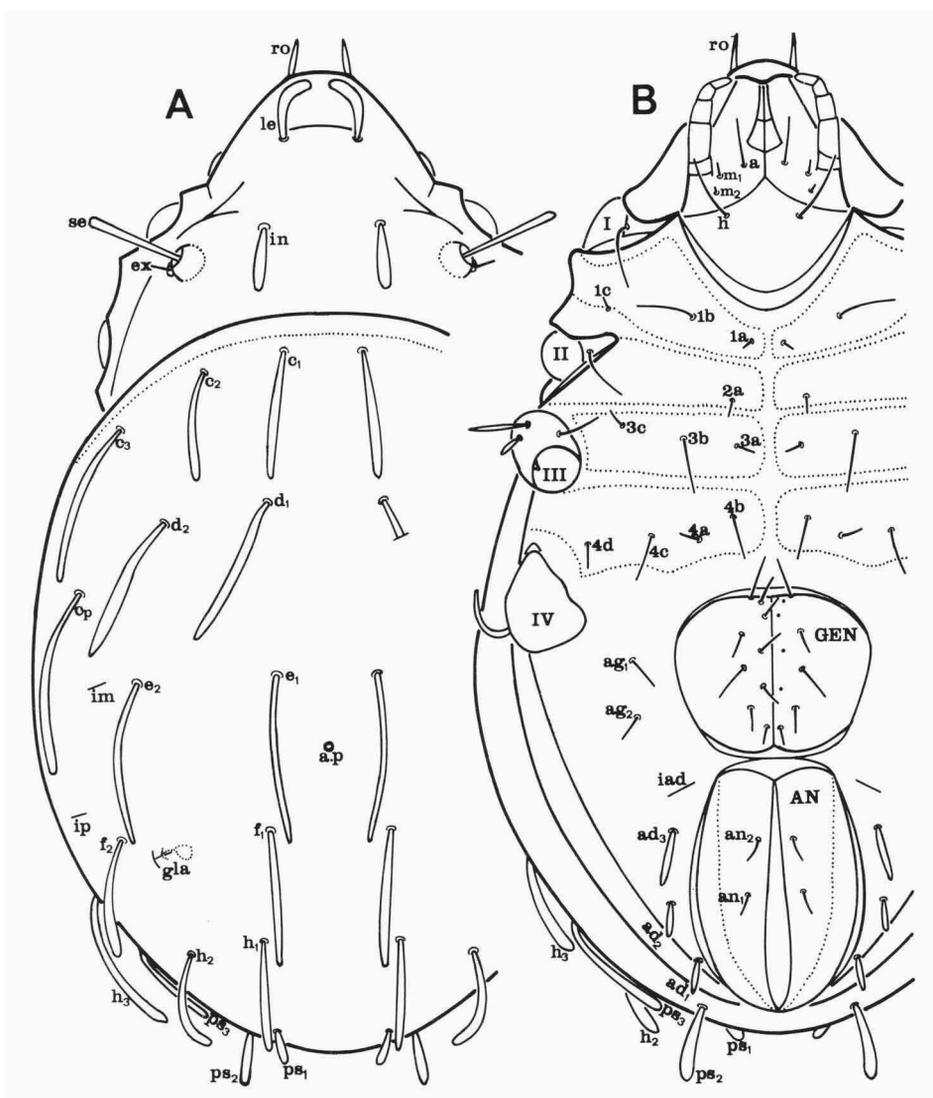


Fig. 1. *Hermannia gibba* (C.L. Koch), adult male, an Oribatid mite presenting more or less basic chaetotactic patterns; A, dorsal view; B, ventral view (legs, with the exception of the trochanter, removed); A, B, $\times 161$.

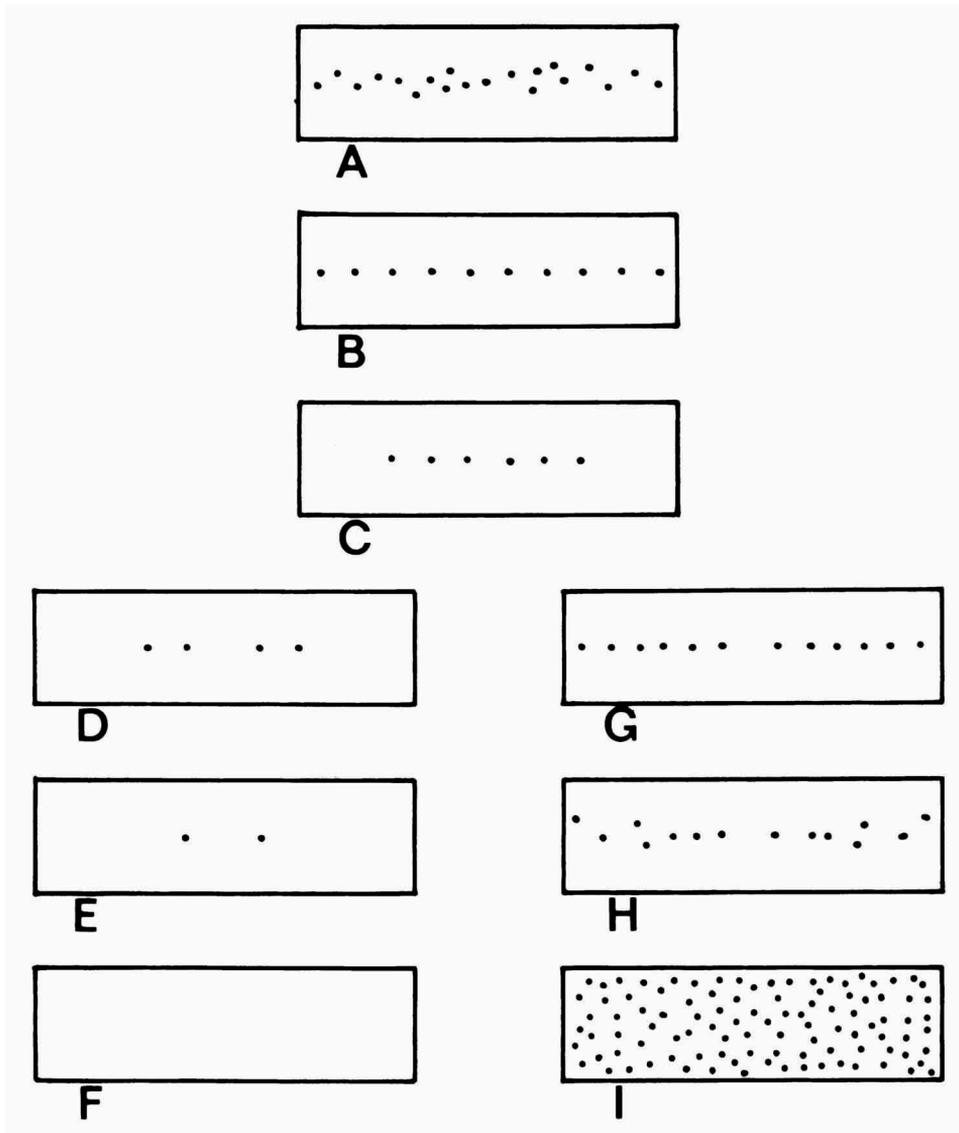


Fig. 2. Schematic representation (a rectangle representing a segment) of the various stages in the evolution of chaetotaxy in Actinotrichida; A, primordiotrichy (hypothetical ancestral chaotic chaetotaxy); B, hypertrichy (presence of setae in regular numbers surpassing that of normal holotrichy); C, holotrichy (chaetotaxy characterized by the presence, in regular numbers, of all the setae normally present in a natural group); D, E, meiotrichy (chaetotaxies characterized by the presence of setae in regular, but reduced numbers); F, atrichosy (absence of setae as a result of regression); G-I, neotrichy (secondary formation of setae by multiplication); G, cosmio-trichy (neotrichy with simple recognizable disposition of setae); H, oligotrichy (weakly developed neotrichy); I, plethotrichy (neotrichy with numerous, chaotically arranged, setae). Primordiotrichy and hypertrichy are not (or not yet, or not always) distinguishable from neotrichy.

genotypic information is not lost, as appears from rare reappearances). In the case of multiplication (see Van der Hammen, 1981b: 25-26), fields of collectively coded setae can gradually take the place of individual setae.

The first dorsal opisthosomatic seta to disappear (from the basic pattern of fig. 1) is f_1 ; this seta is present in several groups of more or less primitive Actinotrichid mites only. Its potential suppression (by parallel evolution) is nearly a general character of the subclass Actinotrichida. In advanced stages of suppression, patterns become increasingly characteristic of lower taxa.

The elements of a group of setae (occurring in a characteristic pattern) are characterized by differences in resistance to regression and multiplication (see Van der Hammen, 1981b: 22-24). For this reason the elements can be arranged, according to relative strength or weakness, in a list of priority. Generally, the most common element of a group is also the element with the greatest strength; often, the strongest element is also the most precocious in ontogeny. As a result of these differences in strength, elements of a group disappear (or are multiplied) in characteristic sequences. Differences in the lists of priority of two or more taxa point to differences in the underlying systems of transformation.

In simple cases, numerical changes can manifest themselves in the course of postembryonic development and evolution, i.e. in ontophylogeny, in three ways (see Van der Hammen, 1981b: 14-22): ascendant (the change first manifests itself at one of the earlier levels of development, and subsequently at the later levels), descendant (the change first manifests itself at one of the later levels, and subsequently at the earlier), or vertical (the change manifests itself, in the course of evolution, simultaneously at all levels concerned). In a taxon, the numerical changes of each of the three types of ontophylogeny can apparently be correlated (see Van der Hammen, 1981b: 32-36) and further investigations will probably reveal very simple systems of transformation underlying these complicated ontophylogenetic patterns of change.

Similar systems of transformation apparently underly other types of numerical changes, such as the evolutionary changes in the number of chelicerate body segments (see Van der Hammen, 1981b: 37n) and in the number of instars in the chelicerate life-cycle (see following section).

IV. LAWS UNDERLYING CHANGES IN THE CHELICERATE LIFE-CYCLE

Changes in the chelicerate life-cycle pertain to the numbers of successive instars as well as to the form of the instars. Several groups of Chelicerata are

characterized by a life-cycle with a fundamental number of six instars (separated by moults); in other groups, the number of instars is greater and more irregular, whilst regression in the number of instars is also known (see Van der Hammen, 1978). In fig. 3, a model is represented of the evolution of the chelicerate life-cycle; it is an ontophylogenetic diagram (t = ontogenetic time; T = phylogenetic time). The hypothesis is that the evolution of the life-cycle has started with stasoids (instars which are morphologically different from the preceding and following instars by discontinuous characters, but which occur in variable numbers, so that they cannot be homologized with instars in other specimens and taxa of the same group) and presented only one immature phase (consisting of nymphoids). It is supposed that a life-cycle with stases (instars which are, as in the case of stasoids, morphologically different from the preceding and following instars, but which occur in fixed number, by which they can be homologized with instars in other specimens and taxa of the same group) arose from a life-cycle with stasoids, by which two evolutionary periods can be distinguished: stasoidy and orthostasy. It is further supposed that the ancestral number of stases has, in all cases, been six (protostasy; as still found in several groups). By the divergent phylogeny of the levels of postembryonic development, different phases can have arisen (prelarval, larval, nymphal). In the course of evolution, various levels of the ancestral protostasic life-cycle can have been subject to changes (alassostasy), including regressive evolution (protelattosis and metelattosis),

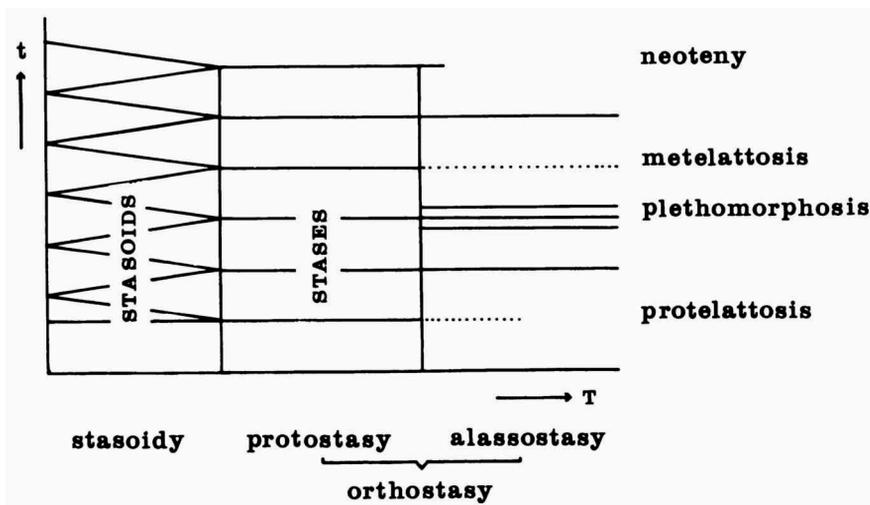


Fig. 3. Model of the evolution of the chelicerate life-cycle (ontophylogenetic diagram; t = ontogenetic time, T = phylogenetic time).

the attainment of maturity at previously immature levels (neoteny), and the formation of isophena, i.e. forms which are the result of growing or repetition moults i.e. moults which are not associated with morphological changes except size (plethomorphosis). It is probable that, at a certain stage of evolution, stasoids and stases can occur in one and the same life-cycle. The possibility cannot be excluded that, as to phylogeny, the model should be read in both directions, and that a third evolutionary period (neostasoidy) should be recognized, which is still undistinguishable from stasoidy.

The fundamental number of six stases has arisen several times in different groups of Chelicerata; the potentiality of an evolution of this number is apparently a general character of the Chelicerata. The general laws of the numerical evolution of instars (chaotic number – fixed number – decrease or increase in number) are apparently similar to that of the numerical evolution of setae. The regressive evolution of the first instar or instars (protelatosis) is a general character of all Chelicerata. In Actinotrichid mites, other instars can also become subject to regression (metelatosis), viz., the deutonymph in Acaridida, and the proto- and tritonymph in Trombidina; in these cases the evolutionary phenomena (and potentialities) are characteristic of the (lower) taxa in question.

V. SUGGESTIONS FOR THE STUDY OF THE LAWS UNDERLYING TRANSFORMATION OF FORM

In my paper on Numerical Changes and Evolution (Van der Hammen, 1981b), I summarized the data with reference to numerical evolution in Actinotrichid mites. In this group, it is now evident that numerical evolution starts as a numerical variation with a low probability of manifestation, whilst this probability increases in the course of evolution. (By a careful analysis of the variation, and a comparison with other related taxa, it must first have become evident that the variation has an evolutionary sense, and does not refer to a normal variation or an anomaly).

In the same paper (Van der Hammen, 1981b: 38), I suggested that the evolution of form could perhaps be very similar to numerical evolution in its first manifestation: it could start as a small discontinuous variation (i.e. as a different form class separated from the preceding class by a small gap) with a low probability of manifestation. (By comparison with other, related taxa it must have become evident that the change has an evolutionary sense.) I suggested that the problem could perhaps be successfully studied in the case of leg segments (the tarsus of species of the Oribatid mite superfamily No-

throidea, for instance). In this connection, the celebrated chapter on Cartesian transformation and the comparison of related forms, in D'Arcy Thompson's famous book *On Growth and Form* (Thompson, 1917), could get a new evolutionary sense. It is evident that, in the case of numerical changes and the variations of presence and absence, laws underlying the changes are simple. These laws must be more complicated in the case of variation in three-dimensional forms. Thompson analysed the transformation of form by the method of coordinates, by which the laws underlying the transformation of form become evident. Up to now, and notwithstanding their fame, Thompson's Cartesian transformations have been used very little. In the detailed comparative analysis of the evolution of form in related species (and the search for laws) they could get a new importance.

VI. LAWS UNDERLYING THE EVOLUTION OF THE CHELICERATE APPENDAGES

The chelicerate appendages and their evolution have repeatedly been the subject of my investigations (see Van der Hammen, 1977a, 1977b, 1985a, 1985b, and in press 2). My insights in this field gradually developed, and not until recently (Van der Hammen, in press 1) have I succeeded in solving the last important problem (that of the homology of epimera and coxae). It has now become possible to give a more or less complete (and partly hypothetical) survey of the laws underlying the evolution of these appendages; in this section my previous views will be summarized, corrected and completed.

Chelicerata (with the exception of Xiphosura) differ from other Arthropods by the fact that the main promotor-remotor movement is at the coxa-trochanter or body-trochanter joint, and not at the body-coxa joint. It is now evident that coxae have evolved, relatively late, from epimera (the sternites of the prosoma) by a gradual separation of these from the sternal exoskeleton, a gradual increase in movability, and a subsequent extension in antiaxial direction (associated with the inclusion of pleural regions). Epimera are present in Palpigradi and Actinotrichida. The "coxae" of Solifugae and Pseudoscorpionida stand about midway between epimera and free coxae. The coxae of Arachnida s. str. (Uropygi, Amblypygi, Araneida) demonstrate the gradual transition from coxae with ventral position and slight movability to coxae with lateral position and increased movability. The problem of the homologization of leg segments (podomeres) is now definitely solved: the main promotor-remotor movement is (with the exception of Xiphosura) at the base of the trochanter, a levator-depressor movement is at the pivot joint be-

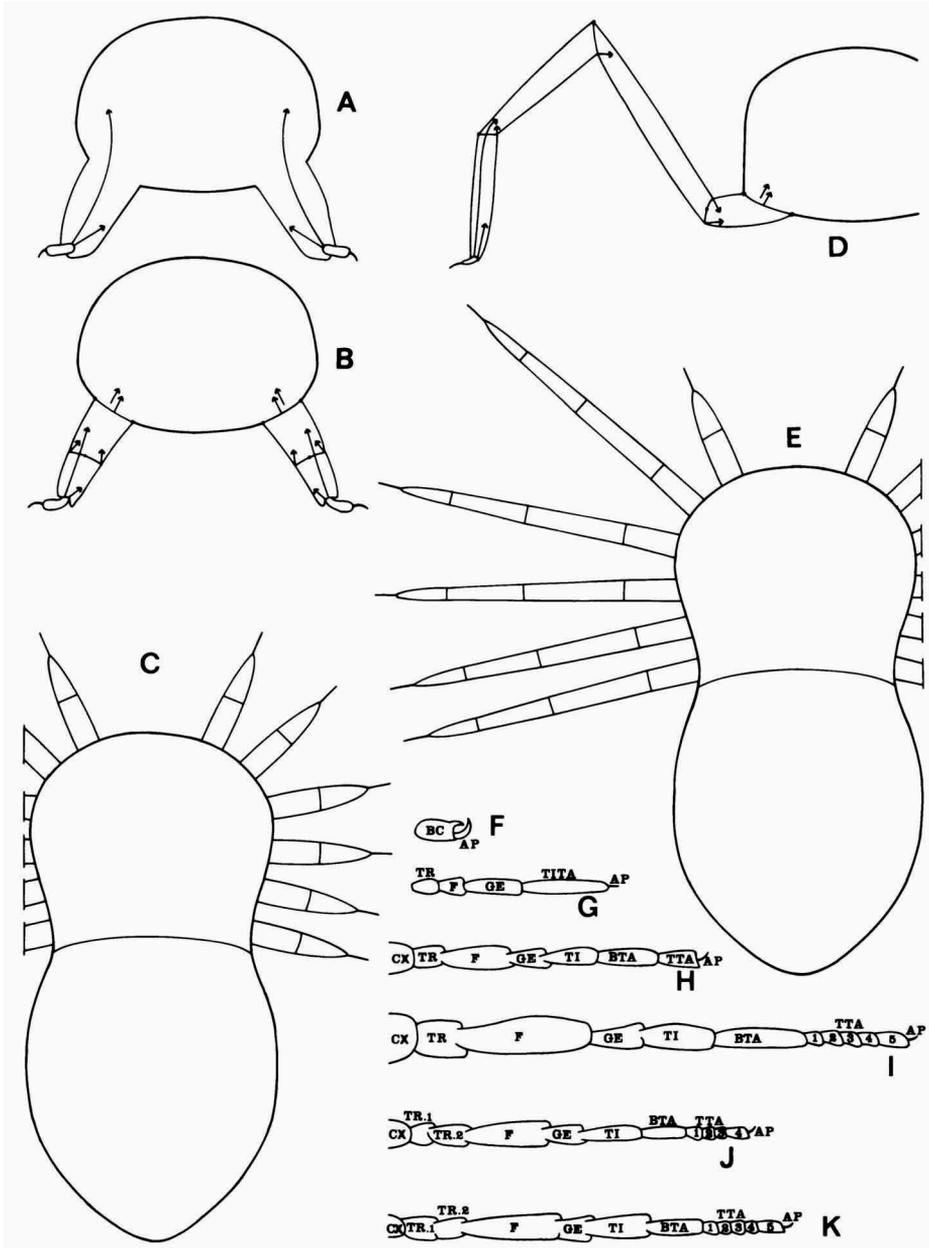


Fig. 4. Stages in the evolution of the chelicerate appendages; A, B, single body-segment, with pair of limbs, of hypothetical Arthropod in transverse section; A, with lobopodia; B, with archepodia; C, dorsal view of hypothetical Arthropod with archepodia; D, single body-segment with left limb, in transverse section, of hypothetical Chelicerate with protopodia; E, dorsal view of hypothetical Chelicerate with three-segmented limb I and five-segmented protopodia (limbs 2-6); F-K, appendages of the adult of a group of extant Chelicerata (Ricinulei) in dorsal view; F, chelicera; G, palp; H, leg I; I, leg II; J, leg III; K, leg IV. Abbreviations: AP, apotele; BC, body of chelicera; BTA, basitarsus; CX, coxa; F, femur; GE, genu; TI, tibia; TITA, tibiotarsus; TR, trochanter; TR.1, trochanter 1; TR.2, trochanter 2; TTA, telotarsus; TTA.1-5, telotarsus 1-5.

tween trochanter and femur (in case this joint is repeated, there is a second trochanter), a knee with a hinge joint is present between femur and patella (genu) or tibia (in the case of a second femur, an extra hinge joint is present between the trochanter-femur and the knee-joint); patella, tibia and tarsus can easily be recognized because of the number of true (eudesmatic) articulations in the descending part of the leg (the articulation between basi- and telotarsus, if present, is adesmatic). This original pattern can be transformed by secondary transformations (the origination of rocking joints from pivot joints, the origination of extensor muscles in hinge joints, etc.), but generally remains recognizable. The following model of the evolution of the chelicerate appendages has now been prepared by me (see Van der Hammen, 1985a, and fig. 4).

Because the six pairs of chelicerate appendages (chelicera, palp and legs) are homonomous structures which have developed by parallel evolution from lobopodia (fig. 4A), the ancestral number of the segments of the chelicera (three) could be the prototypal number for all the appendages (archepodia; see fig. 4B, C); these three segments are usually called trochanter, body of the chelicera, and apotele (or claw-segment). This number of segments could have occurred in short-legged species which stood up on their legs. In chelicerate embryos, palp and leg first divide into four segments: prototrochanter, protofemur, prototibia and prototarsus (it is not impossible that an important translocation of muscles, as in trochanter and femur of Arachnida s. str. and Xiphosura, is associated with important changes in embryonic development). A leg with these four segments and an apotele (i.e. five segments: a so-called protopodium; see fig. 4D, E) could represent the first stage in the evolution of a hanging stance. All types of chelicerate palp and legs can be derived from this primitive type. As mentioned above, free coxae arose from epimera, and can include pleural regions. Protopodia arose from archepodia, either by a further subdivision of segments, or by the addition of projecting parts of the body (see Van der Hammen, 1985a: 50). Because trochanter 2, in Cryptognomae, disappears by suppression (see fig. 5), it must originally have evolved by repetition of information. Because femur 2, in Epimerata, disappears by fusion of femur 1 and femur 2 (see Van der Hammen, 1982: 38; fusion takes place by the regression and disappearance of the muscles, followed by the gradual disappearance of the articulation), it must originally have evolved by subdivision of the femur. Patella (genu) and tibia originally evolved by subdivision of the prototibia; it is interesting that this subdivision has manifested itself in two different ways: the patella (genu)-tibia articulation is, ancestrally, either a hinge joint or a pivot joint. It is also interesting that a second femur arose in Epimerata and Apatellata only; its presence must be

regarded as a unique shared derived character of these two groups (which are now regarded by me as related subclasses). A second trochanter is found in various groups of Chelicerata; its presence is apparently founded on a general chelicerate evolutionary potentiality. The data mentioned in this section demonstrate that it has now been possible to reconstruct all the general laws underlying the evolution of the chelicerate appendages.

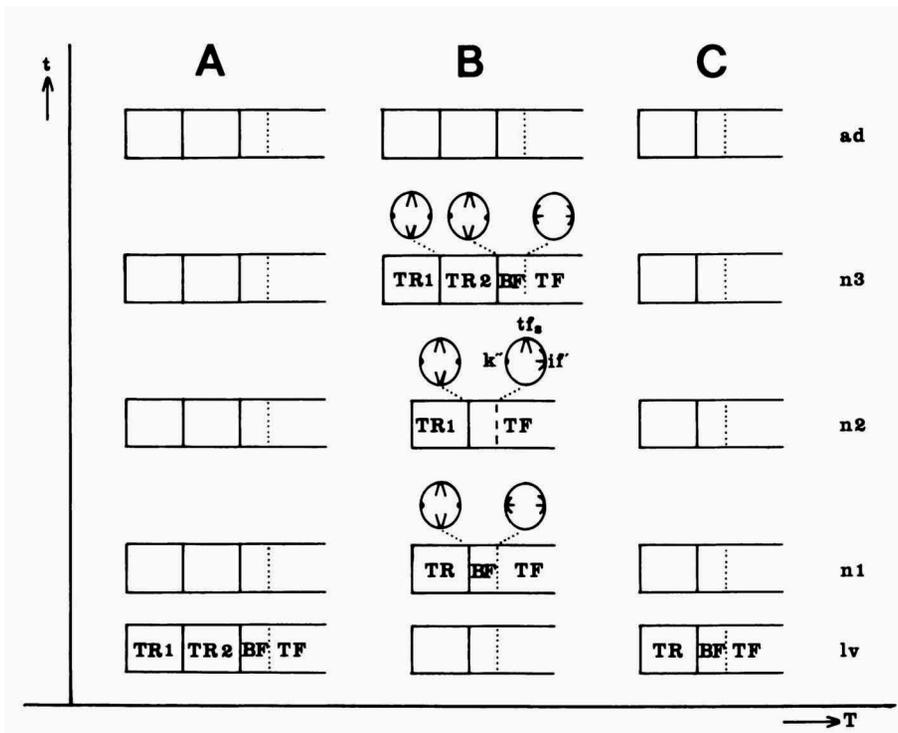


Fig. 5. Ontophylogenetic diagram (not drawn to scale) of the regressive evolution of trochanter 2 in Anactinotrichida. Trochanter 2 disappears by ascendant suppression. In Opilioacarid deutonymphs, the regressive trochanter 2 manifests itself partly (the "basifemoral ring" presents some characters of the trochanter 2-femur articulation, viz., the superior tendon and the posterior condyle; and some characters of a true basifemoral ring, viz., an anterior lyrifissure and the absence of the inferior tendon). A, ancestral Anactinotrichid stage (two trochanters in all instars are still found in other Cryptognomae, viz., Ricinulei, in which group a basifemoral ring is, however, not present); B, Opilioacarid stage; C, Holothyrid, Gamasid and Ixodid stage. Abbreviations: *ad*, adult; *BF*, basifemur; *if'*, anterior lyrifissure of basifemur; *k'*, posterior condyle of femur; *lv*, larva; *n1*, protonymph; *n2*, deutonymph; *n3*, tritonymph; *t*, ontogenetic time; *T*, phylogenetic time; *TF*, telofemur; *tf_s*, superior tendon of femur; *TR*, trochanter; *TR1*, trochanter 1; *TR2*, trochanter 2.

VII. STRUCTURING FORCES AND THE EARLY STAGES OF ORGANIC EVOLUTION

As demonstrated in the preceding sections, it is not impossible, and sometimes (as in the case of numerical changes) even not very difficult to reconstruct the laws underlying the evolution of biological structure, as long as we can start from primitive representatives (or primitive types) of a group, and as soon as we have collected (and carefully analysed) sufficient detailed observational data. Reconstruction of these laws is certainly much more difficult in the case of the early stages of organic evolution, up to the origination of the regna and phyla. Because research in this field is beyond my experience, I must confine myself here to a concise survey of these stages, anticipating an expert analysis of the structuring forces behind the fundamental evolutionary phenomena. The most important problems and phenomena associated with the early stages of organic evolution are: (1) the origin of life, (2) the evolution of the individual, (3) the evolution of sexuality, (4) the increasing complexity of organisms, and (5) the origin of segmentation; these problems are briefly dealt with below.

(1) It is now generally accepted that primordial life must have had two properties: the capacity of harnessing energy, and the capacity of reproduction and growth. Evidently, these completely different properties could not be simultaneously present in a single homogeneous substance. The capacity of harnessing energy required the appearance of complex molecules functioning as catalysts. The capacity of reproduction and growth required the appearance of complex molecules capable of continuous self-perpetuation without diminution. The theory of the origin of life consequently presupposes the associated development of the two completely different and highly complex types of molecules (see, e.g., Bonik, Grasshoff, Gutmann & Maier, 1978: 162-163; Fox, 1984; Good, 1981: 115-158; Matsuno, 1984; Oparin, 1953; Wicken, 1984).

(2) Individuals in organic nature (see Bonik, Grasshoff, Gutmann & Maier, 1978: 163-165; Huxley, 1912; Jeuken, 1952; Koepcke, 1973: 81-116; Medawar, 1957) first arose when living substances began to exist as definite bodies. The single cell must have been the historical basis of organic individuality. To the properties of primordial life (the capacity of harnessing energy, and the capacity of growth and reproduction), the cell added the cell-wall (with double function: protection and absorption). In this way, the first organic individuals constituted unities with an increased independence, consisting of a certain diversity of inter-dependent parts (i.e. parts with integrated functions). Originally, organic individual and individual death were not in-

separably connected. Cells divided, and two new individuals took the place of the parent individual. The life of cell-lineages, which arose in this way (and still arise in the case of extant Prokaryota and Protista), can be characterized as indeterminate. Death, in this case, could be accidental (i.e. arise from any cause whatsoever). Individual death, and the occurrence of a mortal body, apparently first arose in individuals like *Volvox*: colonies of cells, with a differentiation of the members, in which some cells are specialized and have an asexual reproductive function. In the act of asexual reproduction, the major part (the body) of the colony must die. In the course of evolution, natural individual death became increasingly associated with the age-specific decline of vital faculties.

(3) The earliest living organisms certainly had a capacity for self-replication, although this process probably was inexact (the genotype could have been liable to lose identity, so that the progeny departed more or less widely from the condition of their parent). In the course of evolution, more reliable methods of replication arose, but reproduction in ancestral Prokaryotes probably was asexual (in this group, the counterpart of the eukaryote nucleus consists of a circular strand of DNA). Some mechanism of genetic recombination probably arose early in the prokaryotic line. In extant Bacteria, part of a strand of DNA of one individual can be transferred to another (in various ways), and recombination takes place by exchange of material. It can be assumed that the ancestral Eukaryote was a haploid asexual unicellular alga, with a nucleus, a set of linear chromosomes, and an efficient nuclear division resulting in an exact replication of the genome (mitosis). The origin of sex presupposes the fusion of two haploid cells and the attainment of true diploidy, the origination of nuclear divisions which halve the number of chromosome complements (meiosis), and the origination of gametes, followed by fertilization. During meiosis, genetic material can be exchanged between homologous chromosomes (recombination). The primary consequence of sex is the diversification of progeny (see Bell, 1982). In Protista, the somatic cell can develop into a macrogamete (two macrogametes subsequently fuse) or it can develop into a gametangium with several microgametes. In multicellular algae, gametes arise in special cells (gametangia); the gametes can be morphologically similar (isogamy) or present differences in size (anisogamy). In the case of anisogamy, the macrogamete can become a non-motile egg-cell which is fertilized by a free-swimming microgamete or spermatozoid (oogamy).

(4) Starting from Protista, the first important ascent in the scale of increasing complexity of living nature consisted in the origination of multicellular organisms. This step could have been realized in various ways. Colonies of

uniform cells could have arisen from Protista, followed by a division of labours among the cells; the colonies could subsequently have been transformed into true individuals. It is, however, also possible that division of labours set in at the beginning, and that no colony preceded the multicellular individual. According to Bonik, Grasshoff & Gutmann (1976a: 132-136, fig.3), the evolution of multicellular animal organisms must have started from multinucleate, ciliate Protista with internal jelly-formation; by division into compartments, the formation of uninucleate cells constituting an epithelium, and increased solidity (because of the internal jelly-formation), the earliest multicellular animal organisms must have arisen. Although evolution included also regression and extinction, the further ascent generally consisted of an increase in differentiation, complexity, harmonious integration and efficiency, and an increase in independence and individual autonomy. Progressive evolution could be restricted to a perfection of adaptation within the framework of a plan of construction, or pertain to a more important ascent to a higher plan of construction. In the last-mentioned case, various major plans of construction could succeed each other in time (see Huxley, 1912: 99-114; Koepcke, 1973: 99-101; Overhage, 1957).

(5) The origin of many phyla is probably closely connected with the origin of segmentation. In the course of evolution, segmentation probably arose more than once, and perhaps in different ways. It can pertain to one or more internal systems; true segmentation includes segmentation of muscular system and coelom, pseudosegmentation is restricted to other systems. There are several theories pertaining to the origin of segmentation. According to the pseudosegmentation-theory, true segmentation arose from pseudosegmentation (in groups without coelom), and a coelom could subsequently have arisen from gonads. According to the cyclomere-theory (which is associated with the enterocoel-theory, pertaining to the origin of the coelom), segmentation arose from radial symmetry; coeloms originated from caeca (blind diverticula of the alimentary canal), as in the embryonic development of some groups; from a number of radially symmetric caeca, a series of bilaterally symmetric coelom compartments arose. According to the bilaterogastraea-theory (which is also associated with the enterocoel-theory), bilaterally symmetric coelom compartments arose from caeca; this change was associated with the evolution of adult benthic forms from pelagic forms. According to the chain-theory, segmentation originated from asexual reproduction; new individuals arose in the posterior part of a parent individual, and as soon as these remained attached, they became part of a single segmented individual. Bonik, Grasshoff & Gutmann (1976b), who regarded the coelom as a hydroskeleton, connected the origin of segmentation with undulating movements and the associated

origination of coelom compartments and muscular segmentation; the complete internal anatomy must subsequently have been accommodated to this metameric scheme.

VIII. SOME CONCLUDING REMARKS ON DEEP STRUCTURE AND PHYLOGENETIC CLASSIFICATION

In section II of the present paper, it was pointed out that a phylogenetic classification should be based on the hierarchy of deep structures, and that otherwise classification risks to become artificial or, at best, phenetic. It was also pointed out that the deep structures are characterized by the presence of evolutionary potentialities which can manifest themselves separately (and discontinuously) by parallel evolution. It is now evident that branching points in a scheme underlying phylogenetic classification should correspond with the separation of systems of transformation, and not with the manifestation of their evolutionary potentialities at the level of the surface structure. It is also evident that the hierarchy of the natural classification should correspond with the hierarchy of deep structures.

In section III it was demonstrated that, in Actinotrichida, chaetotactic patterns can be arranged, according to evolutionary potentialities, in a hierarchy of systems of transformation. The potentiality of suppression of seta f_1 apparently belongs to one of the deepest Actinotrichid structures, whilst in advanced stages of numerical regression the patterns become increasingly characteristic of lower levels (i.e. less deep structures) in the hierarchy of the natural system.

In section IV it was demonstrated that the attainment of a life-cycle with six instars belongs to the evolutionary potentiality of most groups of Chelicerata, just as the increasing degree of regression of the first instars. Regression of other instars, however, such as that of the deutonymph in Acaridida (one of the four Actinotrichid orders) or that of proto- and tritonymph in Trombidina (a suborder of the Actinotrichid order Actinidida) belongs to the potentiality of the lower levels (less deep structures) of the hierarchy.

In section VI, a complete model was prepared of the laws underlying the evolution of the chelicerate appendages. From this model it can, for instance, be deduced that the potentiality for the development of a second trochanter has been present in most chelicerate ancestors, but that the evolution of a second femur belongs to the potentiality of two groups: the related superclasses Epimerata and Apatellata. The evolution of free coxae with lateral position

apparently belongs to the potentiality of the superclasses Cryptognomae and Arachnida s. str. Several evolutionary changes in the types of joints and in the position of muscles are characteristic of groups at the superclass and class level (Arachnida s. str., Opilionida, Xiphosura, Scorpionida).

IX. DEEP STRUCTURE AND THE STUDY OF EVOLUTION

As mentioned already in the introduction, structuralism is essentially a method; it does not look for causal explanations, but attempts to study the laws underlying transformation. Current neo-Darwinistic studies are based on the hypotheses of random variation and natural selection, which can explain everything, even before the laws underlying evolutionary changes are known. Probably as a result of this premature explanation, very little progress has been made in the discovery of the general evolutionary laws (it is probable that the number of these general laws is relatively small). In the conviction of the author, it is only after the preparation of a complete hierarchic inventory of these general laws of transformation (the deep structure), that a new theory of evolution can be developed.

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